

Observations on Antennal Morphology in Diptera, with Particular Reference to the Articular Surfaces between Segments 2 and 3 in the Cyclorrhapha

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ABSTRACT. The main features of antennal segments 2 and 3 seen in the higher Diptera are described, including many that are not or inadequately covered in available publications. The following terms are introduced or clarified: for segment 2 or the pedicel—annular ridge, caestus, chin, collar, conus, distal articular surface, encircling furrow, foramen of articulation, foraminal cusp, foraminal ring, pedicellar button, pedicellar cup, rim; for segment 3 or the postpedicel—basal foramen, basal hollow, basal stem, postpedicellar pouch, sacculus, scabrous tongue, sub-basal caecum; for the stylus or arista—stylar goblet. Particular attention is given to the occurrence and position of the pedicellar button. The button is the cuticular component of a chordotonal organ, which perhaps has the role of a baroreceptor. It is present in the majority of families of Diptera, and possibly was present in the ancestral dipteran. Some generalizations about antennal structure are made, and a diagram showing the main trends in antennal evolution in the Eremoneura is provided. The general form of the antenna shows a transition from approximate radial symmetry (e.g., in *Empis*, *Microphor*, and *Opetia*) through to superficial bilateral symmetry (in many taxa of Eumuscomorpha), though there is usually much asymmetry in detail. More detailed descriptions and illustrations are given for selected taxa of Cyclorrhapha. The phenomenon of an additional concealed segment-like structure between segments 2 and 3, found among the Chloropidae, Pyrgotidae, etc., and formed from the basally flexible conus, is described. Some antennal features of the Calyptratae suggest a relationship to the Tephritoidea. Critical comments are made with regard to the recently published phylogenetic association of the Ironomyiidae with the Phoridae and the Pallopteridae with the Neurochaetidae. In discussing relationships of some taxa, a few non-antennal features, some needing further study, are mentioned, e.g., variation in separation of abdominal tergites 1 and 2 in the Opetiidae and other lower cyclorrhaphous families; the presence of supplementary claw-like terminal tarsal processes in the Lonchopteridae; the apparent restriction of the presence of barbed macrotrichia to the Phoridae, among lower cyclorrhaphans; variation in structure of the prelabrum in the Pyrgotidae; the microstructure of the facial cuticle in the Syringogastridae as compared with that of other families; the calyptrate-like development of the squama in some tephritoid taxa; variation in the subscutellum in the Conopidae; a feature of the larval posterior spiracles diagnostic for Coelopidae.

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Introduction

From morphological studies relating to my taxonomic research on cyclorrhaphous Diptera, it has become apparent that much of the structural diversity in the antenna of these insects remains unrecorded, and that established terminology does not adequately cover this diversity. Difficulties in observation have occurred because some structures are concealed until careful separation of certain segments is carried out, and in the past access to electron microscopy was more limited.

It is probable that much of the diversity now described has phylogenetic significance, but I do not here propose alterations to current classification. Antennal characters will need to be further checked for consistency and correlated with other data, if such changes are to be made, as I find much evidence of homoplasy. However, the broader trends in at least some aspects of antennal morphology in the higher Diptera seem to follow the course outlined (and simplified) in Fig. 23.

In order to present my more significant findings within a reasonable time, I have limited the range of taxa for detailed study to those of more immediate interest and availability, and some other significant groups have been omitted or given slight attention. Therefore, there remains a large field for investigation by other students, e.g., in the Muscoidea or Calyptratae. Theodor (1967) has described the extraordinary antennal features of the Nycteribiidae. I have omitted my observations on the superfamily Nerioidea and the families Somatiidae and Heteromyzidae s.l. (including Heleomyzidae, Rhinotoridae, Sphaeroceridae, Trixoscelididae, etc.), as these show such diversity as to require separate studies.

Morphological study for this paper has been performed using a stereo light microscope (SLM), a compound light microscope (CLM), and a scanning electron microscope (SEM).

Collections mentioned in the text are: Australian Museum, Sydney (AM); Natural History Museum, London (BMNH); Zoological Museum, Copenhagen (ZMUC).

Terminology—orientation

For descriptive purposes the antenna is assumed to lie, in its primitive position, directed anteriorly from the frontal surface. The terms **dorsal** and **ventral** are applied according to this orientation. The surfaces of the two antennae which are nearest to one another and to the median or sagittal plane of the insect are described as **medial**. The surface of each antenna most remote from the median line is described as **lateral**. The segments are numbered from the basal one (joining the head capsule) to the free distal end, and the adjectives **basal** and **distal** are accordingly applied to the parts of each segment.

Terminology—segmental structure

In the Cyclorrhapha the antenna is most frequently six-segmented and it seems probable (but not certain) that this is the groundplan condition for the Cyclorrhapha (D. McAlpine, 2002). The simplest system of indicating the individual segments is therefore by numbering them 1 to 6 from the base, but names for the differentiated segments or groups of segments are in fairly general use and have application to descriptive morphology, physiology, and taxonomy. I do not use the system of numbering for flagellar segments deduced by Stuckenberg (1999) from study of the reduction series found in extant taxa of Vermileonidae, as the basal eremoneuran was not evolved from that somewhat derived homoeodactylous family. In fact there is no surviving evidence of a multisegmental origin for the postpedicel in the Eremoneura, and, although a very early multisegmental origin is conceivable, it is unlikely that we could ascertain the details of such an origin using present methodology.

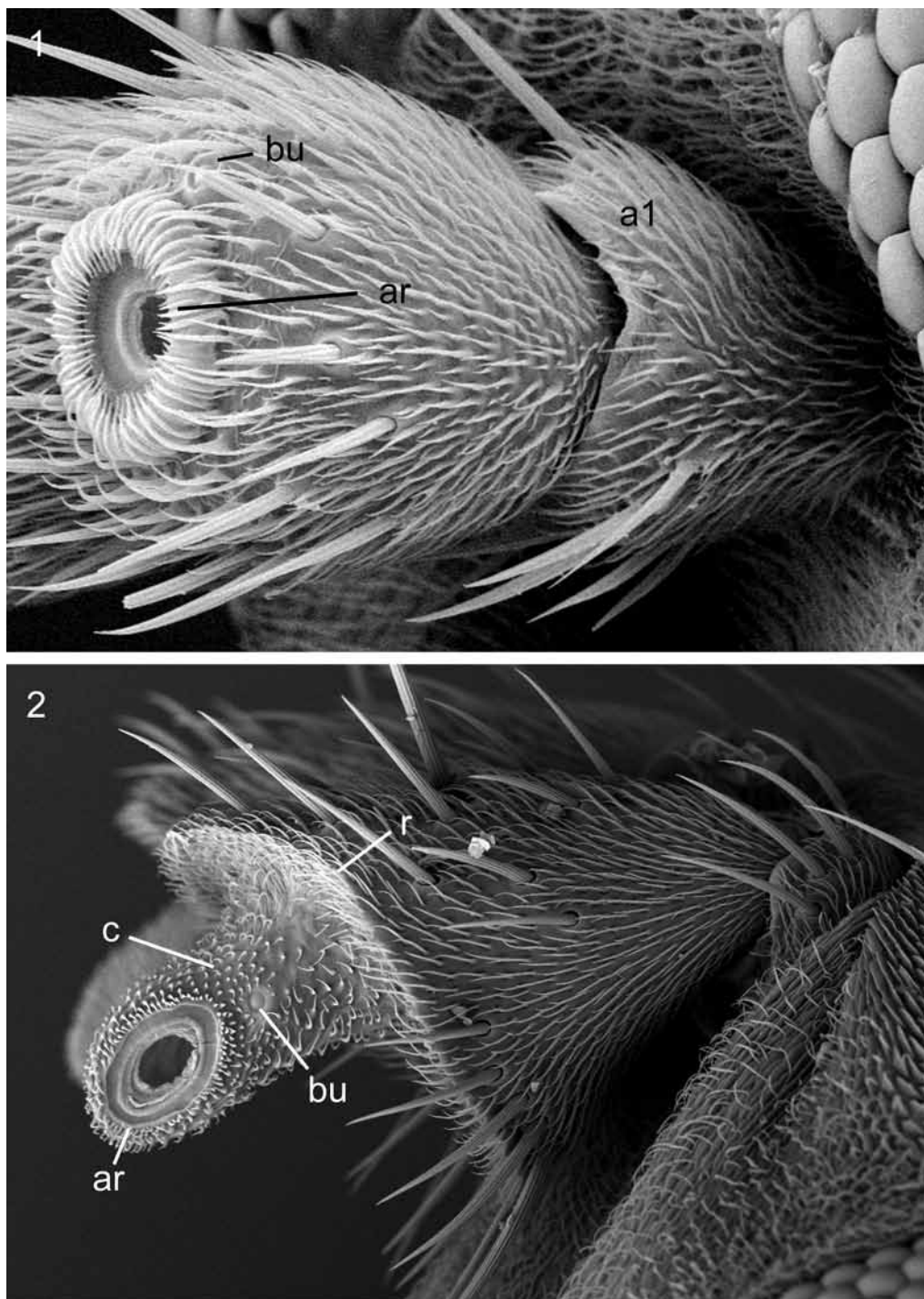
Segment 1 is widely termed the **scape** in insects. It is often relatively short, subcylindrical, and assumed to be of simple structure. Its comparative morphology has therefore received little attention. It probably generally contains muscles arising in its basal part, which connect with the base of segment 2 and effect movement between the segments (Snodgrass 1935: 132; Soenen 1940: fig. 2).

Segment 2 is generally termed the **pedicel**. Its external structure is often complex and taxonomically variable (e.g., Figs 1, 2). Internally it probably usually contains two sensory organs, which have been examined in very few cyclorrhaphans. These are the relatively large Johnston's organ and the outer chordotonal organ or inappropriately "organe de Hicks" (Soenen 1940). The distal surface of segment 2 in the Cyclorrhapha is usually at least partly flattened to concave and encircled by an angular or flange-like **rim** delimiting the **distal articular surface**. This condition contrasts with that of most non-cyclorrhaphous brachycerans, in which segment 2 is generally more or less rounded in distal profile. In some schizophorans the dorsal part of the rim is extended into a pair of **dorsal lobes**, which may be hood-like or cucullate, concealing part of the distal articular surface. This surface is penetrated by the **foramen of articulation** for attachment to the base of segment 3. The foramen is primitively placed in the centre of the distal articular surface and faces distally, but it may be very asymmetrically placed and inclined in advanced taxa. Immediately surrounding the foramen there is often a

slender ridge, the **foraminal ring** (*anneau de renforcement* of Soenen 1940: fig. 2) which is devoid of microtrichia. In some schizophorans the foraminal ring is vertically elongate and may form a dorsal and a ventral projection, each termed a **foraminal cusp** (Figs 95, 101). Outside of this ring there is an often more prominent **annular ridge** (Figs 1, 24, 29, 95). The latter is often armed with spinules, complex denticles, or simple microtrichia. In *Periscelis*, *Neurochaeta* and some diverse other genera there is on each side of the foraminal ring a stout, rounded, and usually nodulose vertical ridge, which I term a **caestus** (Figs 95, 101, 113). The paired caesti are surrounded by the innermost whorl of spinescent microtrichia on the annular ridge. In many taxa of Cyclorrhapha part of the distal articular surface rises into a bulky or elongate projection termed the **conus** (articular peg of Colless, 1994). The conus, which can only be examined adequately after separation of segment 3, bears the foramen of articulation on its distal, lateral, or dorsal surface. The surface of the conus is usually roughened by the presence of numerous hair-like or spinescent microtrichia, denticles, simple or denticulate ridges, or overlapping plates. In some taxa of Schizophora the partly reduced conus is prominent only on the medial side or only on the ventral side of the foramen of articulation, but in these taxa there is no prominence on its outer or lateral side (except sometimes for a slight development of the annular ridge). In some schizophorans the conus is produced into a broad, rounded prominence below the annular ridge, termed the **chin** (Fig. 63). In several acalyptrate families the general region of the conus has become secondarily flattened and almost symmetrical and the region of the annular ridge is sunk into a rounded cavity, termed the **pedicellar cup** when sharply differentiated from the rest of the distal articular surface (Figs 99, 112, 151). A further development of the conus is that described below for the Chloropidae and repeated in at least some taxa of Pyrgotidae. In these forms and some others the conus appears to be moveable in relation to the rest of segment 2, and in extreme forms may resemble an additional segment interposed between segments 2 and 3 (see Figs 63, 66, 67, 134–136).

The **pedicellar button** is a term recently introduced (D. McAlpine, 2008) for a somewhat button-like modification of the cuticle on the distal articular surface of the second antennal segment or pedicel in a majority of families of Diptera. This structure, hereafter referred to simply as the "button", has been generally overlooked by dipterists. There are several apparent reasons for this oversight: it is too small and too slightly prominent to be noticeable in most studies using SLM, and, when slide mounts are examined with higher magnification under CLM the line of view is often almost parallel to the button-bearing surface; the button-bearing surface is normally concealed between segments 2 and 3 until these are artificially separated, and even then the complex articular surface makes detection difficult in some taxa (e.g., in *Musca* spp., *Neurochaeta* spp., *Drosophila* [or *Sophophora*] spp.). For these reasons I have used the SEM on disarticulated antennae in order to locate the button in various dipterous taxa.

The button consists of an almost smooth, bare area, usually in a microtrichose field, and has a central dome or convexity, which is almost circular or tear-drop shaped, and a peripheral ring which is usually also slightly convex (typical examples of button shown in Figs 1, 9, 10, 14, etc.). Although



Figures 1, 2. Segments 1 and 2 (scape and pedicel) of left antenna, after removal of seg. 3, lateral view, of two cyclorrhaphans of different grade. (1) *Opetia nigra* Meigen (fam. Opetiidae). (2) *Huttonina abrupta* Tonnoir & Malloch (fam. Huttoninidae). *a1*, antennal seg. 1; *ar*, annular ridge (surrounding distal articular foramen); *bu*, pedicellar button; *c*, conus (absent in *Opetia*); *r*, rim (absent in *Opetia*).

the central dome is separated from the peripheral ring by an encircling groove, in no case have I been able to detect any slit or aperture associated with the groove, which could lead to a subcuticular cavity. Measurements for greatest diameter of the central dome made over a wide range of dipterous families give a range of c. 2.1 μm (Neurochaetidae) to 8.8 μm (Asilidae). Because the limits of the peripheral ring are often less defined, meaningful measurements of it were not obtained.

In these external features the button conforms to at least some cases of a campaniform sensillum, a sensory structure occurring widely on insect cuticle (Imms *et al.*, 1957; Chapman, 1971; McIver, 1975) and apparently of variable internal structure and function. The button differs from the sensillum placodeum (placoid sensillum) found in the antenna of certain Trichoptera and Lepidoptera (Faucheux, 2004a; 2004b) in the smooth, non-porous surface of the central dome.

The button is, so far as known, the external, supporting component of a special chordotonal sense organ (see Heymons, 1943: 107) which is distinct from the larger Johnston's organ, also contained in segment 2 of the dipterous antenna, and which encircles the central antennal nerve. According to Imms *et al.* (1957: 88), chordotonal sensilla "are stimulated by tension and are used for various purposes, including proprioception, the perception of internal pressure changes, mechanical vibrations, and sound. They have been reported for most orders of insects and occur on various parts of the body..."

The button surface is generally concealed by overlapping structures and often also deeply recessed in a cavity, though not sealed off from the atmosphere. This degree of protection from the exterior seems not to be appropriate for an auditory organ, a role probably fulfilled in most dipterans by vibration of the flagellum in connection with Johnston's organ, nor with detection of substrate vibrations. But such conditions are in accord with the possibility that the organ can detect either internal pressure changes or changes in atmospheric pressure.

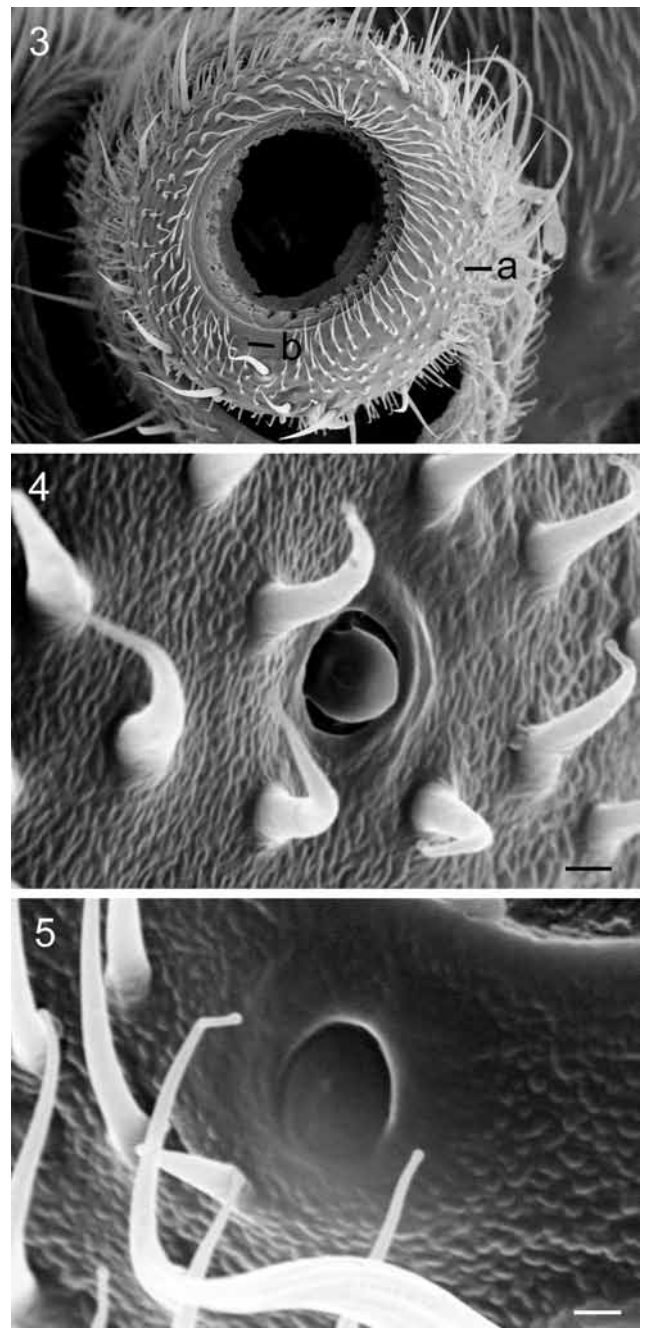
Wellington (1946) recorded reactions of muscoid (or calyptrate) flies to sudden changes in atmospheric pressure produced by a controlled wave of the hand (visual stimuli being excluded), and demonstrated that reception was dependent on the arista. However, he also noted behaviour under differing static levels of air pressure, and stated: "While it is evident that the aristae function as external baroreceptors, it is equally evident that the transmission of the stimulus to the brain is intimately linked with some apparatus present in the pedicels of the antennae. Exposure of the conjunctival plates of these second segments [i.e. of the button-bearing distal articular surfaces] results in partial retention of pressure sensitivity, while the removal of the pedicels or their coverage with collodion results in the loss of wave sensitivity;" —also in general pressure sensitivity in his second (II) set of experiments.

Wellington (1946: 113) inclined to attribute this latter sensory stimulus to Johnston's organ in segment 2, but the various investigations of that organ seem to show that it forms a larger separate body whose chordotonal elements are directly connected to the base of the flagellum via the intersegmental foramen, not to the button-bearing surface (see Heymons, 1943, in particular).

Pending further experimental tests, I propose the hypothesis that the button-connected chordotonal organ is likely to be the pedicellar baroreceptor inferred but not seen by Wellington. Wellington's further discussion (1946: 114–117) gives some indications of the importance of baroreception in dipterous biology.

The tendency for the button to be recessed or protected may be due to the fact that, when its cuticle is perforated by abrasion, no difference is maintained between external and internal pressure, and the baroreceptor becomes inoperative. It is possible that the dorsal cleft or seam of segment 2 in the Ephydroidea, Muscoidea, etc. ensures that, in at least some taxa, complete separation of the button from the atmosphere does not take place, while extensive abrasion of the segment (as in Fig. 87) is unlikely to reach the button.

I am uncertain if a typical pedicellar button occurs on the antenna of any non-dipterous insect. In *Nannochorista dipteroides* Tillyard (order Mecoptera or Nannomecoptera) the pedicel bears some button-like structures (Figs 3–5) but



Figures 3–5. *Nannochorista dipteroides* Tillyard (fam. Nannochoristidae), antenna. (3) Distal view of seg. 2, after removal of seg. 3, showing positions of sensory structures. (4, 5) Detail of sensory structures at positions a, b in Fig. 3; scale = 1 μ m.

these appear to have a lateral or annular opening leading to an internal cavity, and this apparent difference suggests a difference in function in the nannochoristid structure. Somewhat button-like surface features on the pedicel of *Panorpa* sp. and *Chorista* sp. (order Mecoptera) need detailed investigation.

According to Grimaldi & Engel (2005) four extant infraorders of Diptera (or suborders in the modern sense) were present in the late Triassic (at least 210 MYA), and it is clear that the dipterous button must have existed at this time level. Further data are discussed below under Grade Nematocera.

There is some disagreement in available literature on terminology of antennal sense organs. Soenen (1940: 20) stated that he could confirm the absence of the pedicellar chordotonal organ in the rhagionid and chloropid flies which he studied, thus excluding both Johnston's organ and the outer button-connected organ from this category. Wigglesworth (1950: 164–166) appeared to regard Johnston's organ as a special type of chordotonal organ, as did Chapman (1991: 44–45). Soenen (1940: fig. 2) apparently identified the button-connected sensillum in his rhagionid fly as “organe de Hicks”, but this is not the antennal structure (on segment 3) described by Hicks (1857). Wigglesworth (1950: 162, 170) and others have referred to “Hicks' papillae” on the halteres of Diptera, a term arising from other studies by Hicks.

It should be noted that the “antennal pulsating organ” of nematocerous dipterans (Clements, 1956) is in the head capsule, not in the antenna, and is termed the “tambour organ” by Day (1955).

Those segments of the insect antenna distal to segment 2 are collectively termed the **flagellum**, and in their more primitive state (as in the dipterous grade Nematocera) they are little differentiated from one another. However the usual four flagellar segments of cyclorrhaphous flies are strongly differentiated structurally, so that the collective term is less appropriate. While segment 3 is often called the first flagellomere, the term flagellomere or flagellar segment is not generally applied to the succeeding segments, which are taken as constituting the **arista** or **stylus**. The view that the flagellum consists of a single segment, the dipterous antenna thus consisting of only three segments, is expressed by J. McAlpine (1981) and a few other entomologists. However, comparative study reveals no likely three-segmented stage in the ancestral line of the Hexapoda and that of the Insecta (though the intersegmental or intrinsic musculature has been lost in the insect flagellum, it is retained in such basal hexapod groups as the Diplura and Collembola). Treatment of the flagellomeres as segments remains the standard practice in the majority of insect orders, and it does not seem reasonable to designate those concerned as misled. For these reasons, I do not follow J. McAlpine's system.

Segment 3 (postpedicel, funiculus, first flagellomere) is often the bulkiest antennal segment in the Eremoneura (including the Cyclorrhapha). In those cyclorrhaphans which have a substantial conus, this is inserted into the corresponding **basal hollow** of segment 3. Such basal hollow typically contains the articular foramen connecting segment 3 with the conus of segment 2 (Figs 36, 47). Alternatively, in those schizophoran taxa with reduced conus and the distal articular foramen of segment 2 sunk into a concavity of that segment (e.g., *Neurochaeta*, *Psila*, *Cyamops*, *Hydrellia*, *Drosophila*), segment 3 is narrowed into a **basal stem** contained within that cavity. This basal stem (proximale Lappenfortsatz of Hennig, 1971, but unfortunately termed the conus by Grimaldi, 1990, misinterpreting Disney, 1988) is formed by extension of the ventrobasal convexity of segment 3 into a narrow process and migration of the basal foramen on to the process not far from its basal end. This development results in modification of the shape of segment 3 (compare Figs 93, 91). In such forms segment 3 may be considered as divided into the narrow basal stem and the broad **disc**, which constitutes the greater part of the segment, but numerous intermediate states occur. Often, in

these taxa lacking a well-developed conus, segment 3 has the basal hollow much reduced or represented by the **sub-basal caecum** opening on the medial side of the basal stem (Fig. 91). A narrow band of thickened, rough-surfaced cuticle often runs from the medial surface of the basal stem into the extremity of the sub-basal caecum (e.g., Fig. 96). This roughened tract is termed the **scabrous tongue**.

I have seen evidence that the basal stem may be flexible in relation to the disc of segment 3. The cuticle near the junction of the basal stem with the disc is often modified by the presence of transverse ridging with softer interstices (e.g., Fig. 83), and this structure probably confers a limited flexibility.

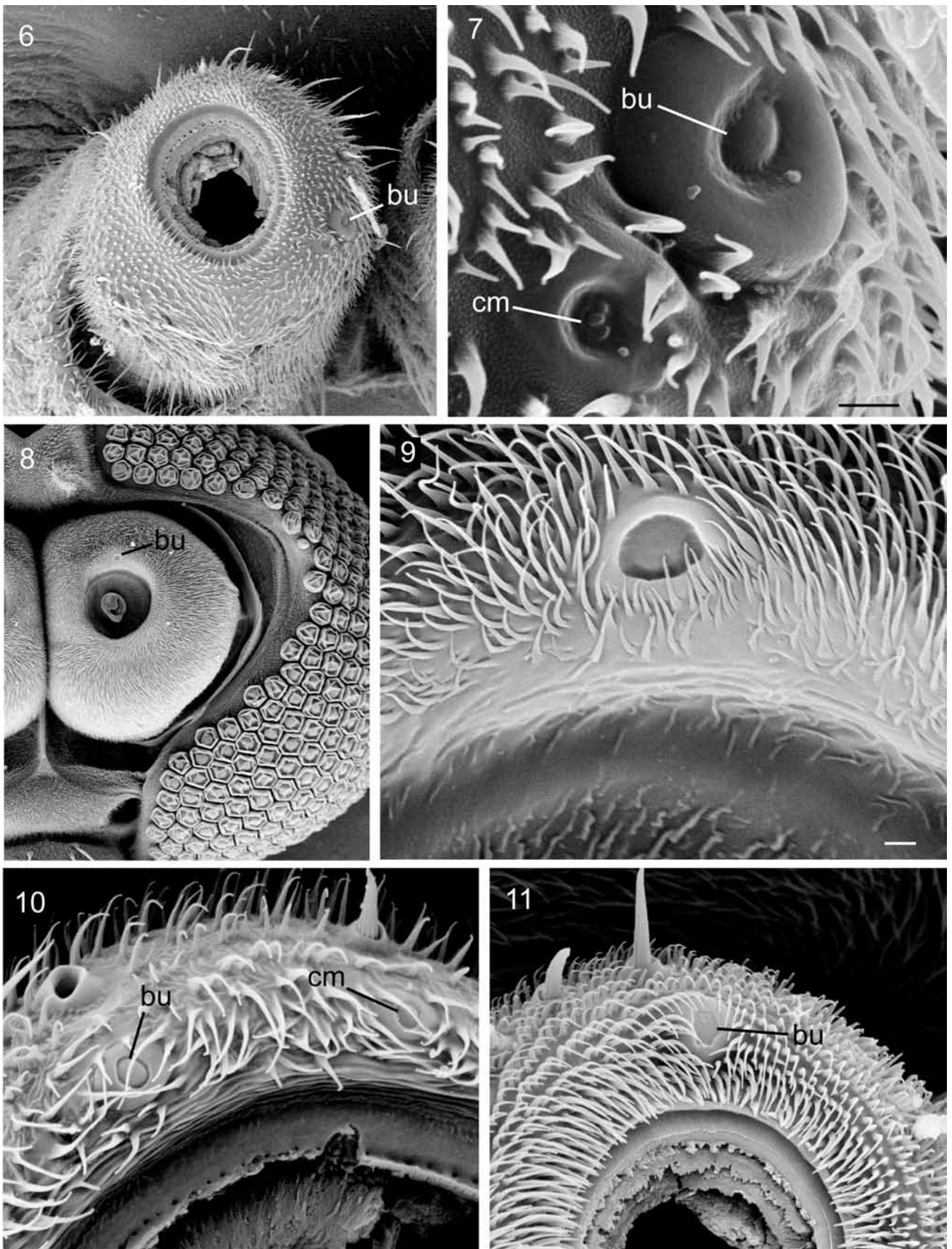
A feature of segment 3 in most eumuscomorphans is the presence of one or few **sacculi** (Lowne, 1895; Shanbhag *et al.*, 1995; D. McAlpine, 2008). A sacculus is a deep, sac-like invagination of the cuticle of segment 3 containing several trichoid sensilla and opening to the exterior by a relatively small pore, most often on the exposed lateral surface. This structure is distinct from the often numerous simple pits in the cuticle, each of which may be associated with a single sensillum, or various saucer-like pits which sometimes contain one or more trichoid sensilla. Smith (1919) has given information on the various sensory pits on antennal segment 3 in various families of Diptera. Where both simple sensory pits and a true sacculus occur together, as in *Musca* (see Smith, 1919: text-fig. 38) and *Cryptochetum* (see below) the two structures are usually very distinct. Stocker (2001) has investigated the distribution of olfactory sensilla on segment 3 of *Drosophila*. Hu *et al.* (2010) characterized the sensilla of segment 3 in certain species of Tephritidae and provided references to much earlier work.

My recent studies (following D. McAlpine, 2008) indicate the possibility that, among the Eremoneura, segment 3 has true sacculi only in the Ironomyiidae (see below) and the Eumuscomorpha (i.e. Syrphidae, Pipunculidae, and Schizophora). In *Hormopeza* (Orthogenya or Empidoidea) and *Microsania* (Cyclorrhapha, Platypezidae), segment 3 has two well-developed sac-like cavities, which I term **postpedicellar pouches**. Though these are suggestive of eumuscomorphan sacculi, they differ in their simple lining and complete lack of trichoid sensilla (author's studies with CLM). Each of these genera seems to be phylogenetically remote from any other known taxon with similar pouches on segment 3, and I am convinced that these structures have evolved independently in each genus. I also use the term postpedicellar pouch below for somewhat similar structures in certain taxa of Conopidae and Muscidae.

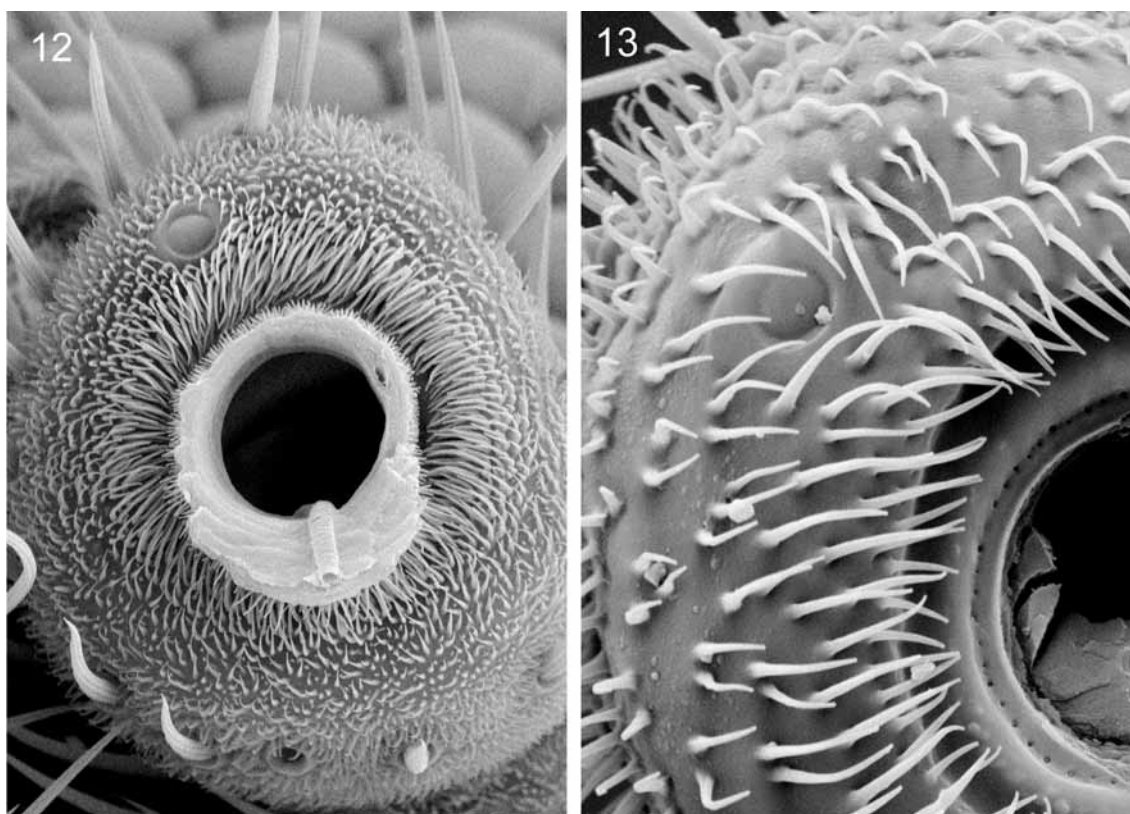
Further information on sacculi is given below under the taxonomic headings (particularly for Ironomyiidae).

Segments 4 to 6 of the cyclorrhaphous antenna constitute the arista or stylus. I have given an account of variation in segmentation of the arista and noted among cyclorrhaphous taxa 29 separate derivations of reduction from the plesiomorphic three-segmented condition (D. McAlpine, 2002). I have now observed some additional cases of segment reduction in the Curtonotidae, Natalimyziidae, Platystomatidae, and Pyrgotidae as noted below, and Buck (2006) has recorded a case for the Inbiomyiidae.

In the Apystomyiidae the basal segment of the stylus has on its terminal surface a capsule-like structure, here termed the **stylar goblet**. See under that family and Fig. 177.



Figures 6–11. Details of antennal seg. 2 in nematocerous dipterans. (6) *Ptychoptera capensis* Alexander (fam. Ptychopteridae), right segs. 1 and 2, distal view. (7) The same, sensory structures; scale = 3 μ m. (8) *Chironomus* (s.l.) sp. (fam. Chironomidae), left side of head after removal of flagellum. (9) The same, part of distal articular surface showing pedicellar button; scale = 2 μ m. (10) *Macrocera* sp. (fam. Keroplatidae), part of distal articular surface (left antenna) showing button and possible campaniform sensillum. (11) *Sciara* sp. (fam. Sciaridae), part of distal articular surface (left antenna) showing button. *bu*, pedicellar button; *cm*, campaniform sensillum (?).



Figures 12–13. Details of antennal seg. 2 in nematoceros dipterans. (12) *Sylvicola* sp. (fam. Anisopodidae), distal view (left antenna), showing button. (13) *Limonia marina* (Skuse) (fam. Tipulidae s.l.), part of distal articular surface (left antenna), showing button.

The grade Nematocera

The non-brachyceran families of Diptera have not been a main focus in this study. General information on the antenna has been given in numerous publications (e.g., Crampton, 1942; Hennig, 1973), and information on Johnston's organ within the pedicel by Eggers (1923), Soenen (1940), and others, who acknowledged that this organ was evidently present in a very early ancestral insect.

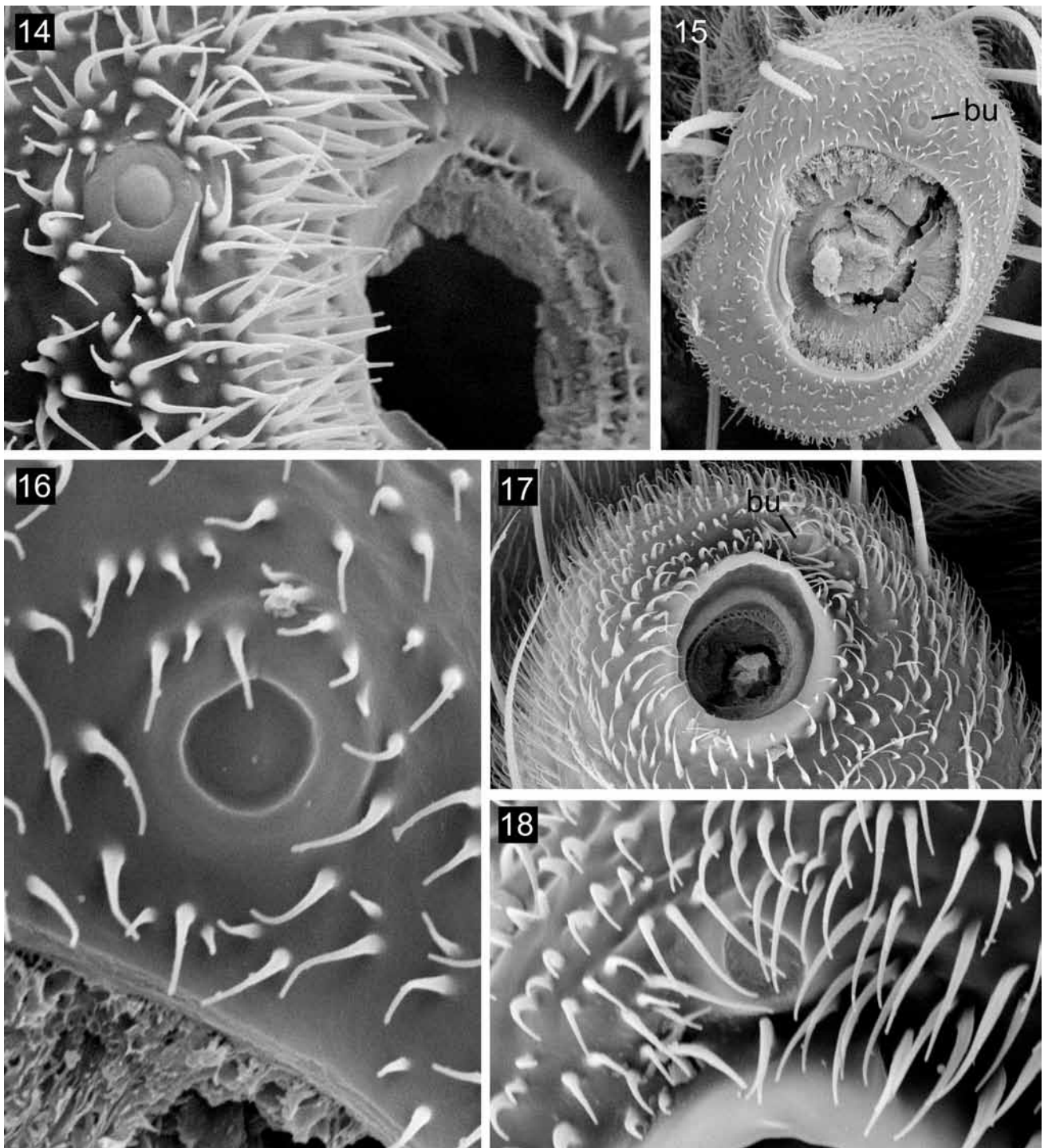
The occurrence and position of the pedicellar button within this grade has not been recorded, and I have made a preliminary survey only of this subject. My observations using SEM on the distal surface of segment 2 shows the button to be present in at least some taxa of the following families: Anisopodidae, Bibionidae, Chironomidae, Dixidae, Keroplatidae, Mycetophilidae (s.str.), Psychodidae, Ptychopteridae, Sciaridae, Tipulidae (s.l.), Trichoceridae (see Figs 6–18). In *Ptychoptera capensis* Alexander (Fig. 7) there are two somewhat button-like structures on segment 2, but probably only one is homologous and functionally equivalent to the typical button. The position of the button in these families varies from medial to dorsal in relation to the distal foramen of the segment.

In examples of several nematoceros families (e.g., the Culicidae) I have failed to demonstrate the presence of a pedicellar button. It is probable that in some of these taxa the button is really absent, but it is also possible that the position or nature of the button has sometimes made it difficult to detect using standard SEM methodology. Rather than listing such taxa at present, I leave detailed interpretations open for future research.

The taxonomic diversity of the above-listed families, for which the presence of the pedicellar button is confirmed, demonstrates its presence within a wide range of nematoceros groupings, whether one uses the cladogram of Oosterbroek & Courtney (1995: fig. 9) or the rather different version of Grimaldi & Engel (2005: fig. 12.25). On the reasonable assumption that the button has not originated more than once in the Diptera, the question arises whether it was present in the groundplan of the order. Of the seven “nematoceros” suborders in the revised classification by Amorim & Yeates (2006), I have found the pedicellar button to occur in five, viz. Tipulomorpha, Psychomorpha (or Psychodomorpha), Ptychopteromorpha, Culicomorpha, and Bibionomorpha. This leaves only the suborders Blephariceromorpha and Axymyiomorpha in which the button has not yet been observed, but the latter is included in the Bibionomorpha by Oosterbroek & Courtney (1995) and Grimaldi & Engel (2005). If the hypothesis of Oosterbroek & Courtney, that the Ptychopteromorpha + Culicomorpha form a monophyletic sister-group to all other Diptera, be confirmed, then presence of the button in the dipterous groundplan would be inferred. Alternatively, under the new system of Wiegmann *et al.* (2011: fig. 1), presence of the button is inferred for the deduced clade that includes all extant dipterous families except the Deuterophlebiidae and Nymphomyiidae (for which antennal microstructure is unrecorded).

The lower brachycerans

I use this designation to include those taxa of the suborder Brachycera other than the Eremoneura (= Orthogenya,

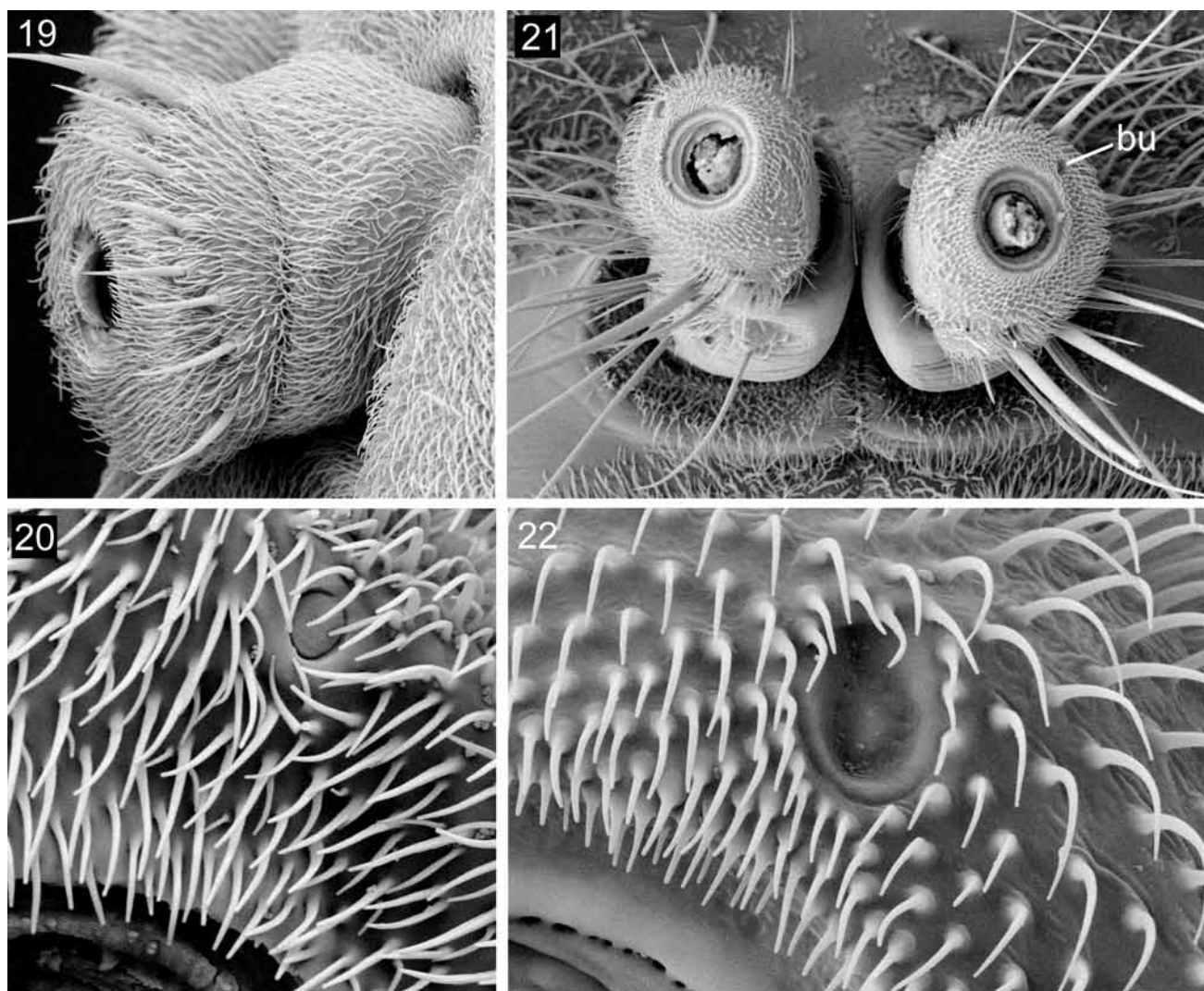


Figures 14–18. Details of antennal seg. 2 in nematocerous dipterans. (14) *Plecia dimidiata* Macquart (fam. Bibionidae), part of distal articular surface (left antenna), showing button. (15) *Nemapalpus capensis* Edwards (fam. Psychodidae), seg. 2, distal view (left antenna). (16) The same, detail of part of distal articular surface, showing button. (17) *Dixella* sp. (fam. Dixidae), seg. 2, distal view (left antenna). (18) The same, detail of button (right antenna). *bu*, pedicellar button.

Cyclorrhapha, and their possible immediate outgroups Chimeromyiidae and Apystomyiidae). These taxa are not usually considered to constitute a clade and are therefore without a formal group name.

Variation in antennal segmentation and external form has been covered in much taxonomic literature. Excellent descriptions and illustrations of antennae of many families can be found in such works as J. McAlpine *et al.* (editors 1981: chapters 30–46), but, as usual, details of the articular surfaces are omitted. I am concerned with only a few points here.

Segment 2 of lower brachycerans is most frequently almost radially symmetrical, with terminal surface somewhat convex and commonly lacking an angular or flange-like rim encircling the distal articular surface (Figs 19, 21). Sometimes a distinct distal rim is present, in which case the distal articular surface is flat or concave. The distal articular surface bears a usually well-developed pedicellar button located almost mid dorsally to laterally in relation to the distal foramen. This is a derived condition relative to the more medially located button generally seen in taxa of nematoceran grade. The distal



Figures 19–22. Details of antennal structure in lower brachycerans. (19) *Spaniopsis clelandi* Ferguson (fam. Rhagionidae), left antennal segs. 1 and 2, after removal of seg. 3, lateral view. (20) The same, detail of distal articular surface, showing button. (21) *Daptolestes* sp. (fam. Asilidae), distal view of antennae after removal of segs. 3, showing button. (22) The same, part of distal articular surface (left antenna) including button. *bu*, pedicellar button.

articular surface generally lacks any prominence comparable with the conus of more advanced cyclorrhaphans. The distal foraminal ring is often slightly recessed to receive the narrowed basal prominence of segment 3. Figs 1, 19, 21, 25 show slight variation in this probably plesiomorphic condition for segment 2 of the Brachycera, including some more basal taxa of the Eremoneura.

In the Stratiomyidae the more basal segments of the flagellum often form a compact unit or may even be fused into an apparent single stoutly rounded segment. These often bear numerous sense organs, sometimes but not always compactly grouped in shallow pits. This subject is touched on by Smith (1919). Schlinger (1981) recorded such a sensory pit, somewhat resembling a shallow sacculus, on segment 3 of some taxa of the family Acroceridae.

The Eremoneura

Since the work of Griffiths (1972) and Hennig (1976) the monophyly of the group Cyclorrhapha + Orthogenya (or

Empidoidea) has gradually achieved general acceptance as the clade Eremoneura. More recently, Grimaldi *et al.* (2009) have added the Cretaceous family Chimeromyiidae to the Eremoneura, but its more precise relationships within this division are undecided. Hennig (1976: 54–56, figs 58–62) described the structural relations between antennal segments 2 and 3 in some lower eremoneurans. The plesiomorphic conditions for Eremoneura, present in what appear to be the most basal examples of Orthogenya and Cyclorrhapha, are described below. My understanding of the main evolutionary stages leading from such basal eremoneuran antennal structure to that of the Eumuscomorpha is shown in Fig. 23.

My studies suggest that the pedicellar conus and prominent rim are absent in the groundplan of both the Orthogenya (see Sinclair & Cumming, 2006) and the Cyclorrhapha, and that they have evolved independently in each of these groups. Thus the general nature of the articulation between segments 2 and 3 found in the Opetiidae and Platypezidae probably resembles the groundplan condition for the Eremoneura (compare my Figs 1, 26 with 24, 25).

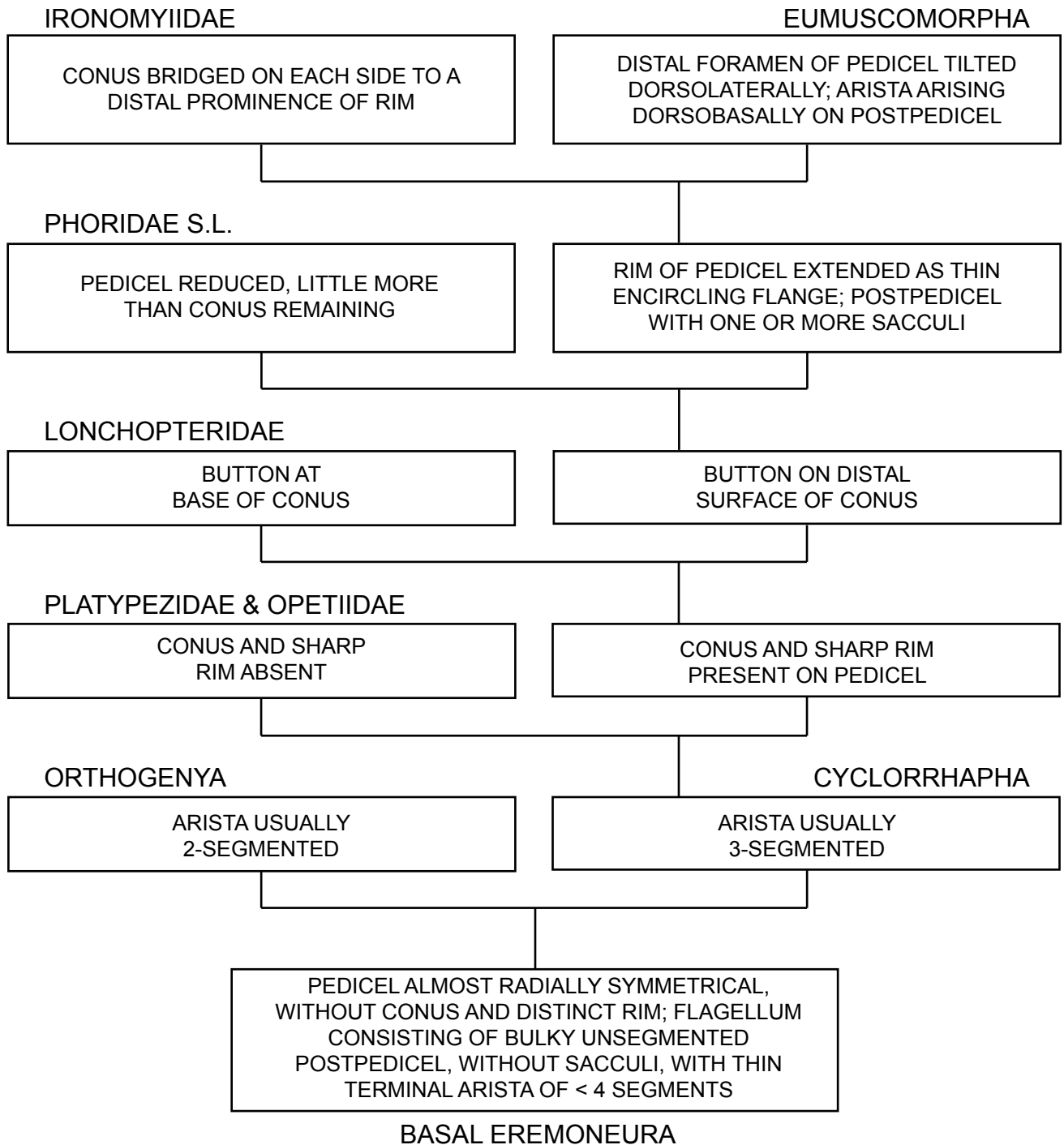
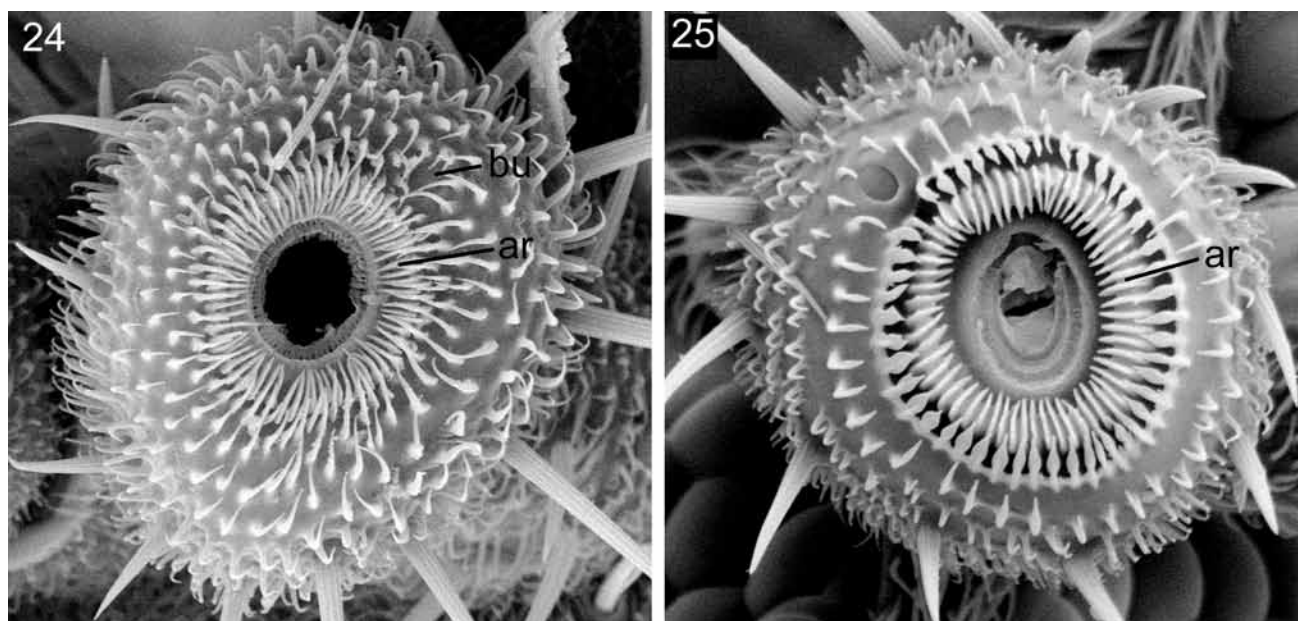


Figure 23. Gradogram, showing possible history of some antennal structures in the Eremoneura. The diagram is intended to show grades as much as clades, and shows the probable basal condition for each broad grouping or taxon, particularly if this condition is a probable apomorphy (polarity of some characters doubtful). As character reversals and convergences occur in numerous taxa, it is not an identification aid.



Figures 24, 25. Antennal seg. 2 of *Orthogenya*, seg. 3 removed. (24) *Empis* sp. (Empididae, Empidinae), distal view of left antenna. (25) *Leptopeza* sp. (Hybotidae, Ocydromiinae), distal view of right antenna. *ar*, annular ridge; *bu*, pedicellar button.

The Chimeromyiidae

The family Chimeromyiidae was established by Grimaldi *et al.* (2009) for the Early Cretaceous genera *Chimeromyia* and *Chimeromyina*. My information on the family is only that provided by these authors.

At least some taxa of Chimeromyiidae have a bulky conus inserted into antennal segment 3 (see figs 7A and 13B in Grimaldi *et al.*, 2009). The pedicel of *Chimeromyia burmitica* Grimaldi & Cumming is described as “cup-shaped” and the basal flagellomere (postpedicel) is described as “possibly with inserted condyle on mesal surface,” presumably referring to a conus arising from the concave distal articular surface of the pedicel. The three-segmented arista may be clearly terminal to dorsal and sub-basal on segment 3 in the various chimeromyiid taxa.

To what degree the presence of a conus in the Chimeromyiidae affects the above hypothesis as to the groundplan state of the eremoneuran pedicel is at present hard to determine, and has not been considered in the design of Fig. 23. The three-segmented condition of the chimeromyiid arista suggested to Grimaldi *et al.* that this is possibly the plesiomorphic state for the Eremoneura.

The Orthogenya (Empidoidea)

If two taxa are sister groups, they should have the same rank, as recognized by Hennig (1973, and elsewhere). As this taxon is widely accepted as the monophyletic sister-group to the Cyclorrhapha (which includes numerous superfamilies), I use the name *Orthogenya* (following Griffiths, 1972; Zatwarnicki, 1996), instead of the superfamily name Empidoidea; it takes priority over the names Empidiformia and Empidiformae sometimes used by dipterists; see Sabrosky (1999) for publication details.

The antennal structure in the apparently primitive forms is essentially similar to that of such basal cyclorrhaphans as Platypezidae, but there are also examples of more complex

antennal types within the group (see Chvala, 1983, and Sinclair & Cumming, 2006, for numerous examples). I am here mainly concerned with the plesiomorphic conditions for the group, which are likely to approach those for the Eremoneura as a whole.

In its simplest form (e.g., Figs 24, 25) segment 2 is moderately compact and maintains an approach to radial symmetry as in many lower brachycerans. The distal profile is rounded, there being neither an encircling rim nor a conus. The pedicellar button is generally present on the distal articular surface, dorsolaterally or laterally to the distal articular foramen. Segment 3 may bear the terminal section of the antenna (arista or stylus) terminally or dorsolaterally, but is not known to have a typical sacculus in any species (see below for comment on *Hormopeza*). The arista is usually two-segmented.

The Apystomyiidae

The Nearctic genus *Apystomyia*, originally placed in the Bombyliidae, was elevated to a separate monotypic family, Apystomyiidae, in the Asiloidea by Nagatomi & Liu (1994). The placement of Apystomyiidae alone as the sister-group to the Cyclorrhapha by Trautwein *et al.* (2010) and Wiegmann *et al.* (2011) has brought this taxon into prominence. Shaun Winterton has generously supplied me with specimens of *A. elinguis* Melander for antennal study from the type locality, Sheep Creek Canyon, Bernardino Co., California.

Nagatomi & Liu (1994) gave a general account of the morphology of *Apystomyia*, including the gross features of the antenna. As in many of the less advanced brachycerans, the general form of the antenna approximates to radial symmetry, except for the bilateral compression of segment 3.

Segment 1 is small, collar-like, with many microtrichia, not evenly distributed, and few dorsal setulae.

Segment 2 (Fig. 174) is considerably larger than segment 1, rotund, slightly bilaterally compressed, slightly higher

than long, without trace of a rim or conus, with the usual covering of microtrichia and a small but variable number of large dorsal and ventral bristles, not forming an encircling series. The annular ridge is scarcely raised above the distal surface of the segment, but bears numerous moderately short, inwardly directed microtrichia. The foraminal ring is slightly raised and finely crenulated. There are two dorsal to dorsolateral buttons (in both sexes) with their peripheral convex rings in contact or partly fused (Fig. 175).

Segment 3 (Fig. 176) is ovoid, slightly bilaterally compressed, with small basal stem fitting into the annular ridge of segment 2. The surface is rugose, more coarsely and irregularly so distally, with many small microtrichia and larger projections, probably trichoid sensilla, but typical macrotrichia are absent. There are no sensory pits, nor anything resembling the sacculi or pedicellar pouches which are present in various cyclorrhaphans.

The slender distal part of the antenna, here termed stylus (though with some doubt regarding its homology with the eremoneuran stylus or arista), arises terminally and symmetrically on segment 3. It consists of two sections (? segments). The more basal section is subcylindrical with its surface broken by many deep grooves into a series of transverse microtrichose plates or sclerites. The terminal surface of the basal section has, ventrally to the base of the terminal section, the structure here termed the stylar goblet (Fig. 177, *go*). The goblet consists in both sexes of a smooth hemispherical cuticular prominence of c. 4.1 µm diameter, with, at its summit, a subcircular aperture of c. 2.1 µm diameter. The aperture clearly leads into a capacious cavity, but further details are not visible because of the condition of the specimens and the minute size of the goblet. On further examination it may be possible to identify the goblet with a particular category of arthropod sense organ. The smaller terminal section of the stylus is articulated with the basal section and has a smooth outer surface (surface contaminated as seen in Fig. 177). Examination with CLM shows it to be hollow, with the inner surface of its cuticle densely micropustulose.

The Apystomyiidae are not morphologically typical of the Cyclorrhapha, because the male postabdomen has a full complement of symmetrical tergites and sternites (which suggests that there is no circumversion of the genital segment), and abdominal plaques can be detected under SEM (which suggests that there is no puparium). I am aware of no other brachyceran with two buttons on each pedicel, but the pedicellar distal articular surface has been examined for very few asiloid flies. I am not aware of any structure resembling the stylar goblet in any other family of Diptera, but this is perhaps due to its minute size and the lack of SEM study of most lower brachycerans. At present I regard the antennal morphology of *Apystomyia* as an ambiguous indicator of relationships, as it resembles that of some more reduced asiloid taxa as well as that of certain more or less basal eremoneurans. The articulation between antennal segments 2 and 3 is unlike that of the Chimeromyiidae and probably more plesiomorphic. If the Apystomyiidae constitute a plesiomorphic sister-group to the Cyclorrhapha, then this would seem to confirm the basal conditions for the eremoneuran antenna indicated in Fig. 23.

The Platypezidae and Opetiidae

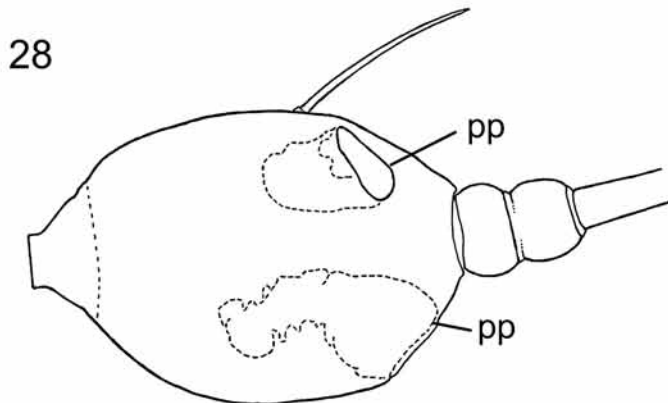
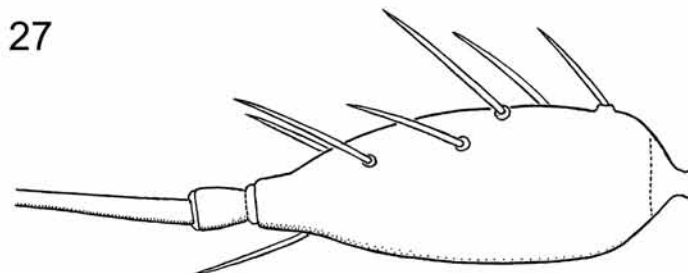
I treat these two families together primarily because of similarity in antennal structure. The molecular study by Moulton & Wiegmann (2004) indicates that they probably together form a clade. See also Chandler (1998) and Collins & Wiegmann (2002a).

Segment 2 in platypezids is generally of primitive form for the Cyclorrhapha, but is variable in some significant characters. I believe that true platypezids, in common with Opetiidae, lack a conus, and that the attribution of a conus to *Plesiocythia* (now included in *Lindneromyia*) by Disney (1988: fig. 5) is due to a slightly prominent annular ridge only. Sometimes the distal articular surface is flattened (as in *Melanderomyia* and *Lindneromyia* sensu Chandler, 1994; see D. McAlpine, 2008: figs 5, 8) but the rim is either indistinct or only slightly angular. The annular ridge in these genera (also in *Agathomyia* and *Microsania*) defines an area of variable size near the centre of the articular surface, and is well marked by its prominent, coarse, incurved microtrichia. In *Opetia* the annular ridge is particularly incassate, but the rim is quite absent (Fig. 1). In *Lindneromyia* the rest of the articular surface is covered with many short, inwardly inclined, tile-like ridges, each bearing a row of microtrichia. The button in the Platypezidae and Opetiidae is located on the dorsolateral part of the distal articular surface, as in most flies of orthorrhaphous grade.

Segment 3 of the Platypezidae and Opetiidae much resembles that of more plesiomorphic taxa of Orthogenya in that it usually tapers distally to the terminal arista and is probably always without true sacculi such as those present in most taxa of Eumuscomorpha. The smoke flies, *Microsania*, are perhaps unique among the platypezids in possessing two deep pit-like hollows, one dorsomedial and one ventral, on segment 3, the postpedicellar pouches (see Fig. 28). However, this condition is almost identical to that of the orthogenyan genus *Hormopeza*, which is also attracted to smoke by odour (Kessel, 1960; Sinclair & Cumming, 2006). The latter authors refer to these hollows as “sensory pits” in their text (2006: 73) and as “pit glands” on their figs 8 and 47. The taxonomic distribution of the pedicellar pouches renders it improbable that they are homologous structures in *Hormopeza* and *Microsania*, or that they can be homologous with the sensory sacculi in typical taxa of Eumuscomorpha. Also, the pouches in *Microsania* and *Hormopeza* do not contain trichoid sensilla, which characterize the sacculi of those eumuscomorphans in which they have been investigated. More detailed examination of ultramicroscopic structure is beyond the scope of the present work. In *Opetia* and some platypezids (e.g., *Microsania*, Fig. 28) segment 3 bears one or more relatively large socket-based bristles or macrotrichia. This is an unusual condition in the Eremoneura.

The arista of typical platypezids is three-segmented, but that of *Opetia* has fewer segments (Fig. 27), as recorded by Hennig (1976), Chandler (1998), and Sinclair & Cumming (2006). In view of the many independent examples of secondary reduction in arisal segmentation in Cyclorrhapha (D. McAlpine, 2002), I have suggested that the condition in *Opetia* may not be plesiomorphic or indicative of wide phylogenetic isolation of the taxon. The Cretaceous *Electrosania cretica* Grimaldi & Cumming, 1999, is also a platypezid-like fly with a two-segmented arista.

While the partial to complete fusion of abdominal tergites



Figures 26–28. Antennal structure in some basal cyclorrhaphans. (26) *Opetia nigra* Meigen, male (fam. Opetiidae), left antennal seg. 2 after removal of seg. 3, distal view. (27) The same, left seg. 3 and arista, lateral view. (28) *Microsania arthuri* Chandler (fam. Platypezidae), left seg. 3 and arista, medial view. *pp*, postpedicellar pouches.

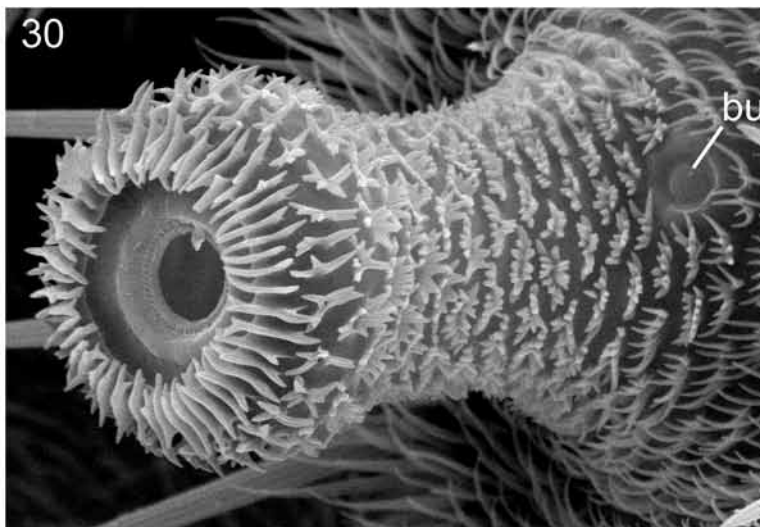
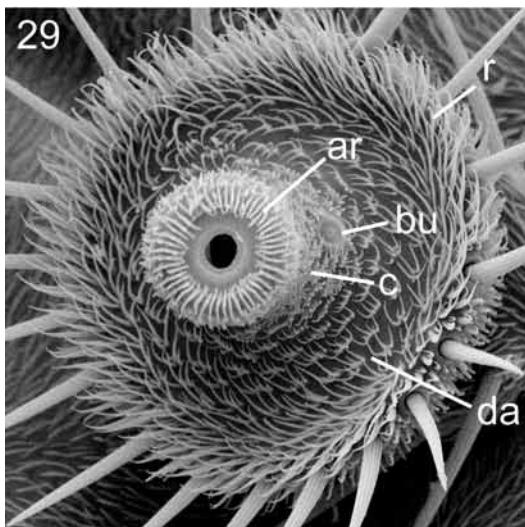
1 and 2 is usual among the Cyclorrhapha (generally quite free in Orthogenya, but also in Phoridae s.l.), *Opetia nigra* Meigen shows sexual dimorphism in this character. The male has tergites 1 and 2 fused so as to leave no intervening intersegmental membrane, but a line of demarcation is generally visible, taking the form of a slight groove in available specimens. This condition is essentially similar to that of both sexes of typical platypezids (e.g., *Lindneromyia* spp.). The female of *O. nigra* has tergites 1 and 2 completely separated by intersegmental membrane so that the posterior margin of tergite 1 is free to overlap broadly the anterior margin of tergite 2, and tergite 1 is shorter than in the male of the species. I have examined dried specimens and others

cleared in lactic acid of both sexes of *O. nigra* for this character. The condition for the female can also be inferred from the illustration by Chandler (1998: fig. 2.12).

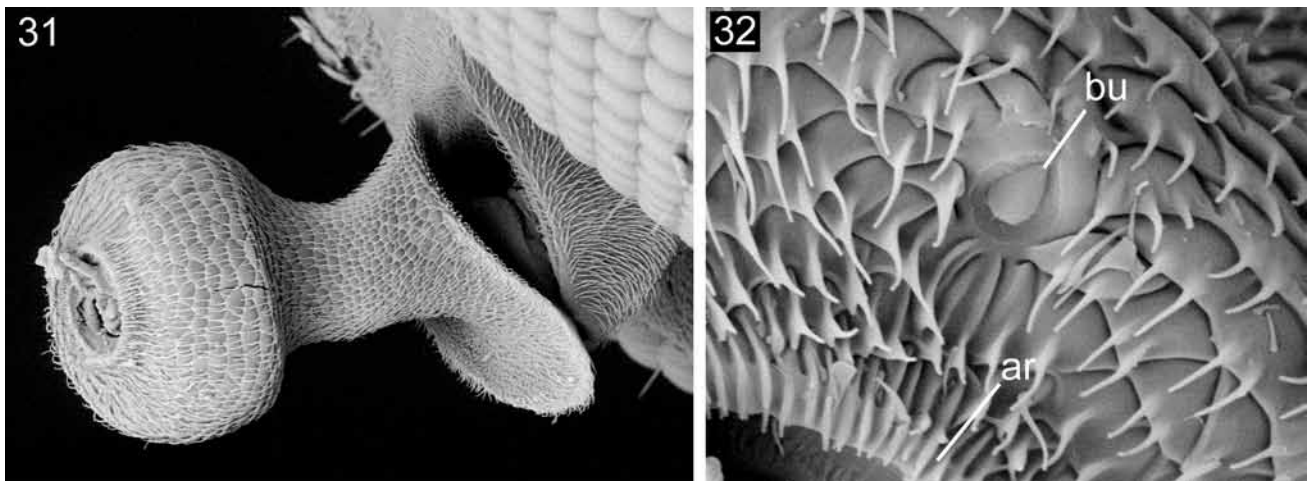
Cyclorrhaphans with a conus

The remaining families of Brachycera-Cyclorrhapha either have a distinct conus on segment 2 (see Hennig, 1976: 54–56) or are derived from forms possessing a conus with subsequent reduction (e.g., *Periscelis*, Fig. 100). Almost all these taxa also have an angular or flange-like, more or less encircling pedicellar rim.

The lower cyclorrhaphous families Lonchopteridae,



Figures 29, 30. *Lonchoptera bifurcata* Fallén (fam. Lonchopteridae). (29) Left seg. 2, distal view. (30) Conus, lateral view. *ar*, annular ridge; *bu*, pedicellar button; *c*, conus; *da*, distal articulation surface; *r*, rim.



Figures 31, 32. *Sciadocera rufomaculata* White (fam. Phoridae). (31) Left antenna, seg. 2 after removal of seg. 3, lateral view. (32) Part of distal surface of conus, showing button. *ar*, annular ridge; *bu*, pedicellar button.

Opetiidae, and Platypezidae are misplaced in the otherwise informative cladogram for the Eremoneura by Grimaldi & Engel (2005: fig. 12.78), through errors regarding the development of the conus (op. cit.: table 12.7, character 19).

The Lonchopteridae

In *Lonchoptera bifurcata* (Fallén) (*L. furcata* auct.), which may be taken as morphologically typical of extant taxa of Lonchopteridae, segment 2 shows an apparent combination of plesiomorphic and derived conditions (Figs 29, 30). The approximate radial symmetry of the segment resembles the plesiomorphic one for the Cyclorrhapha. However, the strongly developed angular rim surrounding the partly concave distal articular surface, and the presence of a well developed, elongate conus arising from the centre of this surface suggest the possibility of apomorphies shared with more advanced cyclorrhaphans, but some features of the conus indicate that this may not be so. The conus in the Phoridae and Ironomyiidae bears the button on its distal surface, and this is the usual and perhaps the primitive position for the button in the Eumuscomorpha. However, in *Lonchoptera* the button is situated at the extreme base of the conus where it adjoins the distal articular surface. I therefore point out the possibility that the lonchopterid conus is an independently derived structure resulting from the simple protrusion of the annular ridge and its associated foramen, in a primitively platypezid-like taxon, into the base of segment 3, without affecting the position of the button. This hypothesis allows for the independent evolution of the conus at least twice in the Cyclorrhapha, but this may not be surprising in view of the fact that a centrally inserted conus has also developed in the orthogenyan genus *Dolichopus* (Sinclair & Cumming 2006), and such concealed structure may well have been overlooked in other non-cyclorrhaphous taxa.

Lonchoptera also differs from the Phoridae in retaining a relatively massive main body of segment 2 with a well developed encircling series of setulae, whereas extant phorid taxa have the segment reduced as explained below. A generally overlooked feature of at least some *Lonchoptera* spp. is the presence of a pair of secondary claw-like structures on the terminal surface of tarsal segment 5. These are

concealed by the true claws so that detailed study is difficult (author's observations with SEM).

The Cretaceous genus *Lonchopteromorpha* (see Grimaldi & Cumming, 1999), though described under "family Lonchopteridae (?)", clearly has a bilaterally subsymmetrical (rather than radially subsymmetrical) antennal type, and possibly separate abdominal tergites 1 and 2 (op. cit. fig. 54); it therefore is probably not closely related to the Lonchopteridae. *Lonchopteromorpha* also differs from *Lonchoptera* in its short, strongly incrassate hind basitarsus.

The Phoridae (including Sciadoceridae)

It has been clear for some time that the Phoridae and Sciadoceridae are very closely related to each other. Disney (2001) combined the two families, and Brown (2007) demonstrated the difficulty of supporting a monophyletic group Sciadoceridae (or Sciadocerinae) when the numerous fossil taxa are considered. Study of phorid antennal structure has been limited because of the difficulty in separating segments 2 and 3 to expose the conus without fragmentation.

Segment 2 of *Sciadocera rufomaculata* White (Figs 31, 32) is very largely concealed in the intact antenna. This is because the main body of the segment is reduced to a narrowly or scarcely visible flange representing the rim, and the large conus is deeply embedded within the basal hollow of segment 3. After removal of segment 3, the conus is seen to be relatively slender basally, with a large, rounded distal club bearing the foramen of articulation on the centre of its apical surface (Fig. 31). The foramen is surrounded by an annular ridge bearing ridge-like denticles. The button is situated dorsolaterally on the distal surface of the conus (Fig. 32). Much of the surface of the conus is covered with tile-like microtrichose ridges as described for *Lindneromyia* sp. above (family Platypezidae). In contrast to that of most cyclorrhaphans, the region of the rim lacks obvious setulae.

In the Phoridae s.str. (or Euphorida of Brown, 2007) segment 2 shows the essential features described above for *Sciadocera* (see also Disney, 1988; 1994). This is the reason why many phorids appear to have only two prearistal segments in the antenna. In specimens of several genera I find the conus to have similar surface sculpture and annular ridge and a similarly situated button to that of *Sciadocera*. The

rim may bear a few moderately small, socket-based setulae.

Segment 3 of *Sciadocera* has a deep basal hollow enclosing the conus and bears a subterminal three-segmented arista (Hennig, 1976: fig. 62; Disney, 2001: fig. 7). It lacks macrotrichia and typical sacculi, but the general surface has diverse microtrichia and sensilla, and the dorsobasal external surface bears numerous (more than 25) saucer-shaped pits packed with trichoid sensilla (author's observations). These pits bear some resemblance to the sensory pits of *Cryptochetum* (family Cryptochetidae, see Figs 69, 70), but in that genus they coexist with a typical schizophoran sacculus. Both *Sciadocera* and *Diplonevra* sp. (examined by me) have neither sacculi (as described above and under Ironomyiidae) nor the subcuticular pit sensilla (SPS) described by Disney (2003) and Pfeil *et al.* (1994) for certain phorids. Sukontason *et al.* (2005) and Chen & Fadamiro (2008) described the surface sensilla on segment 3 of certain phorids, demonstrating some diversity in these.

The arista of various phorids is not consistently terminal and consists of one to three segments, or it may be absent (Peterson, 1987; Disney, 1994).

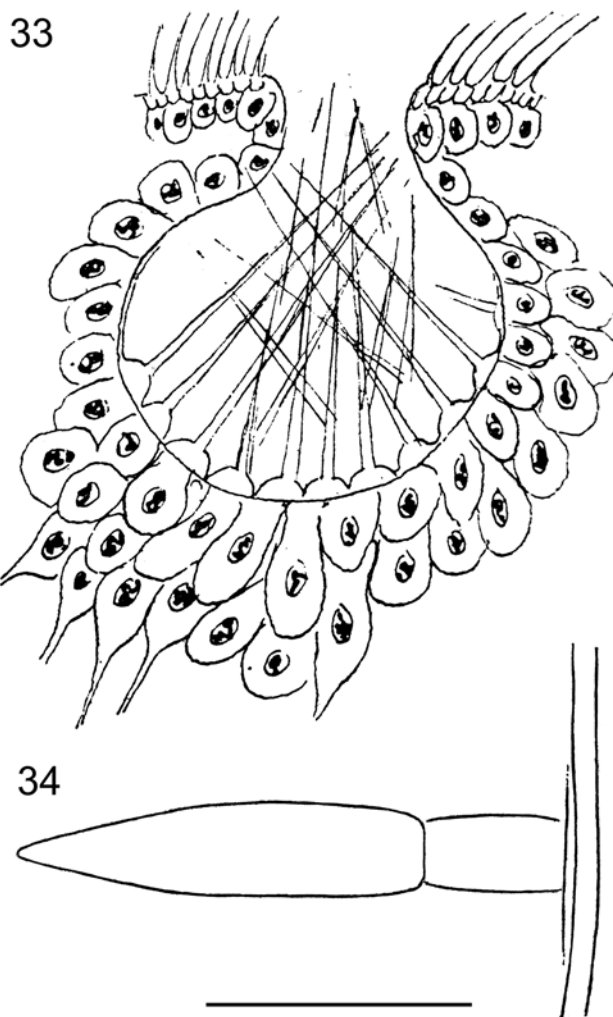
A general condition for the Phoridae, sometimes noted by specialists, is the presence of barbed ("feathered", or "fringed") larger macrotrichia on many parts of the insect (see Peterson, 1987: fig. 99). The barbed condition is confirmed by our SEM work on such phylogenetically diverse phorids as *Diplonevra nigrita* (Malloch) and *Sciadocera rufomaculata*, and is therefore probably in the groundplan of the family. Detailed SEM examination of representatives of each of the other families of lower (non-eumuscomorphan) Cyclorrhapha (Opetiidae, Platypezidae, Lonchopteridae, Ironomyiidae, also Apystomyiidae) suggests the absence of barbs on all macrotrichia for these families. Extensive experience also suggests that barbed macrotrichia may be absent from the numerous other cyclorrhaphous families, but a thorough search has not been made. The barbed condition is therefore likely to be, to a large extent, diagnostic for the Phoridae, though reduced or perhaps lost in some highly derived phorid taxa.

The Ironomyiidae

I have already given some details of the antenna of *Ironomyia nigromaculata* White (D. McAlpine, 2008: figs 1, 2, 6, 7).

Segment 2 of *I. nigromaculata* has the basal body well developed, encircled by setulae and with prominent, flange-like rim surrounding its largely concave distal articular surface. The rim has a pair of opposed angular projections (dorsomedial and ventrolateral). The centre of the distal articular surface bears a large, distally swollen conus with dorsolateral button on its terminal surface. The conus is connected to each of the two angular projections of the rim by a separate bridge.

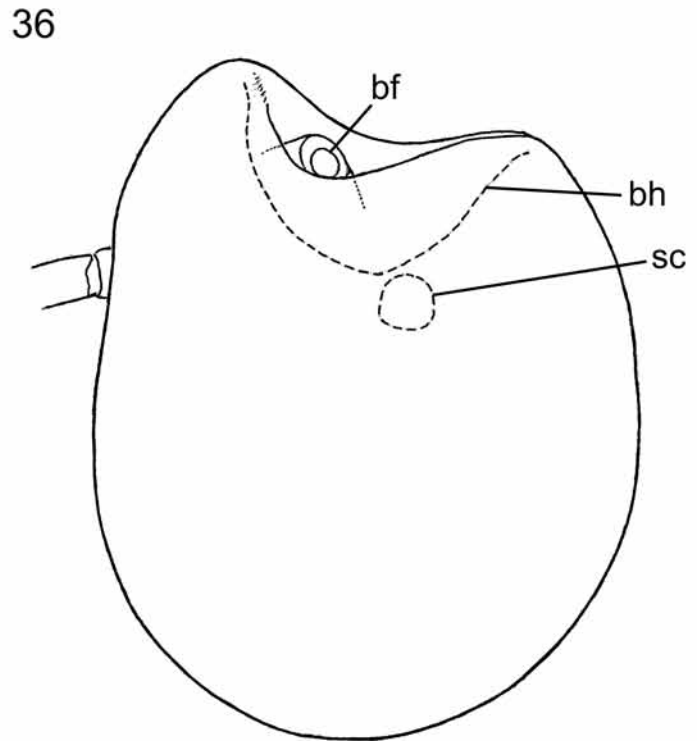
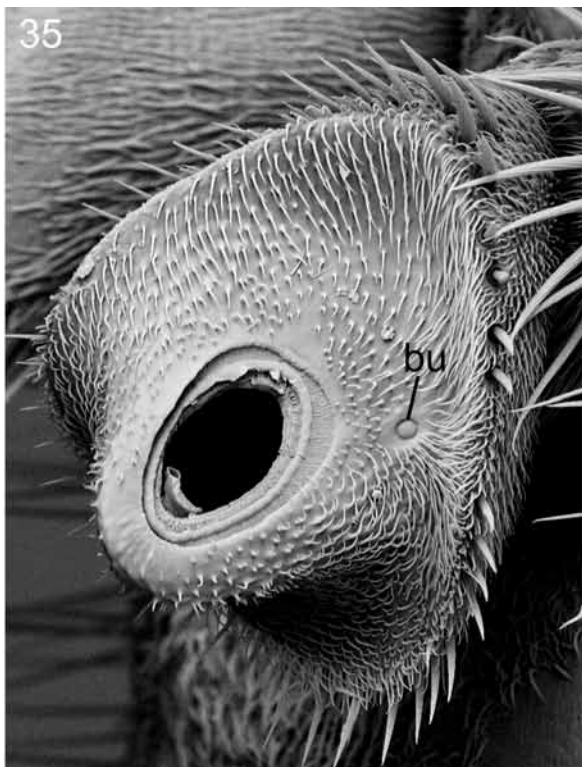
Segment 3 has a characteristic shape, as previously described. Study of more material shows that the number of sacculi in segment 3 can sometimes be more than two, as one male specimen shows two sacculi in the ventral gibbosity of the left antenna as well as one in the dorsal gibbosity, but, as the right antenna has an irregularly divided ventral sacculus, this may be regarded as an abnormal specimen. As this is the first occurrence of sacculi in the standard taxonomic sequence of higher Diptera (or Eremoneura), I have given it some attention.



Figures 33, 34. Details of sacculus. (33) *Calliphora vicina* Robineau-Desvoidy (fam. Calliphoridae), longitudinal section of sacculus (after Lowne, 1895). (34) *Ironomyia nigromaculata* White (fam. Ironomyiidae), sensillum from lining of sacculus, approximate outline as seen with CLM; scale = 5 μ m.

The sacculus contains a large number of slender sensilla. These appear to be of several kinds but detail is at about the limit of resolution of available CLM. Sensilla on the floor and lower sides of the sacculus have the approximate form shown in Fig. 34. These are almost circular in cross-section, without a finely filiform apex, and at least some show a division into two segments. Those on the wall nearer the orifice are closely packed and either more slender than the above or at least very slender and filiform apically. This rather limited information may be adequate to suggest a homology of the ironomyiid sacculus with that of *Drosophila* (Drosophilidae; Stocker, 2001), *Delia* (Anthomyiidae; Ross & Anderson, 1987 and 1991), *Hippelates* (Chloropidae; DuBose & Axtell, 1968), *Calliphora* (Calliphoridae; Fig. 33 reproduced here from Lowne, 1895), and other schizophorans. However, my data are insufficient to draw precise comparisons with the types of sensilla described in the sacculi of these flies.

I have previously summarized evidence for a possible but uncertain close relationship between the Ironomyiidae and the Eumuscomorpha (D. McAlpine, 2008). Alternatively,



Figures 35, 36. *Melangyna* sp. (fam. Syrphidae). (35) Left antennal seg. 2, distolateral view after removal of seg. 3. (36) Right seg. 3. *bf*, basal foramen; *bh*, basal hollow; *bu*, pedicellar button; *sc*, sacculus.

Wiegmann *et al.* (2011) treated Ironomyiidae and Phoridae s.l. as sister groups, which separated c. 90 MYA. However, *Euliphora grimaldii* Arillo & Mostovski, 1999, dating from c. 110 MYA (Early Cretaceous), showed to a significant extent the venational apomorphies of early but not basal phorids (see Brown, 2007), and apparently also (my interpretation of the illustrations by Arillo & Mostovski) the characteristic phorid reduction of antennal segment 2. The Ironomyiidae resemble the Phoridae in the partial fusion of the subcosta and vein 1, but otherwise possess none of these phorid apomorphies. Therefore, if the two families are sister groups, their initial divergence must have occurred at a much earlier time level, especially so if the sinolestine fossils (discussed by D. McAlpine, 2008) are close to true ironomyiids. The date of separation indicated by Grimaldi & Engel (2005: fig. 12.78)—between 130 and 140 MYA—is more credible. Arillo & Mostovski placed *Euliphora*, together with *Prioriphora* (Late Cretaceous), in the phorid subfamily Prioriphorinae. It remains to be recorded whether these fossils have abdominal tergites 1 and 2 quite separate, as in Recent phorids (and apparently the Late Cretaceous *Sciadophora*), or partly fused as in *Ironomyia* and most other cyclorrhaphans.

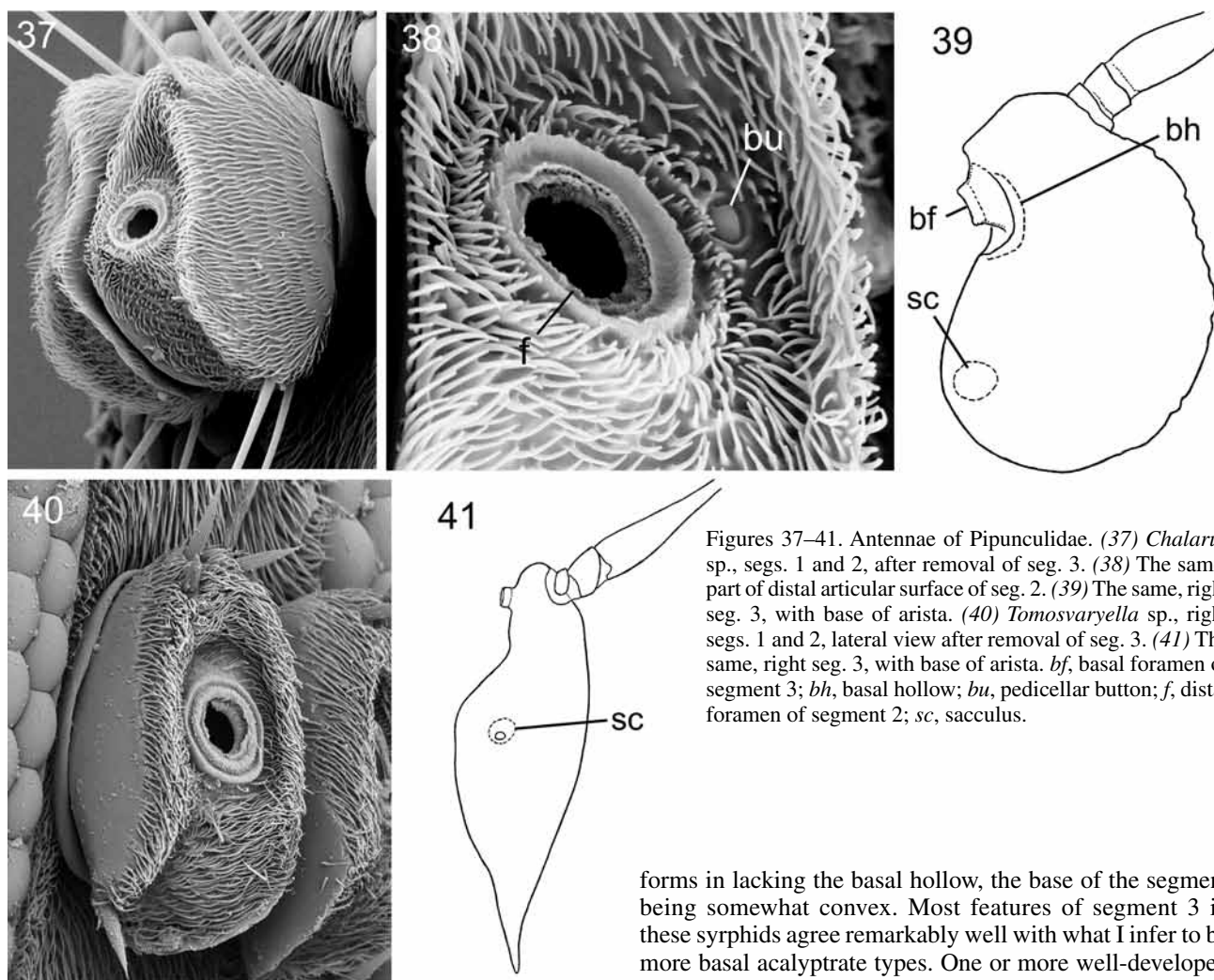
Contrary to the statement of J. McAlpine (1989: 1422), *Ironomyia* differs from almost all Phoridae in the holoptic condition of the males, the derived phorid genus *Postoptica* being an exception. It also differs from the Phoridae in the sexual dimorphism of the prelabrum (a condition met with in many taxa of Eumuscomorpha, see D. McAlpine, 2008: 22–23), and in the absence of barbed macrotrichia on the head, thorax, wing, and abdomen.

The Eumuscomorpha

Following Wada (1991) this apparently monophyletic group includes the Syrphidae, Pipunculidae, and the numerous families of Schizophora. Despite the great present diversity of the Eumuscomorpha, there appear to be very few undoubted fossils of the group from before the Tertiary (Cenozoic era). There is much diversity in structure of segment 2 in the Eumuscomorpha, but the groundplan conditions are probably those shared with certain syrphids and the less modified taxa in several superfamilies of Schizophora, e.g., the Sciomyzoidea. The accumulated antennal apomorphies of the basal Eumuscomorpha, probably absent in the groundplan of the Eremoneura, are as follows: segment 2 with rim extended as encircling flange; conus present, with button on its distal surface; annular ridge and distal foramen of segment 2 tilted dorsolaterally; segment 3 with one or more sacculi; arista arising dorsobasally from segment 3; arista three-segmented (doubtful apomorphy).

The Syrphidae

The Syrphidae, whether they form a sister-group to the Pipunculidae alone or to the whole remainder of the Eumuscomorpha (i.e. Pipunculidae + Schizophora, see Collins & Wiegmann, 2002) must be considered a key group to understanding much of the basal morphology of the Schizophora. I have taken for initial study representatives of the syrphid genera *Melangyna*, *Microdon*, *Psilota*, *Eristalis*, *Chalcosyrphus*, *Ceriana*. These show slight variation, mainly in proportions of certain parts and degree of symmetry.



Figures 37–41. Antennae of Pipunculidae. (37) *Chalarus* sp., segs. 1 and 2, after removal of seg. 3. (38) The same, part of distal articular surface of seg. 2. (39) The same, right seg. 3, with base of arista. (40) *Tomosvaryella* sp., right segs. 1 and 2, lateral view after removal of seg. 3. (41) The same, right seg. 3, with base of arista. *bf*, basal foramen of segment 3; *bh*, basal hollow; *bu*, pedicellar button; *f*, distal foramen of segment 2; *sc*, sacculus.

Segment 2 (Fig. 35) is generally of moderate size, with largely concave distal articular surface and completely encircling rim. The rim is usually notched or sinuate on its dorsal margin, but is scarcely so in *Microdon* and *Ceriana*. Typically, the conus is moderately large, broad, and rather short, with a short ventral chin, and the foramen of articulation is inclined laterally with a tendency to become vertically elongate in some forms. The button is located at the lateral base of the conus where the latter merges with the surrounding articular surface, or is located more dorsally, especially so in *Microdon*.

In *Ceriana ornata* (Saunders) segment 2 is very different from that of other examined taxa. Both the segment as a whole and the conus are elongate and almost radially symmetrical, the latter distally rounded and clavate. As in the Phoridae, the clavate condition of the conus renders the separation of segments 2 and 3 for study difficult, even after the connective membrane is snapped by rotation.

Segment 3 in *Melangyna* (Fig. 36) is typical of a number of syrphid genera. The segment is broadly bilaterally compressed, has a broad, relatively shallow basal hollow, and the basal articular foramen is situated on a slight prominence arising within this cavity, but there is no indication of a sub-basal caecum. The arista arises before mid length of the segment on the lateral surface very close to the dorsal margin. Segment 3 of *Eristalis copiosa* Walker (and possibly that of related species) differs from the above

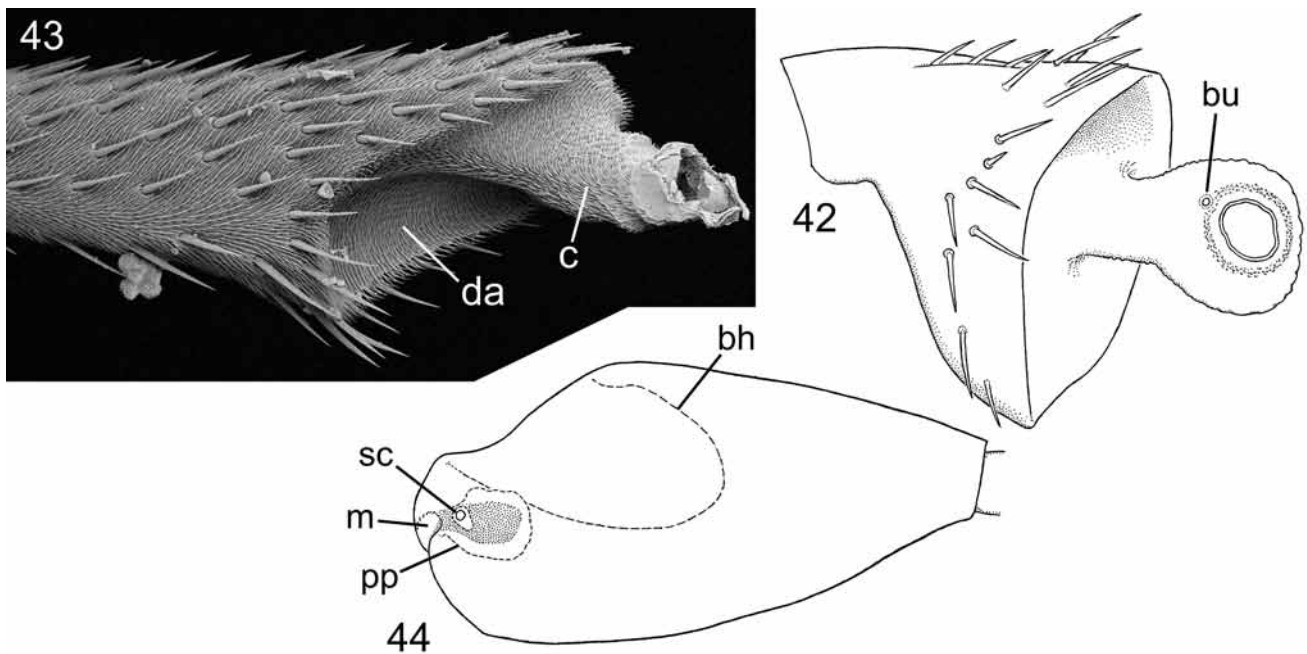
forms in lacking the basal hollow, the base of the segment being somewhat convex. Most features of segment 3 in these syrphids agree remarkably well with what I infer to be more basal acalyptrate types. One or more well-developed sacculi occur on the lateral surface and sometimes also on the medial surface. The number can sometimes differ between the right and the left antenna, but often there is just one sacculus, which is located on the lateral surface as in most acalyptrate taxa.

In *Ceriana* (already noted for its unusual segment 2) and some related genera (see Vockeroth & Thompson, 1987) the arista is much shortened and located apically on segment 3. Comparison with probable outgroups leads me to believe that the peculiarities of *Ceriana* and its allies (tribe Cerioidini) are autapomorphies for this group. Thus, the presence of a terminal arista (or style) on a distally tapered segment 3 is an evolutionary reversal, simulating the conditions present in basal eremoneurans.

The Pipunculidae

I have taken for study antennae of the genera *Chalarus* and *Tomosvaryella*.

In *Chalarus* segment 2 (Figs 37, 38) is bilaterally compressed and otherwise resembles that of the less modified taxa of Syrphidae. The distal articular surface is moderately concave with moderately developed rim, receding ventrally. The conus is broad, little raised, and approximated to the medial side of the segment. The annular ridge and distal foramen are tilted dorsolaterally and the button lies in the relatively slight concavity between the conus and the mid-lateral part of the rim.



Figures 42–44. Antennae of Conopidae. (42) *Myopa* sp., right antennal seg. 2. (43) *Australoconops uncinctus* (Kröber), part of right antennal seg. 2. (44) The same, right antennal seg. 3. *bh*, basal hollow; *bu*, pedicellar button; *c*, conus; *da*, distal articular surface; *m*, mouth of postpedicellar pouch; *pp*, postpedicellar pouch; *sc*, sacculus (seen superimposed on postpedicellar pouch).

Segment 3 in *Chalarus* (Fig. 39) is broadly rounded and bilaterally compressed. The basal hollow is present, but too small to contain the prominence bearing the basal articular foramen and there is no sub-basal caecum. The single sacculus is located on the ventral side of the segment and opens on the lateral surface. Much of the surface is covered with relatively large, saucer-like pits. The arista is inserted dorsally not far from the base of the segment; it is three-segmented with segment 4 forming a complete annulus.

The notable differences in antennal structure of *Tomosvaryella* from the above are probable apomorphies (see Figs 40, 41). The conus is absent and the smooth annular ridge, together with the distal foramen, is sunk into a deep, narrow cavity on the distal articular surface of segment 3. The annular ridge and foramen are located centrally on this surface and are almost symmetrical, not tilted. The button (not visible in the preparation) is apparently concealed in the narrow cavity between the annular ridge and the lateral part of the rim.

Segment 3 is much prolonged ventrally and has no basal hollow. The basal segment of the arista (segment 4) is sclerotized only on the dorsal side.

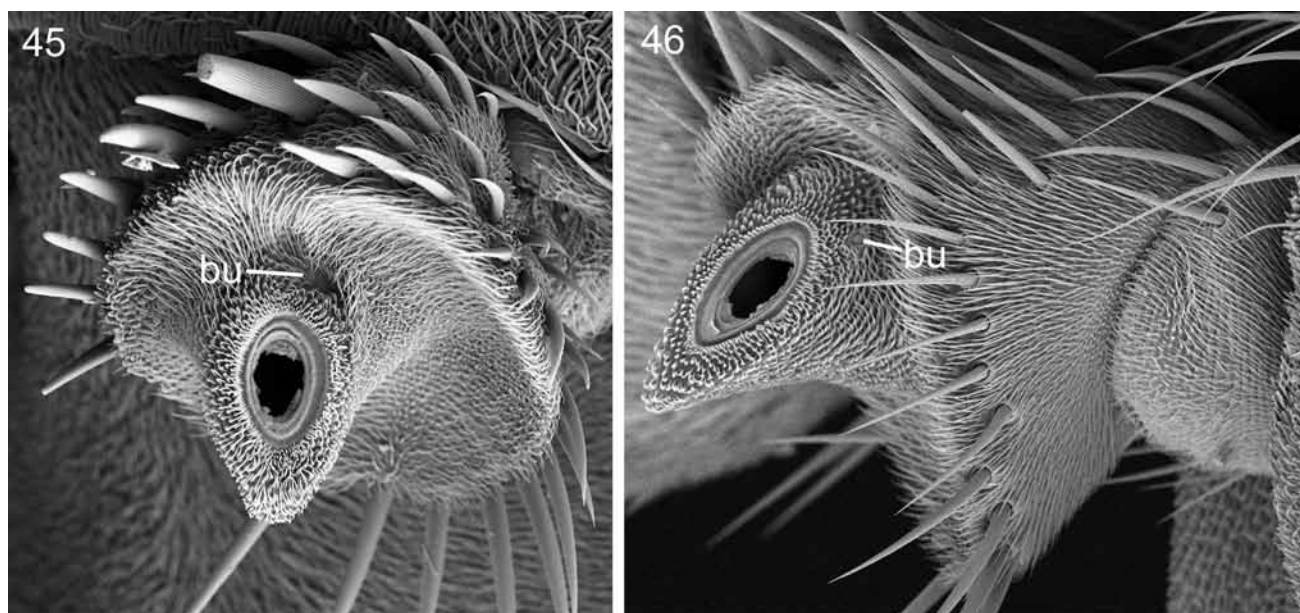
The antenna of the Pipunculidae shows the basic structure of the Eumuscomorpha, but does not appear to provide evidence as to whether this family is the sister group of the Syrphidae or the Schizophora. Neither J. McAlpine (1989) nor Zatwarnicki (1996) gave very convincing synapomorphies for the Syrphoidea (Syrphidae + Pipunculidae) as a monophyletic group. The work of Collins & Wiegmann (2002b) suggested that the Pipunculidae alone represent the sister group to Schizophora, and that the Syrphoidea (*sensu* J. McAlpine, 1989) are paraphyletic. These conclusions are supported by Wiegmann *et al.* (2011).

The Conopidae

Examples used in this study include *Myopa* sp. (subfamily Myopinae), *Australoconops uncinctus* (Kröber), and *Heteroconops* sp. (subfamily Conopinae). Though these species show a range of variation, a wider range of observations will be necessary to make generalizations for the family.

In *Myopa* sp. segment 2 is moderately short and stout, narrowed basally and broadly funnel-like distally (Fig. 42). The flange-like rim is continuous without division into dorsal lobes. The external surface is densely microtrichose and bears a number of stout setulae. In several observed examples the setulae on the medial surface are partly or extensively broken or abraded. The distal articular surface is broadly concave and bears numerous fine, simple microtrichia which are not grouped into combs nor located on ridges. The conus rises from the dorsomedial part of the articular surface. It is narrow basally and dilated and bilaterally compressed distally, apparently well sclerotized and rigid; the distal foramen is located subterminally on the outer lateral surface; it has a narrow foraminal ring; the annular ridge is only slightly prominent and bears a moderate number of small compact tubercles, some rounded, some bearing a minute microtrichium. The general surface of the conus is almost devoid of microtrichia, but bears many short, smooth transverse ridges.

Segment 3 is rather short, inflated, and without basal stem. The apparent sacculus is situated on the outer lateral surface, slightly ventrobasally of its centre, and is only slightly larger than numerous sensory pits on this surface, but it is differentiated by the possession of fine trichoid sensilla in the mouth region, as well as one larger ovoid-cylindrical sensillum arising from the floor of the cavity. The arista is shorter than segment 3, inserted slightly laterad of mid-dorsal position on segment 3, and is three-segmented.



Figures 45, 46. Left antennal seg. 2. (45) *Maorimyia bipunctata* (Hutton) (fam. Helcomyzidae), distolateral view. (46) *Napaeosciomyza* sp. (fam. Helosciomyzidae), lateral view. *bu*, pedicellar button.

In *Australoconops* segment 2 (Fig. 43) is elongate, gradually expanding distally, with the distal articular surface oblique, concave ventrally and bearing the conus dorsally. The conus is elongate, irregularly subcylindrical, weakly sclerotized and apparently flexible. The distal foramen is exceptionally large, subcircular, without a marked annular ridge, and terminal on the conus. The button was not located, probably because of the irregular surface of the conus. Segment 3 (Fig. 44) is somewhat elongate, bulbous basally and tapered distally. There is a large basal hollow into which the conus is inserted. The apparent sacculus opens on to the lateral surface near the base of the segment. There is a relatively large opening facing basally on the basal swelling of segment 3, which leads into a cavity much larger than that of the sacculus. This cavity (Fig. 44, *pp*), which I term the postpedicellar pouch, in analogy with that of the orthogenyan genus *Hormopeza*, has a thick transparent wall with a pigmented lining. Its mouth, though microtrichose, lacks the scabrous surface of the sub-basal caecum of some families, and is unlikely to be homologous with that structure. The microstructure of the pouch is not visible in my preparations, and it is not evident whether its function is sensory or glandular. Under CLM the sacculus appears to be superimposed on the pouch (in lateral view), but it is not clear if there is any connection between their walls.

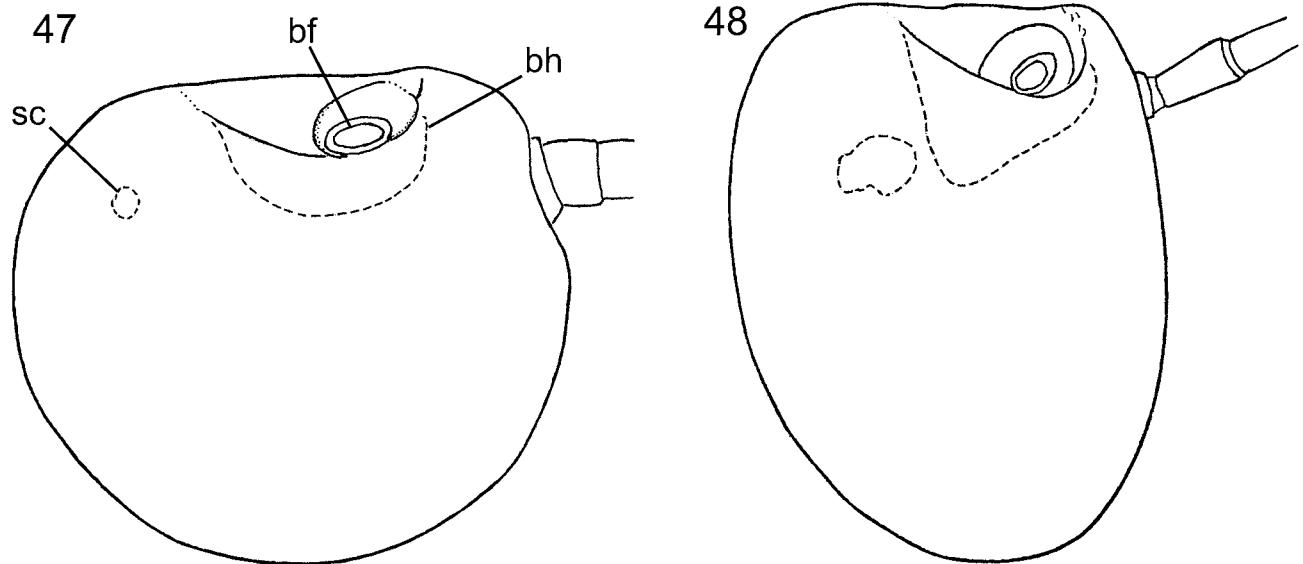
The postpedicellar pouch is present in both sexes of *Australoconops uncinatus*. It is also present in *Heteroconops* sp. and probably at least some other taxa of Conopinae. Its opening is usually concealed in whole specimens, as it is on the surface which faces into the concavity of the distal articular surface of segment 2, but it is readily visible in cleared antennae under CLM. The condition in *Physocephala texana* (Williston) appears to be more complex but has not been examined in detail. The conus of *Heteroconops* is similar to that of *Australoconops* but is more elongate. The remarkable resemblance in structure of segment 2 between certain taxa of Conopidae and Pyrgotidae is mentioned under the latter family. I have previously noted variation in the number of arisal segments in the Conopidae (D. McAlpine, 2002).

Various studies of the Conopidae have failed to demonstrate convincingly its nearest relatives among the schizophoran families. The peculiarities of the conus and postpedicellar pouch appear to be apomorphies restricted to the subfamily Conopinae, and are therefore not relevant to the broader problem of relationships.

During this rapid selective check of conopid morphology, I have noticed major differences in the subscutellum (*sensu* J. McAlpine, 1981) between taxa. In *Stylogaster* spp. the subscutellum is large, deep, and medially extended so as almost to divide the postscutellum; in other conopid taxa examined the subscutellum is quite narrowly transverse or vestigial above the large postscutellum. This variation may have taxonomic significance.

The Sciomyzoidea (including Lauxanioidea)

J. McAlpine (1989) gave detailed reasons for separating the superfamilies Sciomyzoidea and Lauxanioidea and, at first glance, particularly regarding his table 116.4, he seems to have made a strong case (comparable to his now refuted case for monophyly of the Acalypratae). However, careful assessment of the 16 character differences given indicates that their reliability as indicators for a pair of sharply defined monophyletic sister groups is at best very weak. Some ambiguous characters seem to be interpreted in a particular way to support a desired hypothesis, when they could be as readily interpreted as supporting an alternative one. J. McAlpine's identification of character states "that are apomorphic with respect to ground plan of Acalypratae" is invalid as there is no such monophyletic taxon. What is apparent to me is that his lauxanioid families Lauxaniidae s.l. and Chamaemyiidae form a more apomorphic group, which could be a clade, whereas the remaining sciomyzoid family collection is most probably paraphyletic. If J. McAlpine (1989) and Wiegmann *et al.* (2011) are correct in including *Cremifania* within the lauxanioid family Chamaemyiidae, then it is clear that the protandrial structure supposed by the former to indicate the apomorphic groundplan condition for



Figures 47–48. Left antennal seg. 3, medial view. (47) *Maorimyia bipunctata* (Hutton) (fam. Helcomyzidae). (48) *Napaesciomyza* sp. (fam. Helosciomyzidae). *bf*, basal foramen; *bh*, basal hollow; *sc*, sacculus.

the Lauxanioidea (as distinct from the Sciomyzoidea) has no validity. Presentation of a more detailed analysis would be out of place here, but I retain the system used by Colless & McAlpine (1991) wherein the Lauxaniidae are placed in the Sciomyzoidea.

Those sciomyzoid taxa with antennal features more basic (and probably plesiomorphic) for the superfamily seem likely, from comparison with the outgroup Syrphidae, to retain the conditions most like the groundplan for the Schizophora. In *Maorimyia bipunctata* (Hutton) (family Helcomyzidae, Figs 45, 47) the rim is moderately developed for the Schizophora and does not form a pair of dorsal lobes. The conus is stout and prominent, located slightly medially of the centre of the distal articular surface, so that it encroaches slightly on the medial part of the rim-flange, with its distal surface and foramen very obliquely tilted dorsally and slightly laterally, with prominent ventral chin. The annular ridge is not prominent, and lacks any special development of microtrichia. The button is dorsolateral in position, more nearly dorsal than in related families (other than Coelopidae), and there is no dorsal longitudinal sulcus on the conus. Segment 3 is short, rounded, with moderately large basal hollow, the basal foramen on a marked, rounded gibbosity near the medial margin of the hollow. The sacculus is located ventrolaterally. *Napaesciomyza* sp. (family Helosciomyzidae, Figs 46, 48) has the antenna structurally very similar to that of *Maorimyia*.

In typical Coelopidae (subfamily Coelopinae), e.g., *Gluma* (Fig. 49), *Coelopa*, and *Coelopella*, segment 2 resembles that of the Helcomyzidae in having the large conus situated almost centrally on the distal articular surface, almost symmetrical, and with distal foramen facing more dorsally than laterally. However, the coelopid conus, though slightly variable, is more elongate, and the button is situated dorsally at the base of the conus, where the latter merges with the distal articular surface, and is sunken into a shallow pedicellar sulcus, which extends distally on the dorsal surface of the conus for a variable length. Segment 3 of the coelopid antenna is short, rounded, and decumbent at rest, but is similar structurally to that of the

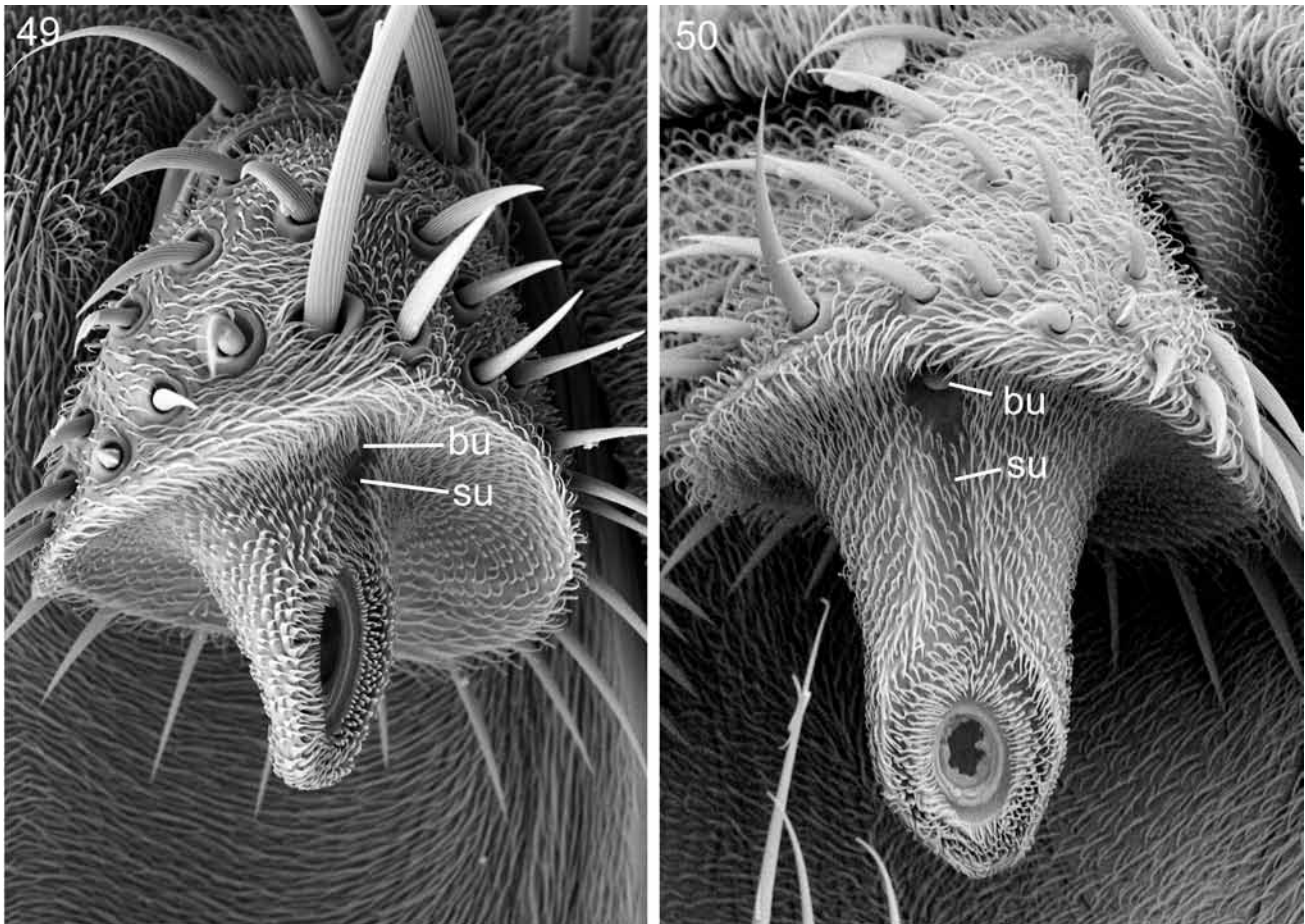
Helcomyzidae, Helosciomyzidae, etc.

The position of the genus *Lopa* in the Coelopidae has been queried by Meier & Wiegmann (2002) from their molecular data. *Lopa* was originally placed in a separate subfamily, Lopinae, from other coelopids, the Coelopinae. The antenna of *Lopa convexa* McAlpine (Fig. 50) shares the peculiar apomorphic conditions of the Coelopidae, not known in other sciomyzoid families: conus large, centrally situated, with foramen dorsolateral; button dorsally situated at base of conus and at basal end of dorsal pedicellar sulcus. The last instar larva of *Lopa* also possesses the complete circle of hydrofuge hairs surrounding each posterior spiracle (D. McAlpine, 1991: 46), apparently absolutely diagnostic for the Coelopidae (larva of *Lopa* examined by both R. Meier and author). I consider that the sharing of these unique antennal and larval apomorphies between Lopinae and Coelopinae is strong evidence for their monophyly.

The sciomyzoid family Natalimyidae (only genus *Natalimyza*, see Barraclough & McAlpine, 2006) is endemic to Africa, but a species has recently been recorded from Baltic amber (Eocene of Europe, Tschirnhaus & Hoffeins, 2009). I have examined antennal structure in *Natalimyza* “sp. B” (flagellar segments; Mount Elgon, Kenya) and *Natalimyza* “sp. A” (pedicel; Ukulinga Reserve, Natal). Segment 2 (Figs 51, 52) is of the basic sciomyzoid type with conus large, asymmetrical, prominent on median side, with foramen facing laterally and armature of annular ridge not particularly developed. Segment 3 (Fig. 53) is broad with broad, capacious basal hollow containing the basal foramen on its median side. The arista (Fig. 54) lacks segment 4, and segment 5 is short, rotund, and asymmetrical.

I have examined antennal structure in the following species of the family Lauxaniidae: *Minettia maculithorax* (Malloch), *Sapromyza sciomyzina* Schiner, *Rhagadolyra handlirschi* Hendel, *Trigonometopsis binotata* (Thomson), and *Homoneura* sp. (Figs 55–57).

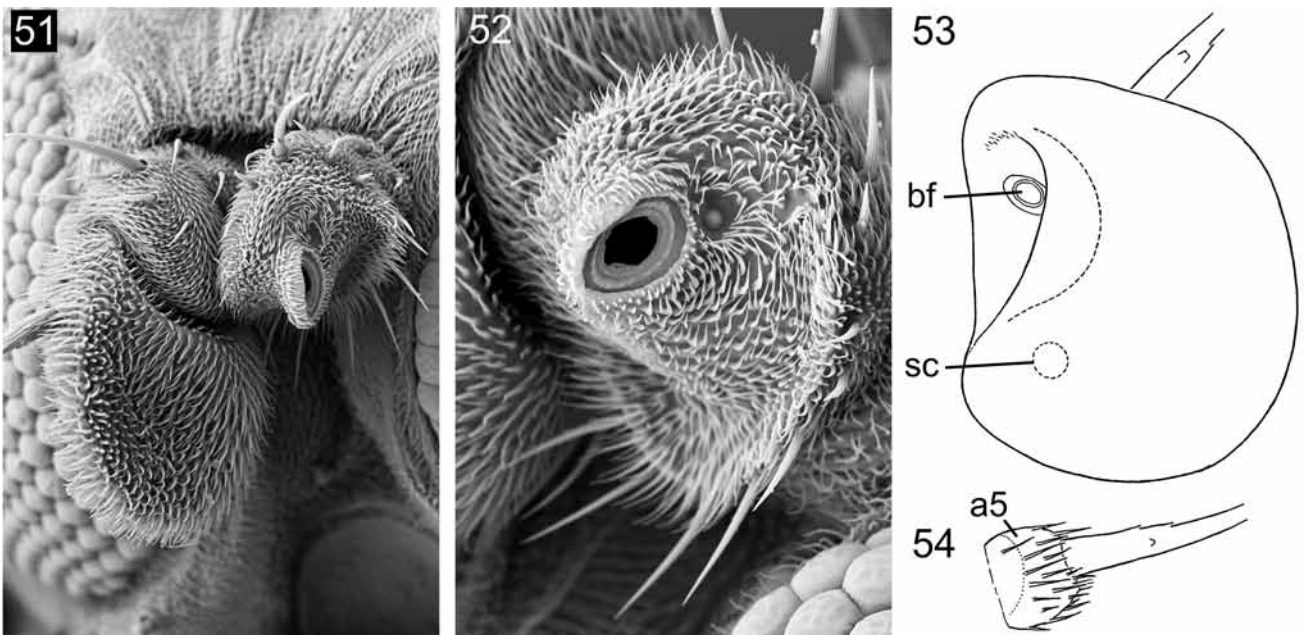
The conus in these taxa is very asymmetrical, short, attached to the medial side of the distal articular surface and inclined so that it is little raised above that surface on



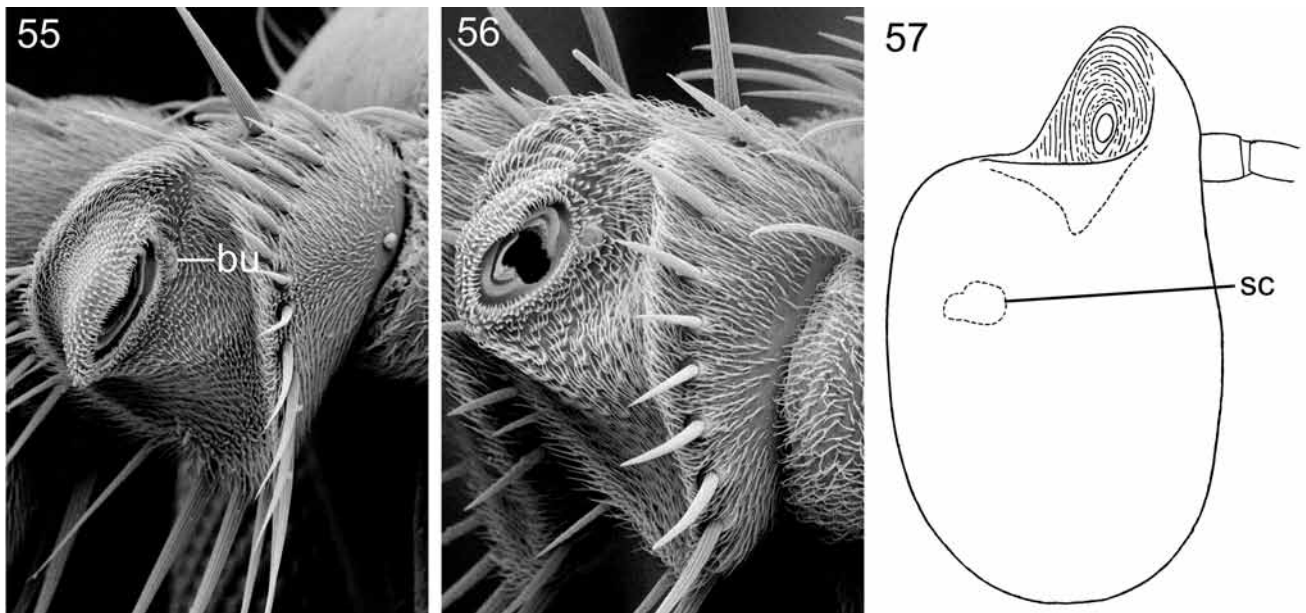
Figures 49, 50. Antennal seg. 2 of Coelopidae. (49) *Gluma keyzeri* McAlpine. (50) *Lopa convexa* McAlpine. *bu*, pedicellar button; *su*, pedicellar sulcus.

its lateral side. The distal foramen is so strongly inclined laterally as to be invisible when the segment is viewed distally. The microtrichose armature on the annular ridge is not differentiated from the general surface of the conus. The button is situated close to the upper lateral part of the

annular ridge. Segment 3 differs from that of *Maorimyza*, *Napaosciomyza*, and less markedly, from *Natalimyza* in that the basal outline is more oblique because of the prominent asymmetrical dorsobasal region bearing the foramen (Fig. 57).



Figures 51–54. Antenna of *Natalimyza* sp. (Ukulunga Reserve Farm, Natal; fam. Natalimyzidae). (51) Pair of antennae, left seg. 3 removed. (52) Left seg. 2, lateral view. (53) Left seg. 3, medial view. (54) Basal part of left arista. *a5*, seg. 5; *bf*, basal foramen; *sc*, sacculus.



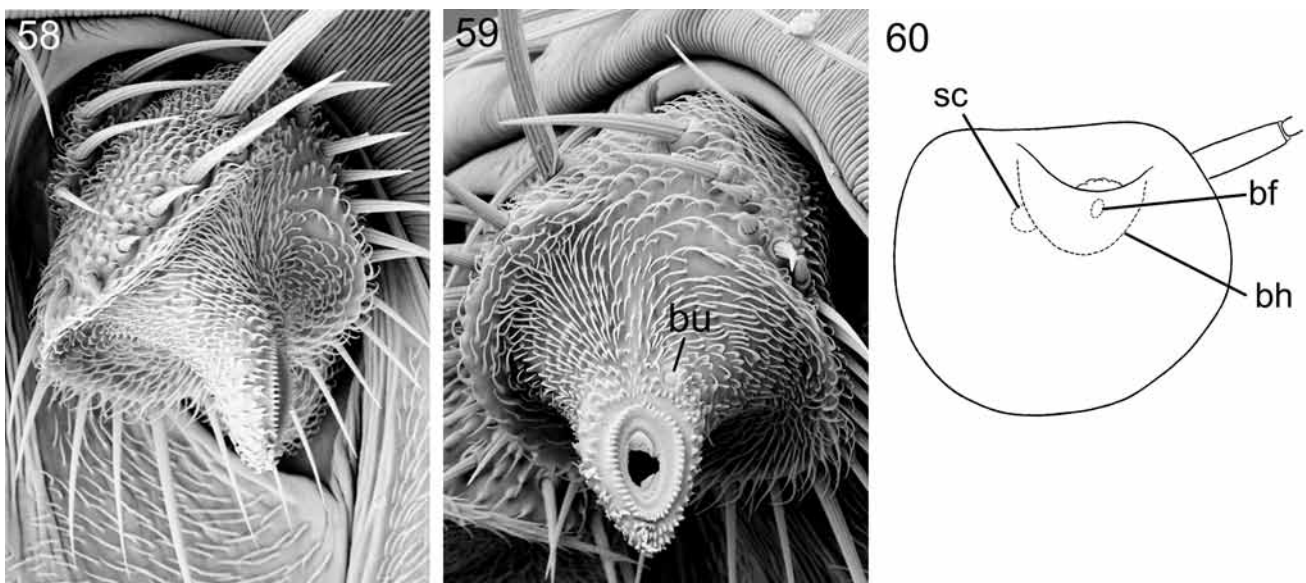
Figures 55–57. Antennae of Lauxaniidae. (55) *Sapromyza sciomyzina* Schiner, left seg. 2, lateral view. (56) *Trigonometopsis binotata* (Thomson), left seg. 2, lateral view. (57) *Homoneura* sp., left seg. 3, medial view. *bu*, pedicellar button; *sc*, sacculus.

The question arises as to whether antennal structure supports the segregation of Lauxaniidae and Chamaemyiidae together as a separate superfamily from the Sciomyzoidea. The above description suggests some differences between the Lauxaniidae and basal members of the Sciomyzoidea, but the sciomyzid genus *Pherbellia* has a conus somewhat approaching that of typical lauxaniids in shape. In the chamaemyiid genus *Pseudoleucopis* segment 2 and the conus are much more like those of *Maorimyia* than any of the lauxaniids examined, and segment 3 is almost transverse in basal outline. Thus, my very limited antennal studies for these families do not at present provide support for a superfamily Lauxanioidea *sensu* J. McAlpine.

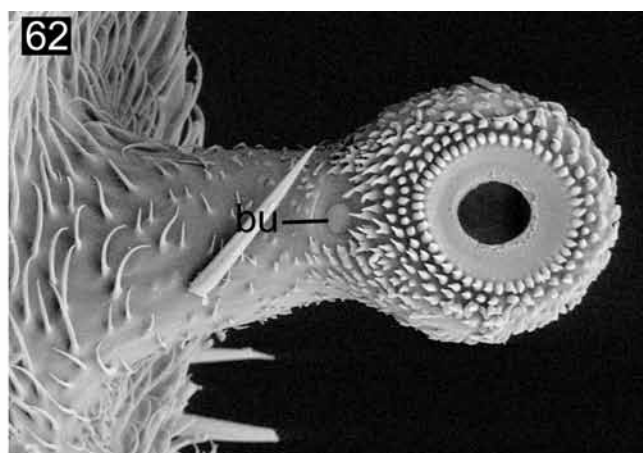
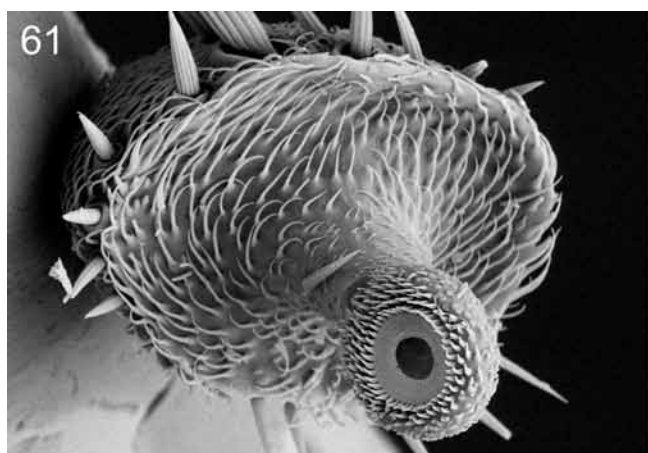
The Milichiidae

Examples used for this study include *Stomosis* sp., *Milichiella* sp., and, in less detail, *Desmometopa* sp. In some species separation of segments 2 and 3 without damage to the conus is difficult.

In *Stomosis* (Figs 58–60) antennal structure retains many of the basal schizophoran features seen in various taxa of Sciomyzoidea and Canacidae s.l. The rim of segment 2 is prominently developed, without differentiated lobes, but is rather broadly interrupted dorsally. The distal articular surface is concave all around the conus, but has no differentiated cup or cavity. The conus is



Figures 58–60. *Stomosis* sp. (fam. Milichiidae). (58) Left seg. 2, distodorsal view. (59) Left seg. 2, distolateral view. (60) Left seg. 3, medial view. *bf*, basal foramen; *bh*, basal hollow; *bu*, pedicellar button; *sc*, sacculus.



Figures 61, 62. *Milichiella* sp. (fam. Milichiidae). (61) Right seg. 2, distal view. (62) right conus, lateral view. *bu*, pedicellar button.

located near the centre of the distal articular surface and is large and prominent, with oval, dorsolateral annular ridge and foramen, and ventral chin; the button is situated dorsolaterally to the annular ridge. Segment 3 is short and compact with moderately deep basal hollow into which the conus is inserted and no basal stem; the basal foramen is contained within the hollow; the pore of the sacculus is situated on the lateral surface a little before mid-length of the segment.

Milichiella (Figs 61, 62) and *Desmometopa* differ mainly in having the rim uninterrupted dorsally and the conus more elongate and apically thickened, as in the Phoridae and Heteromyzidae-Sphaerocerinae; the annular ridge and associated foramen are subcircular, laterodistally located, and there is no chin.

The Milichiidae are often considered to be the possible sister group to the Chloropidae (e.g., Griffiths, 1972; Brake, 2000), but the few examples examined of the former show the distal articular surface of segment 2 to have no trace of cavity or cup and the conus to be rigidly sclerotized basally.

The Chloropidae

Study of the disarticulated pedicel of the following examples was carried out with SEM: *Apotropina ornatipennis* (Malloch) (subfamily Siphonellopsinae); *Chloropella bipartita* Malloch, *Lipara lucens* Meigen, *Pachylophus rufescens* (de Meijere), *Pemphigonotus mirabilis* Lamb (subfamily Chloropinae); *Batrachomyia atricornis* Malloch, *Cadrema* sp., *Merodonta* sp., *Rhodesiella magna* (Becker), *Tricimba carinifacies* Malloch, gen. and sp. undetermined, near *Elachiptera* and *Monochaetoscinella* (subfamily Oscinellinae); see Figs 63–67. In addition, the pedicel of several other taxa of Chloropidae has been examined on dry specimens with high magnification of a SLM, after removal of the postpedicel.

The distal articular surface of segment 2 is concave within the bounds of the well-developed, uninterrupted rim, but centrally a pedicellar cup is encircled by a sharply elevated ridge or collar. The conus is based within the cup which it almost fills, leaving a narrow encircling furrow. The conus is prominent and produced as a chin below the dorsolaterally facing foramen, and is armed with many denticles or spinules and sometimes with transverse ridges basal to the dentulate zone. The button is dorsolaterally located on the conus just clear of the collar. In *Apotropina* (subfamily

Siphonellopsinae) and *Chloropella* (subfamily Chloropinae) the collar is not very prominent and the general covering of simple, separate microtrichia on the collar extends near the edge of the furrow. In *Rhodesiella*, *Cadrema*, and *Tricimba* (subfamily Oscinellinae) the collar is markedly higher and more prominent with smooth surface.

The condition in *Apotropina* and *Chloropella*, where the collar is relatively little raised and largely clothed with microtrichia, like those on the adjacent articular surface, somewhat resembles that of the possible outgroup Canacidae s.l. (*sensu* D. McAlpine, 2007a) and is probably plesiomorphic within the Chloropidae. The relatively high, glabrous collar, seen in *Rhodesiella*, *Cadrema*, and *Tricimba*, is perhaps an apomorphic state, but is not present in *Lipara* and *Batrachomyia*, also of the subfamily Oscinellinae.

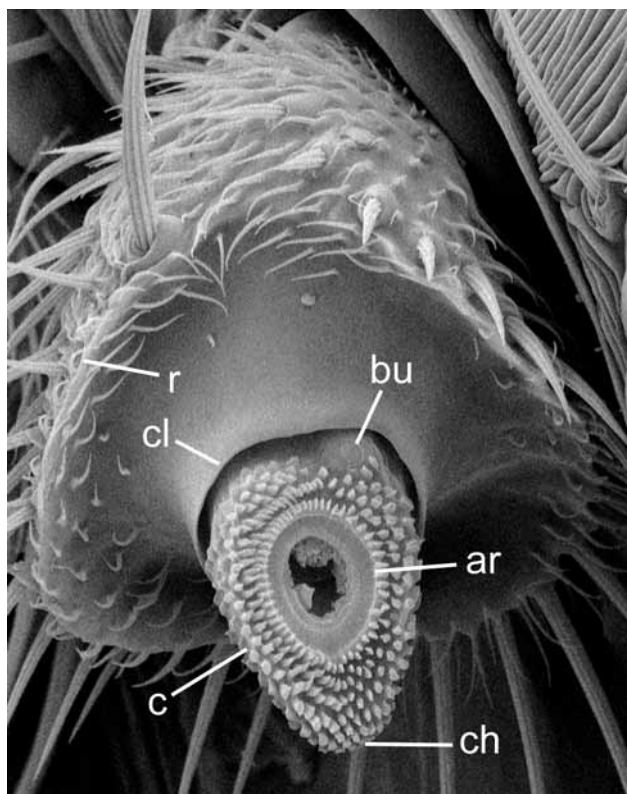
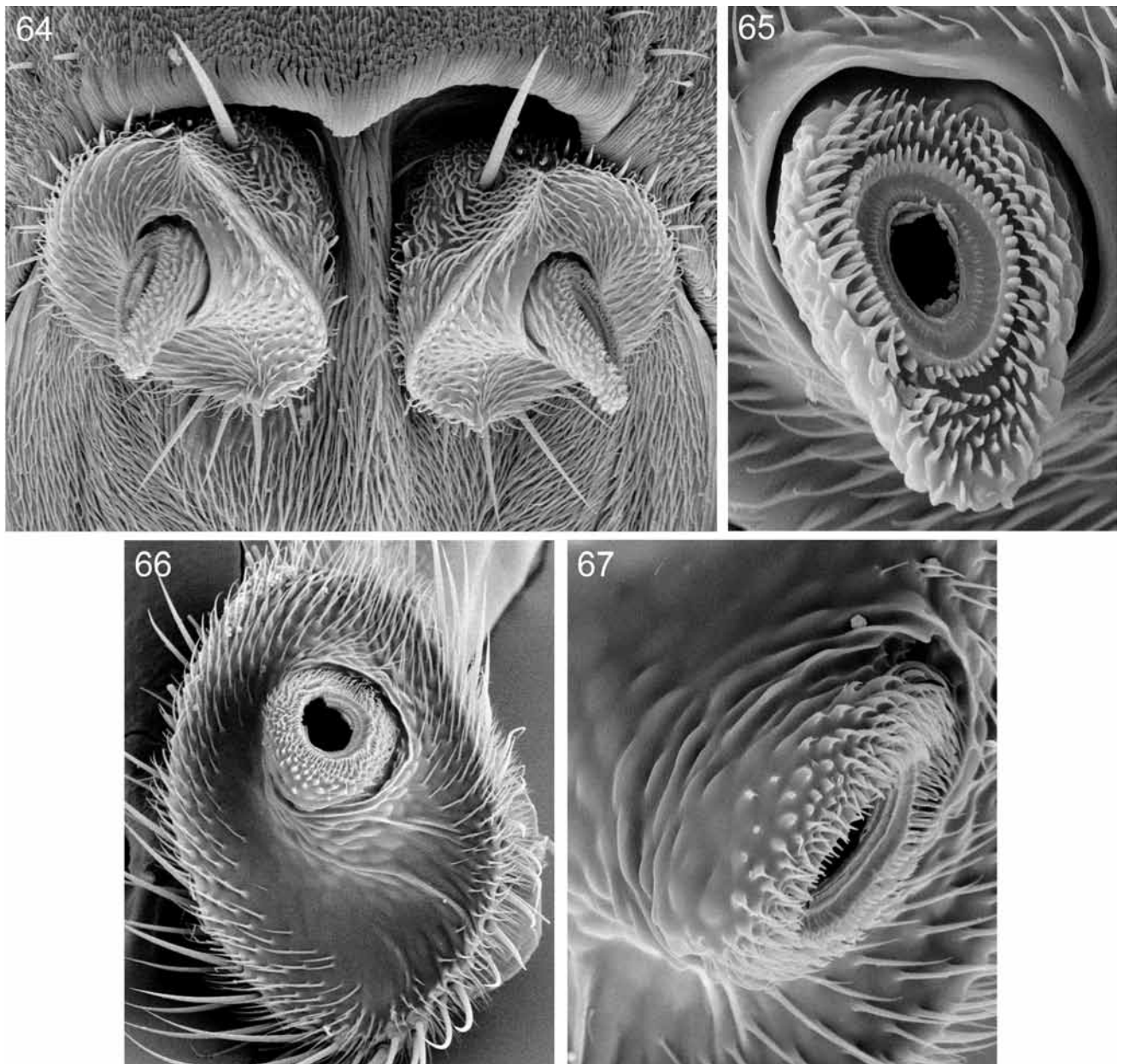


Figure 63. *Rhodesiella magna* (Becker) (fam. Chloropidae), left antennal seg. 2, seg. 3 removed. *ar*, annular ridge; *bu*, pedicellar button; *c*, conus; *ch*, chin; *cl*, collar; *r*, rim.



Figures 64–67. Antennae of Chloropidae. (64) *Apotropina ornatipennis* (Malloch), antennae in situ, disarticulated. (65) *Chloropella bipartita* Malloch, left conus. (66) *Batrachomyia atricornis* Malloch, distal articular surface of left seg. 2 with conus. (67) *B. atricornis*, laterally flexed conus of left antenna, part of collar and furrow thus obliterated.

I have seen evidence suggesting that the lining of the furrow is flexible, and that the collar system effectively provides another joint to the antenna. The illustrated pedicel of *Batrachomyia* (Figs 66, 67), shows how the cuticular fold forming the collar on the medial side of the conus can be stretched when the conus is flexed laterally, and the furrow is no longer apparent.

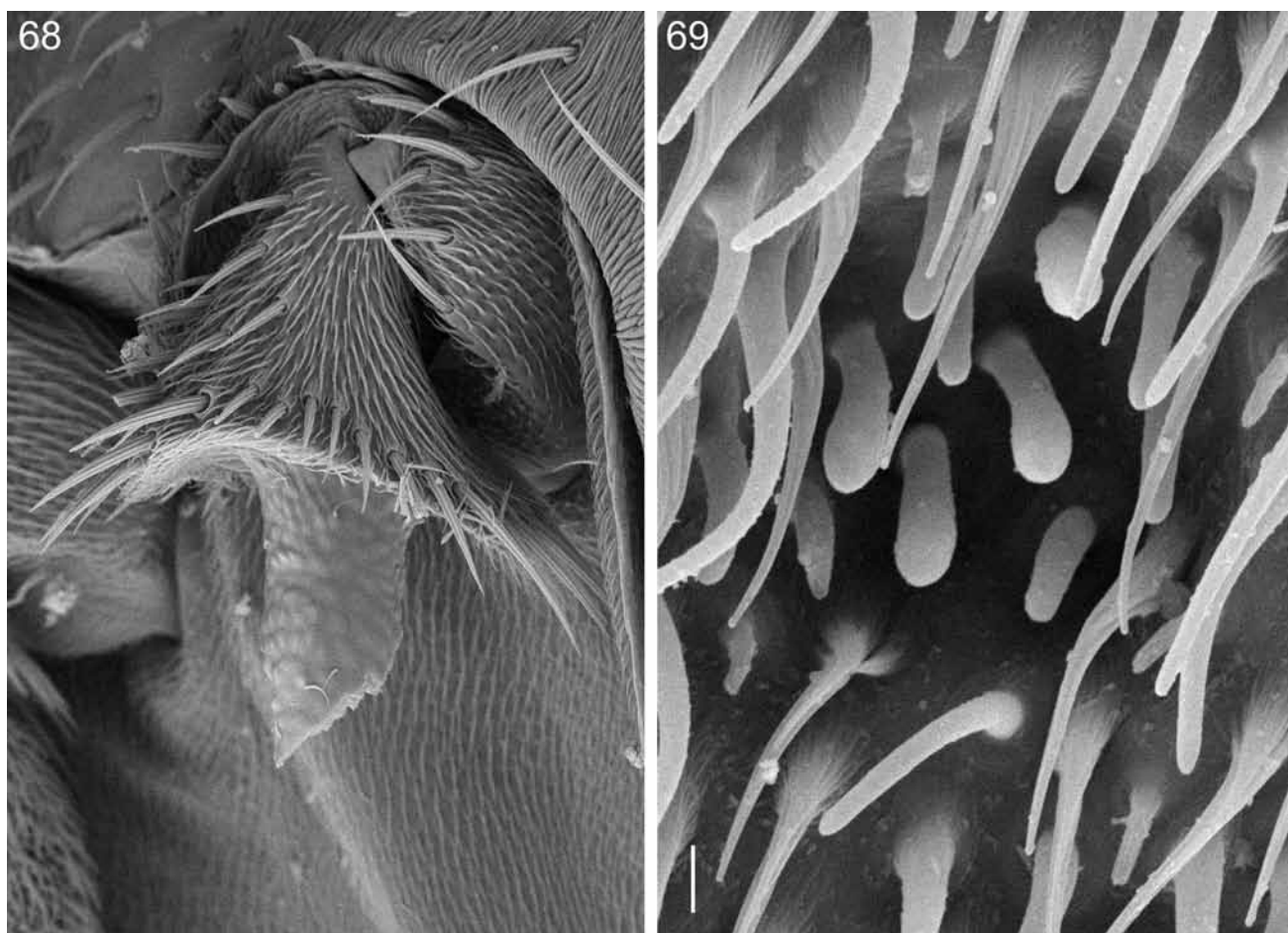
In view of the fact that the chloropid genera studied represent a wide range of relationships within the family, including examples of all three recognized subfamilies, it is probable that they are adequate to show both the groundplan conditions of the conus for the Chloropidae and the generally diagnostic features. I therefore suggest that the presence of a collar enclosing a narrow encircling furrow around the base of the conus is an autapomorphy for the family, and is a condition unknown in presumably closely related families

(e.g., Milichiidae, Canacidae), but a similar condition occurs in some Pyrgotidae and some other Tephritoidea through convergence (see below).

The Cryptochetidae

This Old World family includes the polytypic genus *Cryptochetum*, also doubtfully the Australian *Librella* and the fossil *Phanerochaetum*. I have examined the antenna of all these genera, but the material has been inadequate for a detailed study.

Antennal structure in *Cryptochetum* is distinct from that of any other acalyptrate taxon (Figs 68–70). Segment 2 is completely encircled by the prominent, sharp-edged rim without an incision, notch or marked sinuosity. The distal articular surface is slightly concave, with large, elongate,



Figures 68–69. Antenna of *Cryptochetum* sp. (fam. Cryptochetidae). (68) Left seg. 2, dorsolateral view, conus broken. (69) Sensilla in sensory pit of seg. 3; scale = 2 μ m.

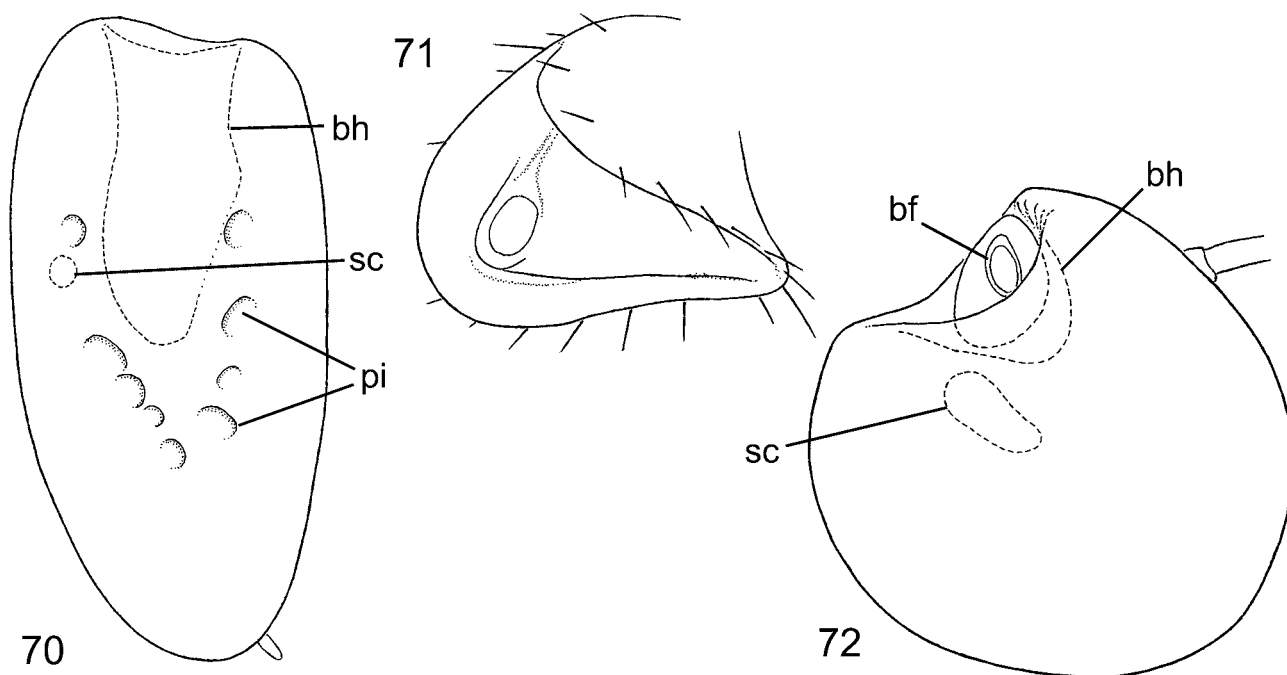
erect, central conus. Because the conus is fragile and deeply embedded in segment 3, I am unable at present to describe it in detail, and the precise positions of the button and distal foramen have not been observed. Segment 3 is large, elongate, bilaterally compressed, with minute, unsegmented, subterminal arista or none and with the sacculus opening by a small pore on the ventrolateral surface before mid-length; the lateral and medial surfaces each support a number (9 to 12 or more) of shallow pits. These sensory pits each contain several club-like sensilla with thick, rounded apices (Fig. 69), probably to be classed as basiconic sensilla. Though such pits are of uncommon occurrence in acalyptrate schizophorans, similar ones are present on segment 3 of *Maorimyia bipunctata* (family Helcomyzidae), but they are differently distributed.

In *Cryptochetum* the elongate, centrally based conus, deeply inserted into the basal hollow of segment 3, resembles that of some conopids, some diopids, and some milichiids (but probably not the more plesiomorphic taxa among the latter). Also, in the lower cyclorrhaphous family Phoridae the conus is deeply embedded in the centre of segment 3. The only claim of *Cryptochetum* to relationship to any of these families is to the Milichiidae, particularly in view of the interpretation of the venation of the anal region of *Cryptochetum* given by J. McAlpine (1989: 1476–1477). However, my thorough and prolonged investigation of the venation leaves no doubt that J. McAlpine was mistaken (see D. McAlpine, 2002), and that the venation of *Cryptochetum*

(like that of *Librella*) approximates to that of the Ephydroidea (including Curtonotidae and Drosophilidae), not to that of the Milichiidae and Canacidae. Undoubtedly this development of the conus has evolved in a number of separate eremoneuran lineages, and is not always a reliable indicator of relationships.

The antennal structure of *Librella* is very different from that of *Cryptochetum*. Segment 2 is of a much more primitive form (Fig. 71). The rim expands on each side forming a broad lateral and a medial lobe, but these lobes are not approximated dorsally to produce the cucullate or cup-like condition as in most Ephydroidea (including Drosophilidae), but diverge from their origins on each side of the dorsal notch. The conus is stout, deep, and asymmetrical, slightly displaced on to the medial lobe of the rim, with the foramen facing dorsolaterally. Segment 3 (Fig. 72) is deep and bilaterally compressed, with medium-sized basal hollow and the foramen on a broad prominence near the margin of the hollow. The arista is three-segmented and of normal length.

I have examined the holotype (in amber) of *Phanerochaetum tuxeni* Hennig (ZMUC), and the most significant addition I have to add to the original description (Hennig, 1965) regards the relation of the free anal vein (vein 6, CuA+A1, or cu1b+1a) to the cell cup (or anal cell). Interpretation is difficult because there is partial separation of the wing surface from the amber, but reflected light off the wing surface gives an apparently more accurate representation than in Hennig's fig. 263, and indicates



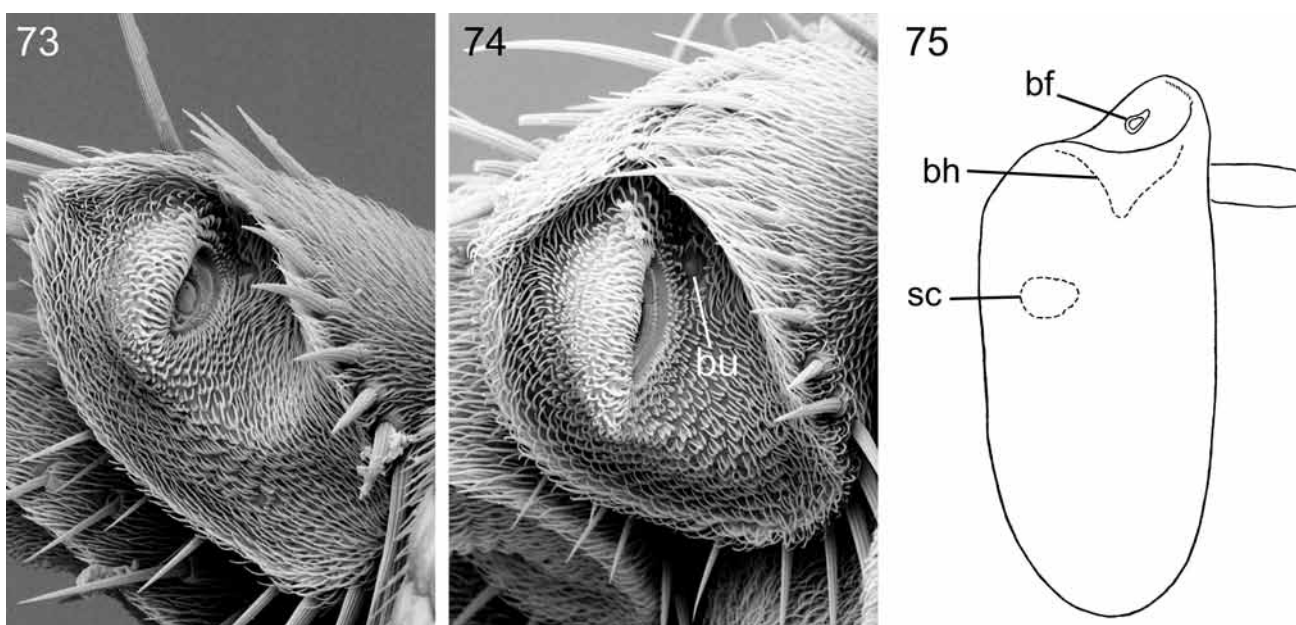
Figures 70–72. Antennae of Cryptochetidae. (70) *Cryptochetum* sp., seg. 3 of left antenna, medial view. (71) *Librella* sp., left seg. 2, lateral view. (72) The same, left seg. 3, medial view. *bf*, basal foramen; *bh*, basal hollow; *pi*, sensory pits; *sc*, sacculus.

that the anal cell is more like that of *Cryptochetum* and some ephydroid taxa, with anal crossvein strongly inclined distad and the vein delimiting the anal cell posteriorly little sclerotized. There is no trace of the basal crossvein, though Hennig (1969: fig. 43) found this to be distinct in a further specimen of *Phanerochaetum* (perhaps a second species).

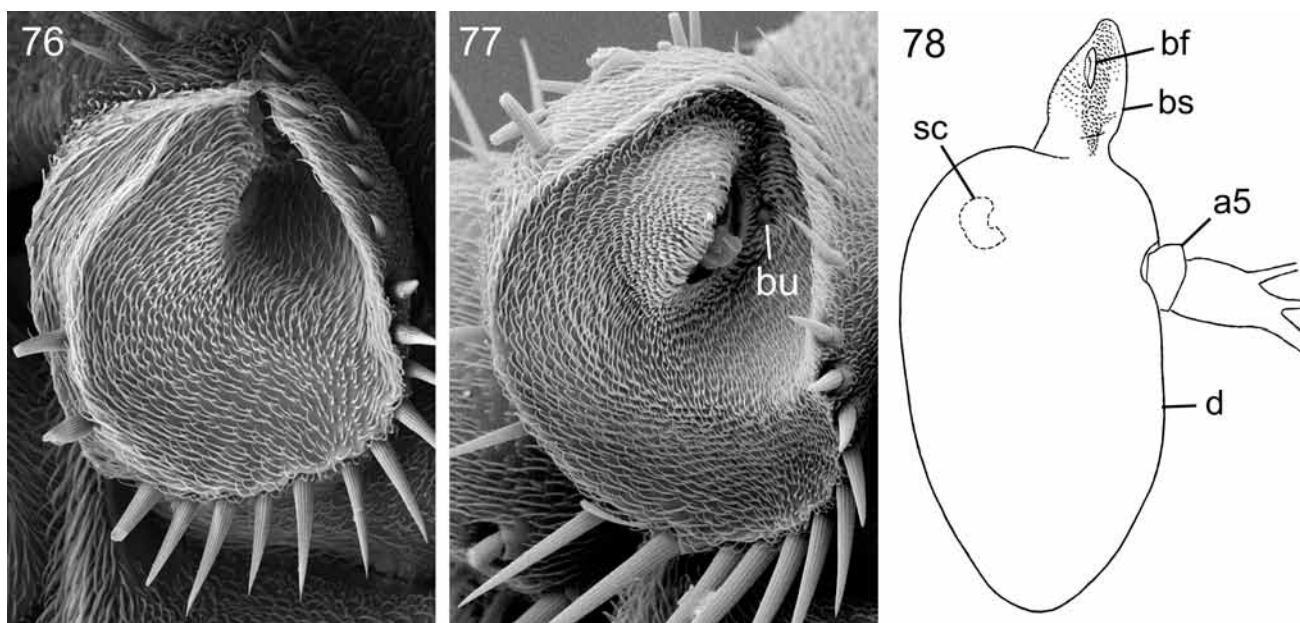
The Ephydroidea

The following families of this superfamily are discussed below: Campichoetidae, Diastatidae, Curtonotidae, Drosophilidae, Ephydriidae.

Some features and variation in the ephydroid antenna have been previously described, e.g., by Hennig (1971), and, in more detail, by Grimaldi (1990). Features common to all families include the great dorsal development of the pedicellar rim to form a pair of lobes separated by a narrow dorsal cleft (seam or slit), the adjacent margins of the two lobes usually appressed so that the cleft may not be obvious at low magnification, and the very asymmetrical conus. Typical caesti (separate from the annular ridge) are absent. The distal articular surface is particularly concave on its dorsolateral quarter (Fig. 73), or may abruptly give way to a deep cup containing the button and the sometimes much reduced conus



Figures 73–75. Antennae of Diastatidae and Campichoetidae. (73) Left antennal seg. 2 of *Diastata fuscula* (Fallén) (fam. Diastatidae), lateral view, seg. 3 removed. (74) *Campichoeta punctum* (Meigen) (fam. Campichoetidae), lateral view of seg. 2, seg. 3 removed. (75) The same, medial view of seg. 3. *bf*, basal foramen; *bh*, basal hollow; *bu*, pedicellar button; *sc*, sacculus.



Figures 76–78. Antennae of Curtonotidae. (76) *Axinota pictiventris* Wulp, left seg. 2, seg. 3 removed, distolateral view. (77) *Cyrtona* sp., left seg. 2, similar view. (78) *A. pictiventris*, left seg. 3, medial view. a5, antennal seg. 5; bf, basal foramen of seg. 3; bs, basal stem; bu, pedicellar button; d, disc of seg. 3; sc, sacculus.

(Fig. 80). Several taxa show evidence of abrasive action using the dorsomedial surface of segment 2 (see p. 163).

Some of the apomorphies listed by J. McAlpine (1989: 1486) appear not to indicate accurately the groundplan condition for the superfamily, or are present in possible outgroups.

The Campichoetidae and Diastatidae

The antennae of *Campichoeta punctum* (Meigen) and *Diastata fuscata* (Fallén) have been studied.

In *Campichoeta* the distal articular surface of segment 2 (Fig. 74) is extensively concave, more deeply so on its lateral part, but there is no defined cup. The conus is located towards the medial side of this surface and is very asymmetrical. While the medial part of the conus is quite prominent, the part lateral to the foraminal ring is obsolete, so that the foramen and foraminal ring face laterally. The foraminal ring is crenulate laterally, but this condition is probably not homologous with the caestus of Neurochaetidae etc. The button is located on the articular surface a little laterally to the foraminal ring. Segment 3 (Fig. 75) has not a typical basal stem, but is more prominent dorsobasally than ventrobasally. The basal hollow is moderately large; the basal foramen is situated just beyond its medial margin and faces laterally. The sacculus is located slightly before mid length and has the usual lateral pore. The arista is three-segmented, with short annular segment 4 and long cylindrical segment 5.

The antenna of *Diastata* (Fig. 73) agrees in all essential details with that of *Campichoeta* as given above, the main differences being in proportions.

The Curtonotidae

The antennae of *Axinota pictiventris* Wulp (Figs 76, 78) and *Cyrtona* sp. (Karen, Kenya, Fig. 77) are here considered.

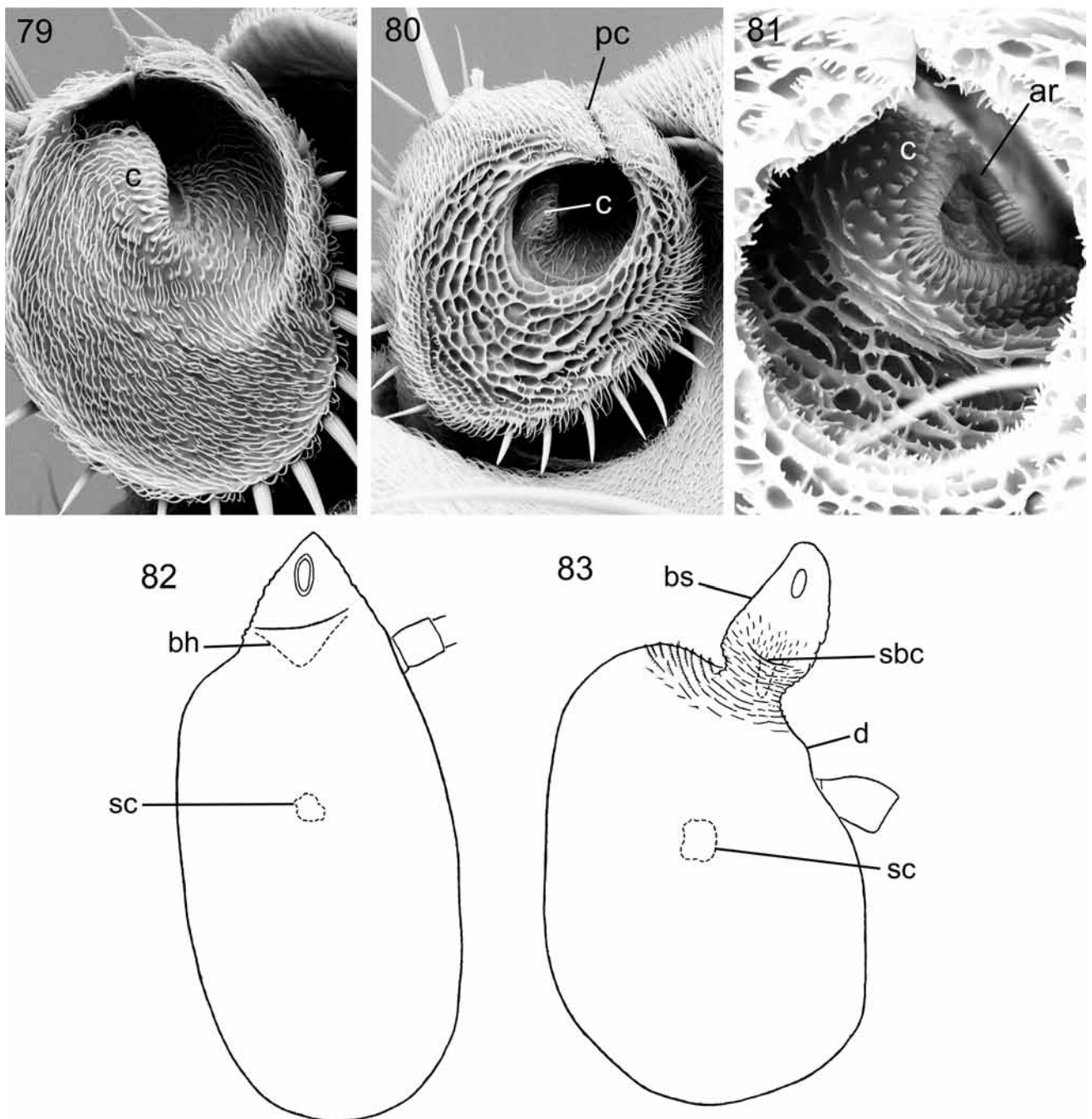
In *Axinota* segment 2 has the rim represented by a double ridge on its medial side. The distal articular surface is concave and more deeply recessed laterally to the conus. The conus is asymmetrical, broad and very short, with the foramen facing laterally. The foraminal ring is crenulate laterally as in *Campichoeta*, but is not entirely visible in the preparation. Segment 3 has a very marked differentiation into basal stem and distal disc. There is no basal hollow, and the caecum on the basal stem is minute. The basal stem bears the basal foramen on its ventromedial surface not far from its extremity. The arista lacks segment 4; segment 5 is very short and stout, and segment 6 is swollen basally.

The antenna of *Cyrtona* has a general resemblance to that of *Axinota*, with a few notable differences. Segment 2 lacks the additional ridge of the rim; the lateral part of the distal articular surface is less narrowly recessed so that the button is readily detected, just laterally to the foraminal ring; segment 3 has a less attenuated basal stem; segment 4 is distinctly sclerotized so that the arista is three-segmented.

The Drosophilidae

I have examined for this study the antenna of the following species: *Leucophenga scutellata* Malloch, *Scaptomyza australis* Malloch, *Drosophila (Drosophila) immigrans* Sturtevant, *Drosophila (Sophophora) melanogaster* Meigen, *Tambourella endiandrae* Wheeler. Grimaldi (1990) has given information and figures for some additional species. The true drosophilids (*sensu* Grimaldi, 1990) have many features in common with the Campichoetidae and Diastatidae, as discussed above, but are, to varying degrees, more apomorphic. All those studied by me have the conus short, asymmetrical, and undeveloped on the lateral side of the asymmetrically directed foramen.

In *Leucophenga* (Fig. 79) segment 2 has no well defined cup, but the distal articular surface deepens much dorsolaterally so that the button is almost concealed. Segment



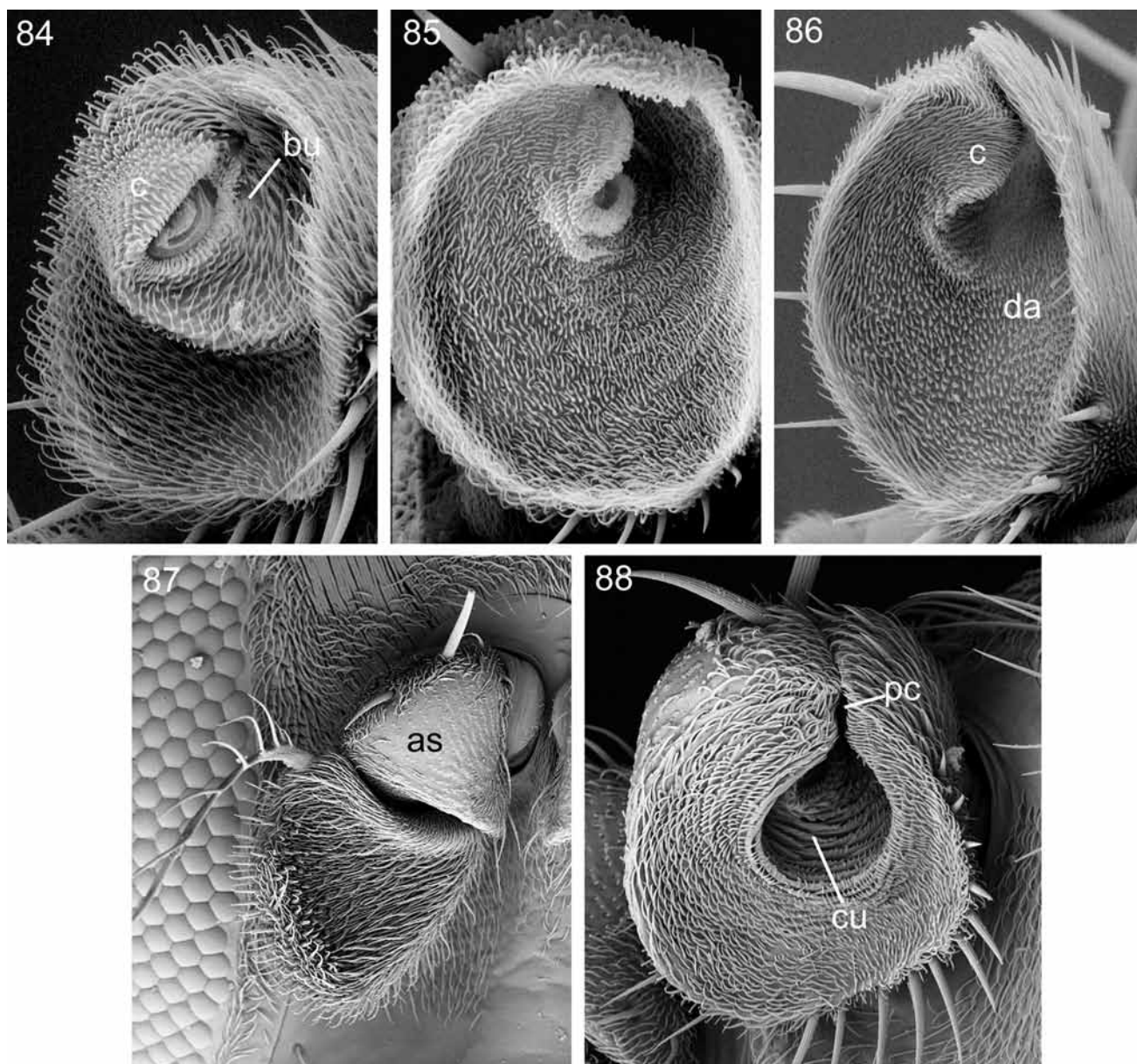
Figures 79–83. Antennae of Drosophilidae. (79) *Leucophenga scutellata* Malloch, distal articular surface of seg. 2. (80) *Drosophila immigrans* Sturtevant, the same. (81) *Tambourella endiandrae* Wheeler, contents of pedicellar cup. (82) *L. scutellata*, left seg. 3, medial view. (83) *T. endiandrae*, the same. *ar*, annular ridge of seg. 3; *bh*, basal hollow; *bs*, basal stem; *c*, conus; *d*, disc of seg. 3; *pc*, pedicellar cleft; *sbc*, sub-basal caecum; *sc*, sacculus.

3 (Fig. 82) has a basal stem, but this is broad where it joins the disc and less sharply defined than in the other genera. The moderately developed basal hollow opens on the broader part of the basal stem.

In *Drosophila* spp. and *Tambourella* the distal articular surface gives way much more abruptly to a deep, narrow cup into which the very short conus is sunken, but there is no raised collar (Figs 80, 81). Usually segment 3 has the basal stem well defined and more or less attenuated (Fig. 83). The basal hollow is generally present in some form, in contrast to the Curtonotidae, but may be contracted to a narrow caecum located on the basal stem. The arista is usually three-segmented.

The Ephydriidae

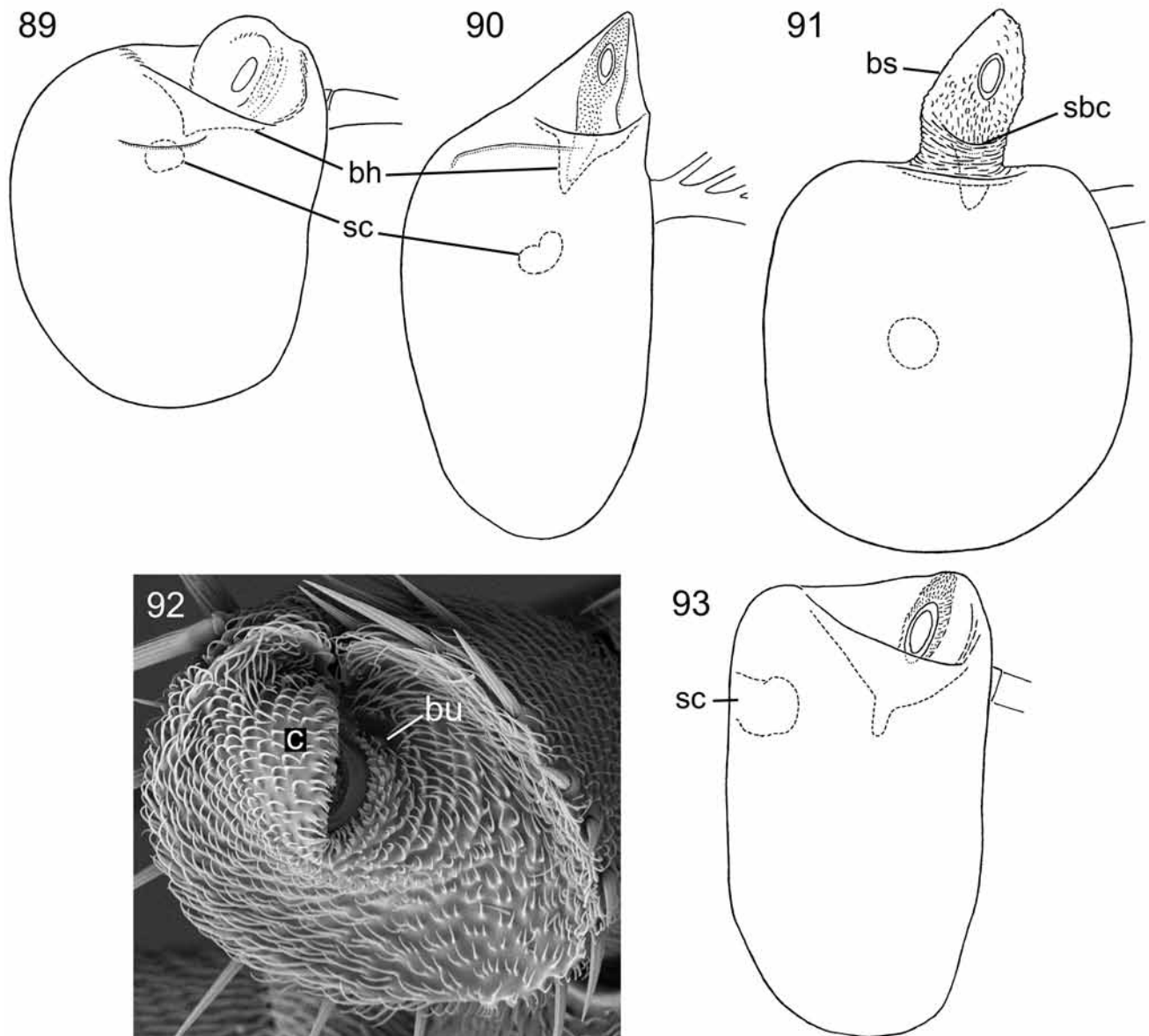
For this study I examined the antennae of the following species: *Ochthera pilimana* Becker, *Scatella* sp., *Ephydrella marshalli* Bock, *Paralimna calva* Bock, *Hydrellia tritici* Coquillett, *Stratiothyrea cheesmanae* Cogan, *Risa longirostis* Becker, “ephydrid genus E”, which includes several Australian species living in saline habitats. I previously examined the arista of numerous ephydrid taxa (D. McAlpine, 2002), and found it to be usually two-segmented through loss of segment 4, but in a few cases it is even further reduced. Wirth *et al.* (1987: particularly figs 41–44) show some of the variation in antennal form in the family.



Figures 84–88. Antennae of Ephydridae. (84) *Ephydrella marshalli* Bock, left seg. 2, seg. 3 removed, distolateral view. (85) *Paralimna calva* Bock, the same view. (86) *Hydrellia tritici* Coquillett, the same view. (87) *Stratiothyrea cheesmanae* Cogan & Wirth, right antenna. (88) The same, left seg. 2, distal view, seg. 3 removed. *as*, abraded dorsomedial surface of seg. 2; *bu*, pedicellar button; *c*, conus; *cu*, pedicellar cup; *da*, distal articular surface; *pc*, pedicellar cleft.

Antennal structure in the family Ephydridae shows most of the range of variation occurring in the superfamily Ephydroidea (Figs 84–93). In *Scatella* and *Ephydrella* the conus arises from the medial side of the distal articular surface and is seen to project markedly beyond it in medial view; a ridge extends from the ventral base of the conus across the articular surface, defining a shallow cup-like depression which occupies the dorsolateral part of the surface. The annular ridge and foramen are asymmetrical and face laterally. Segment 3 has a shallow basal hollow, deepening to a central pit. The basal foramen is located in a concavity on a broadly rounded prominence on the margin of the hollow, which could be regarded as an incipient basal stem. The pore of the sacculus is located laterally, far from the ventral margin. In segment 2 of *Ochthera* the conus is somewhat similar but there is no transverse ridge

extending from its base. Segment 3 has a distinct but short basal stem. *Hydrellia* and *Paralimna* have a more reduced conus, and, although the distal articular surface is markedly and narrowly deeper dorsolaterally, there is no defined cup. Segment 3 has a definite basal stem which is not strongly narrowed, though tapering to a point in *Paralimna*. In *Stratiothyrea* the distal articular surface of segment 2 is almost flat on much of its extent, with narrow dorsal cleft and very deep abrupt subcentral cup quite unlike any of the above examples. The conus is almost absent and the annular ridge is located only slightly asymmetrically on the floor of the cup. Segment 3 is markedly differentiated into the narrow, digitiform basal stem and broad disc; the rather narrow sub-basal caecum opens on to the medial surface of the stem a little distance from the disc; there is a slight indication of a separate basal hollow on the medial side of



Figures 89–93. Antennae of Ephydridae. (89) *Scatella* sp., left seg. 3, medial view. (90) *Paralimna calva* Bock, the same. (91) *Stratiomyia cheesmanae* Cogan & Wirth, the same. (92) Ephydrid genus E, Innaminka, S. Aust., left seg. 2, distal view, seg. 3 removed. (93) Ephydrid genus E, Lake Hindmarsh, Vic., left seg. 3, medial view. *bh*, basal hollow; *bs*, basal stem; *bu*, pedicellar button; *c*, conus; *sbc*, sub-basal caecum; *sc*, sacculus.

the broad basal surface of the disc. The antennal structure of *Stratiomyia* is remarkable for its resemblance to that of such advanced drosophilids as *Tambourella*, evidently through detailed convergence. Like these two genera, *Camilla acutipennis* (Loew) (family Camillidae) also has an elongate basal stem (Hennig, 1971: fig. 8).

In “ephydrid genus E” segment 2 (Fig. 92) is more elongate than that of many ephydrids, with the lobe on the medial side of the dorsal seam more prominent than that on the lateral side; the distal articular surface is less deeply concave than that of most ephydrids and without any suggestion of a cup-like cavity; the conus is relatively narrow, but strongly projecting and arising close to the medial dorsal lobe; the foramen faces entirely laterally. Segment 3 (Fig. 93) has no basal stem; the basal foramen is on a slight scabrous prominence on the lateral margin of

the basal hollow; the hollow is capacious, tilted medially, and its floor has a narrow caecum-like extension; the pore of the sacculus is in a ventral position, as in *Risa*, but in contrast to other examined ephydrids, which have it in a lateral position. The arista lacks segment 4; segment 6 is numerous and irregularly pubescent on *c*. the basal 0.4 of its length, but beyond this has only a dorsal series of *c*. 10 very short rays. The arista is thus fairly typical of the Ephydridae, while some other features, including the ventral position of the sacculus, the elongate prementum of the proboscis, the characteristic facial contour, the prominent vibrissa, the milky-white wing membrane, the rather long unpigmented but slightly sclerotized crease representing vein 6, and the almost complete suture separating abdominal tergites 1 and 2, suggest placement in the subfamily Risinae, which was formerly given separate family status.

The Mormotomyiidae

There has been difficulty in determining the relationships of this family within the Schizophora (see Kirk-Spriggs *et al.*, 2011, for most recent discussion). The only included species, the subapterous *Mormotomyia hirsuta* Austen, is only known from the type locality, Ukasi [Ukazzi] Hill, Eastern Province, Kenya, where all stages are associated with bat dung. Ashley Kirk-Spriggs has generously supplied adult males for antennal study (Figs 178–181, see p. 162). Hennig (1971) has described some features of the antenna.

Segment 2 is subconical in outward form; the cleft is long and deep, completely dividing the paired dorsal lobes of the rim, but their adjacent margins remain in contact (Fig. 178). The distal articular surface (Fig. 179) is deeply concave, extensively microtrichose, with some of the microtrichia grouped into combs, but without parallel or reticulate ridging. There is no well defined pedicellar cup, but the laterodorsal part of the surface has a deeper bowl-like concavity containing the conus, somewhat as in *Leucophenga*. The conus is asymmetrically developed, obsolete on the lateral side of the foramen, moderately prominent on the medial side, and well removed from the medial margin of the rim. The annular ridge is indistinct and the foramen is inclined laterally. The pedicellar button (Fig. 180) is located near the dorsolateral part of the annular ridge, but is weakly developed or almost indistinguishable externally.

Segment 3 (Fig. 181) has a broadly rounded, not well defined basal stem, with the basal foramen facing medially. The basal hollow is broad and of moderate depth. The sacculus is capacious, with relatively small pore near centre of lateral surface of disc. The three-segmented arista arises laterodorsally towards the base of the disc.

The deep pedicellar cleft of *Mormotomyia* is similar to that occurring in both the Ephydroidea and the Calypttratae. However, the asymmetrical conus, with laterally (not dorsally) inclined foramen, and the sclerotized prothoracic precoxal bridges are typical of the Ephydroidea, not of the Calypttratae. The general structure of the antenna is reminiscent of *Leucophenga*, a somewhat plesiomorphic example of the Drosophilidae, or could be classed between the more plesiomorphic and more apomorphic taxa of the Ephydridae (Figs 84–93). The three-segmented arista, the location of the preabdominal spiracles in the pleural membrane, and, in the male, the large tergite 6 and asymmetrical sternite 6 place *Mormotomyia* outside the limits of the Ephydridae, but general antennal structure supports its position in the Ephydroidea suggested by Kirk-Spriggs *et al.* (2011).

The Neurochaetidae and Periscelididae

These families share a distinctive antennal structure including possible synapomorphies, but only if the genera *Cyamops* and *Stenomicro* are omitted from consideration. The two last genera are so different that their antennae will be described separately (as subfamily Stenomicroinae). For comment on the recently published phylogenetic association of the Neurochaetidae with the Pallopteridae see p. 150.

Because of availability and ease of exposure of parts of segment 2, I describe the antenna of *Nothoasteia clausa* McAlpine first (Figs 94–96), and then draw comparisons with other taxa. Segment 2 is deflexed so that its broad distal

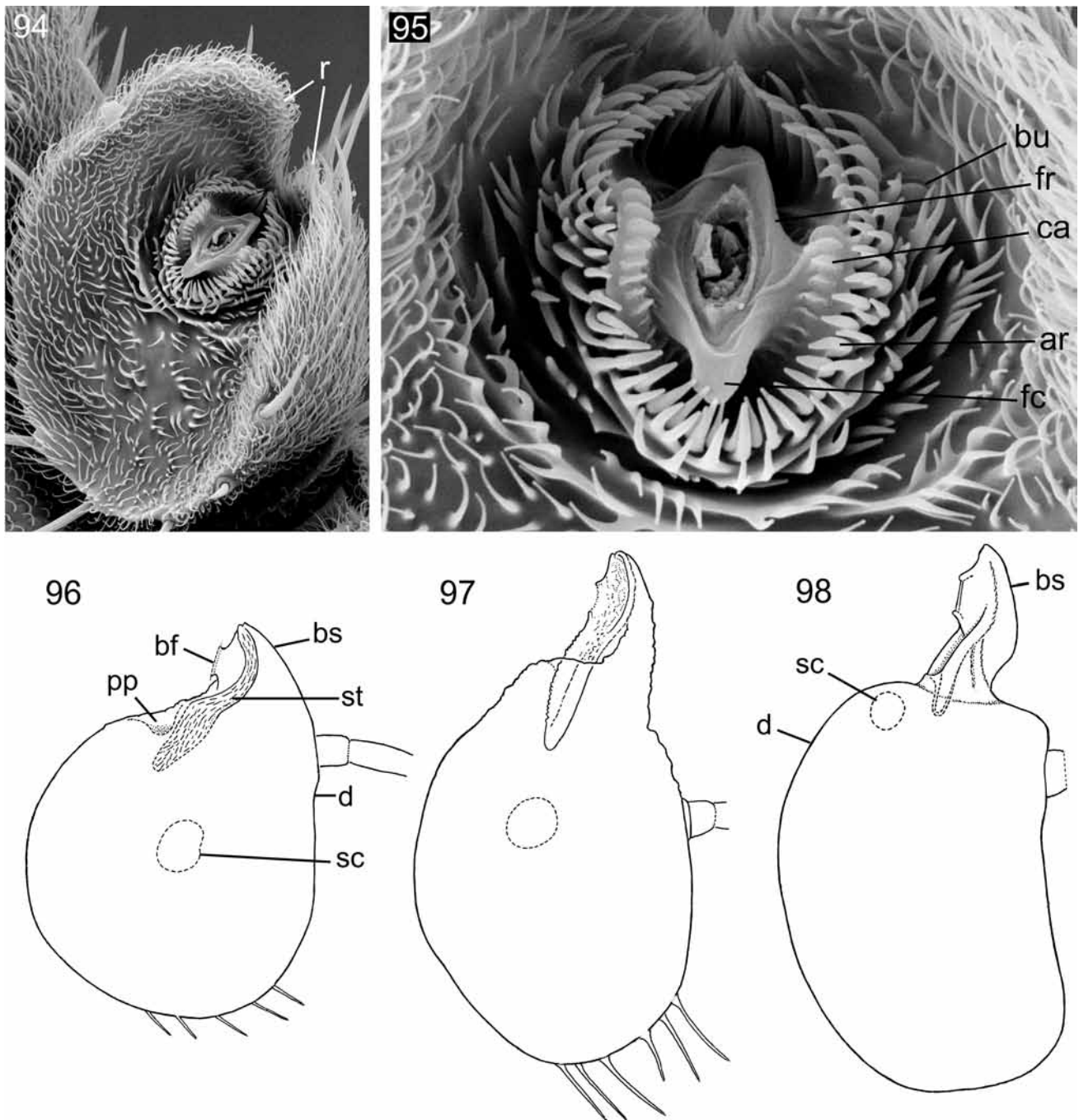
articular surface faces downwards (Fig. 94). The rim forms a pair of dorsal lobes separated by a deep slit, or cleft, but their margins are not appressed as in the Ephydroidea. The medial lobe is larger than the lateral lobe, but the lobes are not as large and cucullate as in some related genera (e.g., *Neurochaeta*), so that most details of the articular surface are exposed by disarticulation (Fig. 95). The conus is absent. The distal articular surface is extensively microtrichose, with the ventral part extensively almost flat, the dorsal part with centrally placed shallow concavity almost filled by the nearly symmetrical, distally facing, complete annular ridge. The annular ridge is armed with two to three dense irregular encircling series of incurved spinescent microtrichia. A well-developed button is located just outside the annular ridge slightly dorsad of a mid-lateral position. There is a well-developed nodulose caestus on each side between the annular ridge and the foraminal ring. The latter is rather prominent and produced into a blunt cusp dorsally and ventrally. The short oval foramen faces distally and is approximately symmetrically placed, both within the annular ridge and on the segment as a whole.

Segment 3 of *Nothoasteia clausa* (Fig. 96) consists of a short, stout basal stem and rounded disc. The basal foramen is on the mid-ventral surface of the basal stem, in accordance with the symmetrically placed distal foramen of segment 2. The scabrous tongue is finely, irregularly ridged and runs from the basal extremity of the medial surface of the basal stem distad into the basal caecum of the disc. The ventrobasal surface of the disc has a shallow secondary cavity or postpedicellar pouch just beyond the opening of the basal cavity. Such secondary cavity has not been observed in other genera. The sacculus opens near the centre of the lateral surface of the disc.

The arista of *Nothoasteia clausa* lacks any trace of segment 4. Segments 5 and 6 are symmetrical, without trace of the oblique base of segment 6 seen in *Cyamops*, *Periscelis*, and some other genera. Segment 6 and the short segment 5 are both pubescent, the hairs beyond the basal enlargement of segment 6 tending to form slightly differentiated but not seriate rays which extend to the apex. In one specimen examined segments 5 and 6 appear to be fused, leaving no visible suture under high magnification of CLM, but in other specimens there is a visible suture but no annular membrane between these segments.

In the neurochaetid *Neurotaxis primula* McAlpine the essential structure of segment 2 resembles that of *Nothoasteia* with some difference in proportions. The dorsal lobes are larger than in *Nothoasteia* but do not conceal much of the distal articular surface. The part of the dorsal articular surface immediately below the annular ridge is almost devoid of microtrichia but bears a reticulate pattern of fine, prominent ridges, which give way to an irregular covering of separate microtrichia towards the ventral margin. The button is larger than that of *Nothoasteia* but similarly located. The annular ridge is more vertically elongate than in *Nothoasteia* but has similar armature. The caesti are more vertically elongate and diffuse, with weak, almost horizontal nodulation.

I previously mentioned (D. McAlpine, 1993) the general features of segment 3 and the arista in *Neurotaxis* spp., and illustrated the antenna of *Neurotaxis freidbergi* McAlpine (D. McAlpine, 1993: fig. 8). This and *N. primula* have the basal stem longer than in *Nothoasteia* and the disc narrower and more ovate. In *Neurotaxis freidbergi* the arista is three-



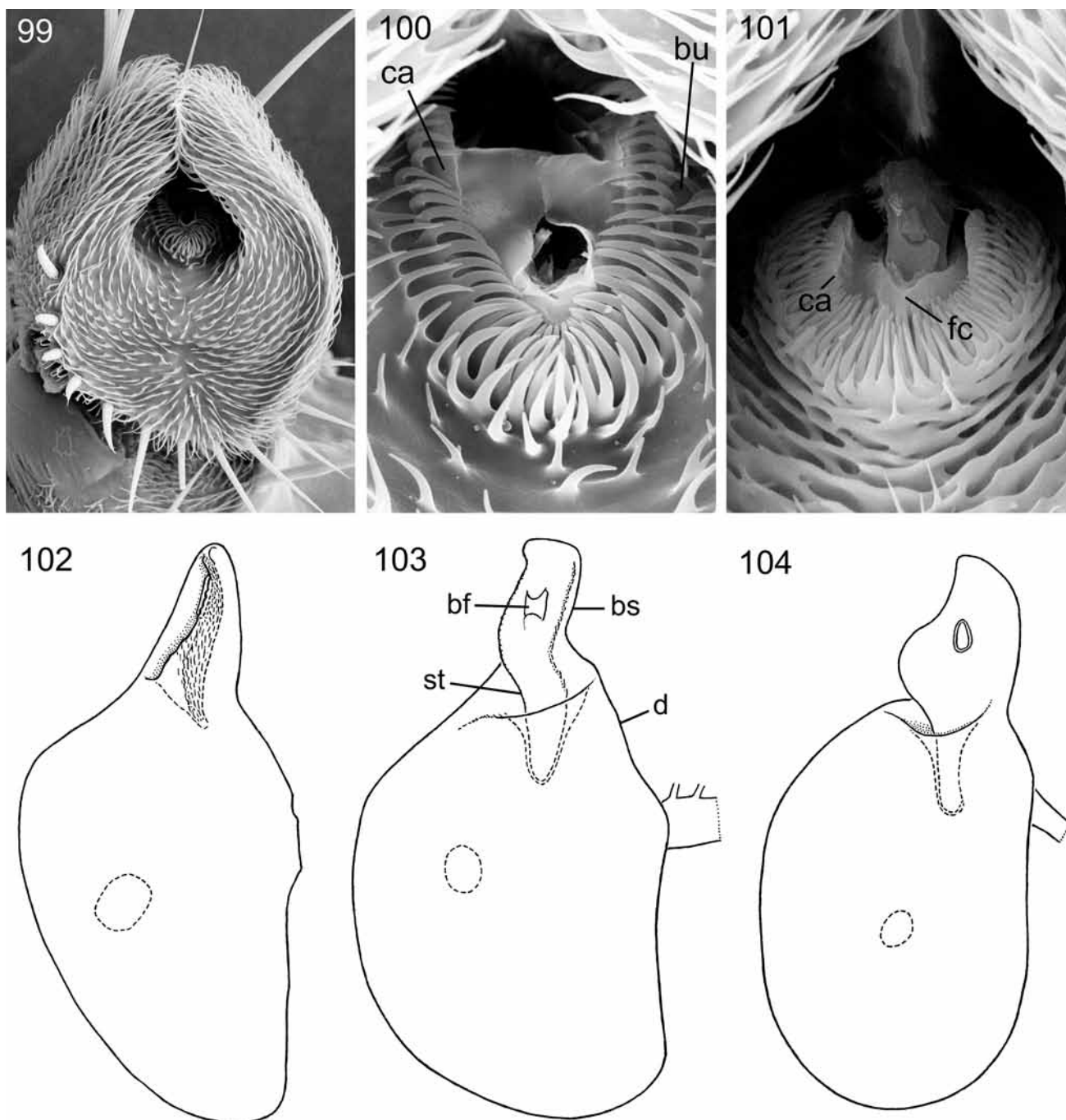
Figures 94–98. Antennae of Neurochaetidae and Periscelididae. (94) *Nothoasteia clausa* McAlpine, left seg. 2, distal view, seg. 3 removed. (95) The same, annular ridge of seg. 2 and associated structures. (96) The same, left seg. 3, medial view. (97) *Neurochaeta inversa* McAlpine, left seg. 3, medial view. (98) *Periscelis fasciata* Mathis, the same. *ar*, annular ridge; *bf*, basal foramen; *bs*, basal stem; *bu*, pedicellar button; *ca*, caestus; *d*, disc of seg. 3; *fc*, foraminal cusp; *fr*, foraminal ring; *pp*, postpedicellar pouch; *r*, dorsal lobes of rim; *sc*, sacculus; *st*, scabrous tongue.

segmented, with segments 4 and 5 small; in *N. primula* segment 5 is very short and distinct, but segment 4 is not clearly defined, perhaps fused with segment 3. Segment 6 has long dorsal and ventral rays and fewer short medial rays. It has not been possible to locate the sacculus in preparations because of the irregularly roughened cuticle of segment 3.

The antenna of *Neurochaeta inversa* McAlpine resembles that of *Neurotaxis primula* in most features. The dorsal lobes of segment 2 are more deeply cucullate than in that species making examination of the dorsal part of the distal articular surface more difficult. The part of this surface ventral to

the annular ridge is almost devoid of microtrichia, but has a reticulate pattern of ridges resembling *N. primula*. The incurved spinescent microtrichia on the annular ridge are particularly large and dense on the more ventral part of the ridge, but are less developed dorsally. The button could not be located, possibly because of difficulty in exposing the more dorsal part of the articular surface. The caesti are short, compact, and prominently raised, with relatively few nodules.

Segment 3 of *Neurochaeta inversa* (Fig. 97) resembles that of *Neurotaxis primula* in most features, but the basal cavity, with its contained extension of the scabrous tongue, is



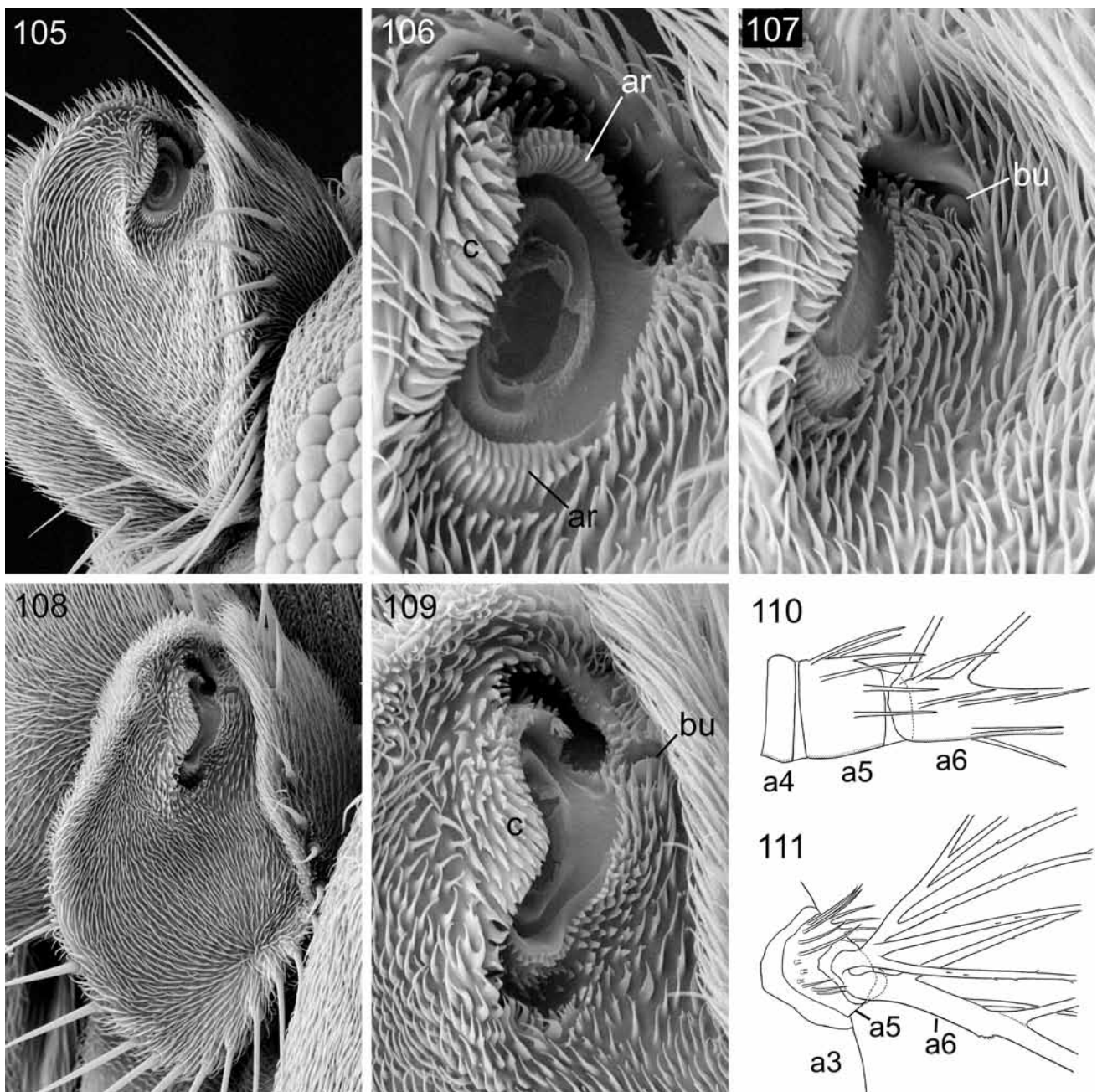
Figures 99–104. Antennae of Periscelididae. (99) *Periscelis fasciata* Mathis, right seg. 2, distal view, seg. 3 removed. (100) The same, annular ridge and associated parts. (101) *Planinasus* sp. (Brazil), annular ridge and associated parts of left antenna. (102) *Planinasus* sp. left seg. 3, medial view. (103) *Stenomicroa* “sp. B” (Upper Allyn, N.S.W.), the same view. (104) *Cyamops* sp. (Tuglo, N.S.W.), the same. *bf*, basal foramen of seg. 3; *bs*, basal stem; *bu*, pedicellar button; *ca*, caestus; *d*, disc of seg. 3; *fc*, foraminal cusp; *st*, scabrous tongue.

deeply elongate, and none of the larger, fringing microtrichia is forked. There is a well-developed sacculus opening near the centre of the lateral surface of the disc.

The arista of *Neurochaeta inversa* resembles that of *Neurotaxis* spp. in general features. Segments 4 and 5 are both very short, microtrichose, and approximately symmetrical.

I have examined segments 2 and 3 in *Periscelis fasciata* Mathis, and segment 3 and the aristal segments in *Periscelis annulata* (Fallén). Segment 2 of *P. fasciata* (Figs 99, 100) has much in common with that of the neurochaetids described above. The paired dorsal lobes are subequal, large

and appressed, so that part of the distal articular surface is sunk in a cup, which is well differentiated from the rest of the distal articular surface. The part of the distal articular surface ventral to the annular ridge is clothed with many simple irregularly placed microtrichia and has no ridges. The structures on the distal articular surface are approximately symmetrical and symmetrically placed. The annular ridge resembles that of *Nothoasteia* and other neurochaetids, but its dorsal part is not visible in the preparation. The button is small and located near the outer lateral side of the ridge. The caesti are present, but elongate and not very prominent.



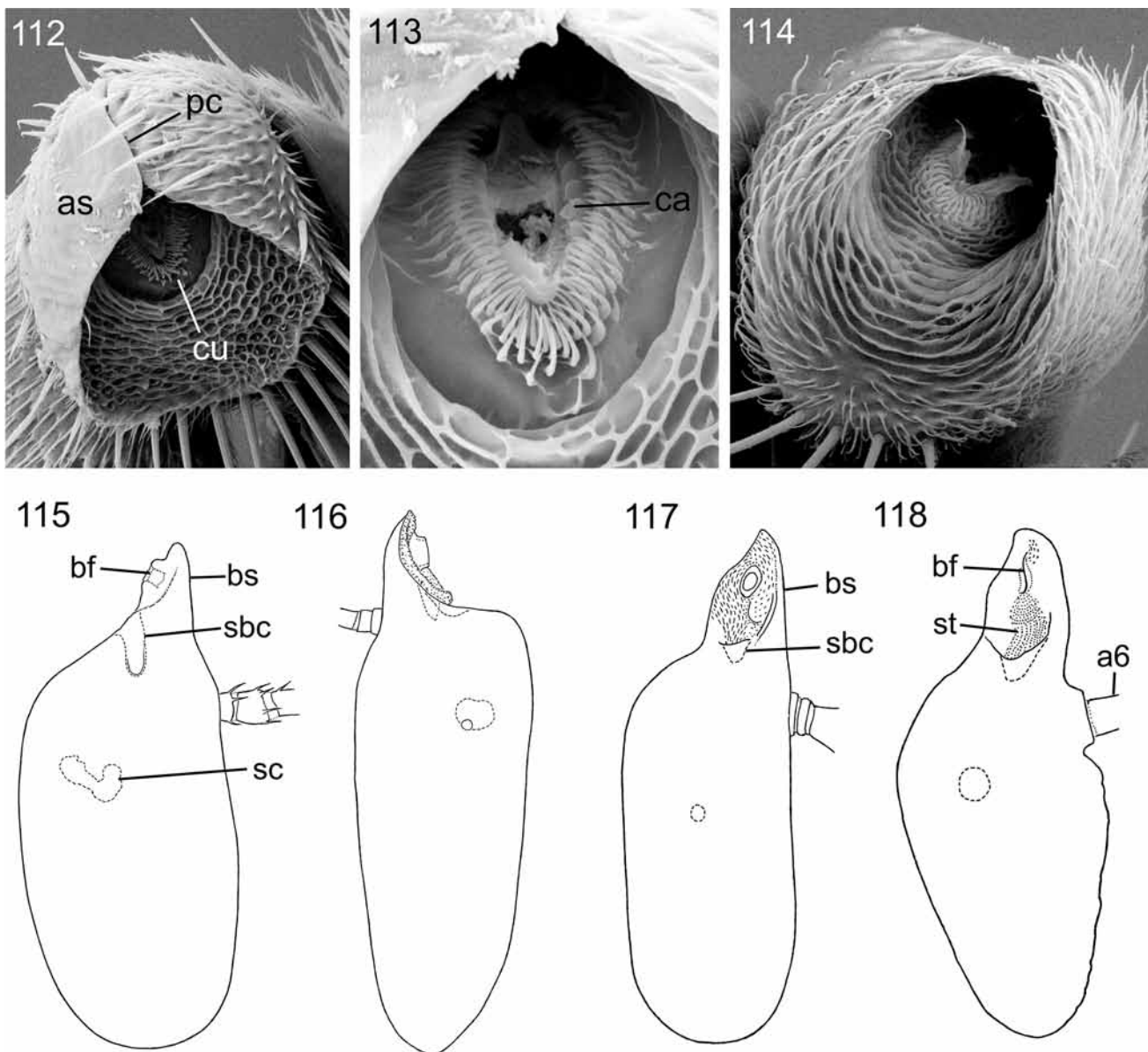
Figures 105–111. Antennae of Periscelididae. (105) *Stenomicroa* “sp. NB” (Woitape, P.N.G.), left seg. 2, lateral view, seg. 3 removed. (106) The same, detail of annular ridge and adjacent parts. (107) The same, more distal view of same region. (108) *Cyamops* sp. (Tuglo, N.S.W.), left seg. 2, lateral view. (109) The same, detail of annular ridge and adjacent parts. (110) *Periscelis annulata* (Fallén), part of right arista. (111) *Planinasus* sp. (Brazil), part of right arista. *a3*–*a6*, antennal segments three to six; *ar*, annular ridge; *bu*, pedicellar button; *c*, vestige of conus.

In both *Periscelis fasciata* (Fig. 98) and *P. annulata* the basal stem of segment 3 is more abruptly narrowed and set off from the disc than in *Neurotexis* and *Neurochaeta*. The sacculus is located very near the ventral base of disc in both species (as it is also in *Scutops fascipennis* Coquillett), instead of the more central position on the lateral surface as in the other periscelid taxa studied and in the neurochaetids.

As previously pointed out (D. McAlpine, 2002) the arista of the more typical Periscelidinae (e.g., *Periscelis* and *Scutops*) is three segmented with asymmetrical segment 5, and the base of segment 6 is obliquely fitted to the distolateral surface of segment 5 (Fig. 110). I have noted also that in a

paratype of the periscelidid *Diopsosoma primum* Malloch (in BMNH) segment 6 is asymmetrical basally.

The genus *Planinasus* is placed in the Periscelididae in most recent literature, and sometimes in the subfamily Stenomicroinae (e.g., Grimaldi & Mathis, 1993). I find the antennal structure of *Planinasus* sp. (N. Friburgo, Brazil) to resemble more closely that of the subfamily Periscelidinae (Figs 101, 102). Segment 2 shows most of the features seen in the Periscelidinae and Neurochaetidae. These include the pair of large, cucullate dorsal lobes, the nearly symmetrical structure of the distal articular surface and annular ridge, the pair of prominent caesti, and the centrally located, distally



Figures 112–118. (112) *Chyliza* sp. (Imbia, P.N.G.; fam. Psilidae), left antennal seg. 2, distal view, seg. 3 removed. (113) The same, annular ridge and associated parts within pedicellar cup. (114) *Syringogaster* sp. (Costa Rica; fam. Syringogastridae), left antennal seg. 2, distal view. (115) *Chyliza* sp., left antennal seg. 3, medial view. (116) *Syringogaster* sp. left antennal seg. 3, lateral view. (117) *Nothybus decorus* de Meijere (fam. Nothybidae), left antennal seg. 3, medial view. (118) *Gobrya cyanea* (Enderlein) (fam. Gobryidae), the same. *a6*, antennal seg. 6; *as*, abraded surface; *bf*, basal foramen; *bs*, basal stem; *ca*, caestus; *cu*, pedicellar cup; *pc*, pedicellar cleft; *r*, dorsal lobes of rim; *sbc*, sub-basal caecum; *sc*, sacculus; *st*, scabrous tongue.

facing foramen. The part of the distal articular surface below the annular ridge has many, more or less transverse ridges supporting many microtrichia. The button is present just outside the lateral part of the annular ridge. The basal cavity of segment 3 opens obliquely along the basal stem (Fig. 102). It thus contains the elongate, somewhat obliquely facing basal foramen and the greater part of the scabrous tongue. The sacculus is located near mid-length of the disc.

The arista of *Planinasus* (Fig. 111) lacks segment 4. Segment 5 is dilated to cover much of the membranous socket of segment 3. It is asymmetrical and partly microtrichose. Segment 6, with its complex branching, is bifurcate from the base which is oblique—desclerotized on its medial side—to fit the oblique distal articular foramen of segment 5.

The most typical genera of the subfamily Stenomicrocrinae here considered are *Stenomicrocra* and *Cyamops* (Figs 103–109). In these segment 2 has the distal articular foramen and associated parts much more asymmetrical than in the Periscelidinae and Neurochaetidae, and more like that of the ephyrid genera *Hydrellia* and *Paralimna*. The reduced conus is present only on the medial side of the foramen as an irregularly rounded ridge, and the foramen faces laterally from inside this conus-remnant. The annular ridge with its dentate armature is variably developed, and is concealed by the conus-remnant from most angles. The button is located near the lateral margin of the foramen. Caesti are absent. Segment 3 has a very prominent basal stem (when disarticulated), with its basal foramen located

asymmetrically on its lateral surface (Figs 103, 104). Some *Stenomicroa* spp. have the annular ridge and button more deeply recessed than in Figs 105–107 and difficult to examine.

These facts suggest that a rearrangement of genera within the currently recognized taxa Stenomicroinae (*sensu* Grimaldi & Mathis, 1993), Perisclidinae, and Neurochaetidae may be necessary. I do not formally make this reclassification because (1) I do not have access to a wide enough range of material, (2) the degree of symmetry in the articulation between segments 5 and 6 suggests a different segregation of taxa from that indicated by the structure of segment 2, (3) some other schizophoran families (e.g., Ephydriidae) possess a comparable range of variation to that of Perisclididae s.l., (4) some of the distinctive features shared by Neurochaetidae and Perisclididae appear in other acalyprate families (e.g., the Psilidae, see below), and (5) any major reclassification should take into consideration further evidence in addition to antennal morphology. Also, the Neurochaetidae should perhaps retain family status as a derivative or close relative of the Eocene genus *Anthoclusia*, possessing a more complete series of fronto-orbital bristles and a symmetrical antennal segment 5, in contrast to the genera recently placed in both the Perisclidinae and Stenomicroinae (see D. McAlpine, 1983).

The Psilidae and Syringogastridae

These families have been placed in the superfamily Diopsoidea by D. McAlpine (1997). Examples of Psilidae used for detailed antennal study include *Chyliza* sp. (from Imbia, Papua New Guinea, Figs 112, 113, 115) and *Psila fimetaria* (Linné) (from Switzerland). Specimens of *Syringogaster* spp. (from Costa Rica, Figs 114, 116, and Brazil) were used.

The Psilidae have often been characterized as having segment 2 with a dorsal cleft, slit, or seam, i.e. the rim is strongly produced to form a pair of broad, narrowly separated cucullate dorsal lobes, as in numerous other schizophoran families (see D. McAlpine, 1997). This structure produces a cap-like appearance with the hollowed distal articular surface facing distoventrally or ventrally. Much of the concave distal surface is covered with a reticulation of raised ridges and is microtrichose to a variable degree. The conus is virtually absent. The annular ridge forms an almost symmetrical convexity sunk within a deep median cavity of the upper part of the articular surface, sheltered or almost concealed by the lobes of the rim, and bearing numerous stout, incurved microtrichia. The button is located dorsolaterally, just outside this circle of microtrichia in *Chyliza* sp. It could not be found in *Psila fimetaria*, apparently because of the extremely irregular and deeply recessed cuticular surface. The foraminal ring is vertically elongate, with a variably developed dorsal and ventral cusp. A caestus, consisting of a series of prominent, almost separate tubercles is present on each side of the foraminal ring.

These features coincide to a quite remarkable degree with those described for the Neurochaetidae and some taxa of Perisclididae. Though this may suggest at first glance a close relationship between these families, I can find no

particular shared non-antennal characters to support such a relationship, and many of the antennal features also occur in other families.

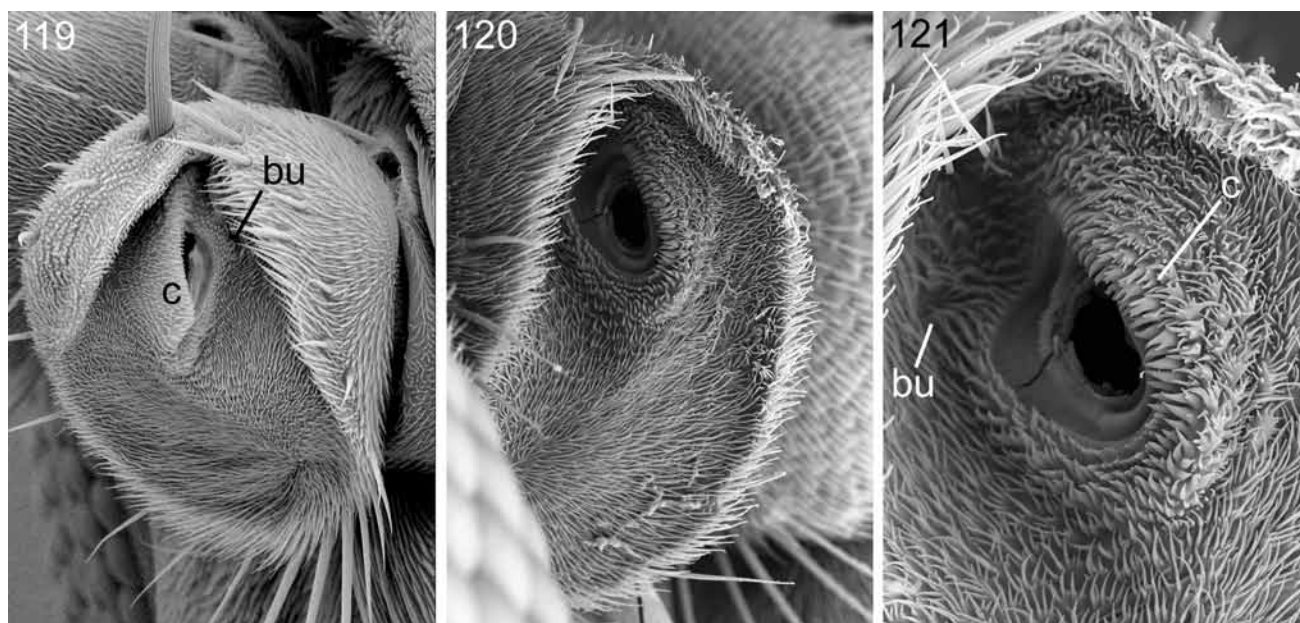
In *Syringogaster* sp. (family Syringogastridae) both segments 2 and 3 are very similar to those of the Psilidae in essential structure. The distal articular surface of segment 2 (Fig. 114) is deeply concave because of the pair of large incompletely separated lobes formed from the rim; there is no elevated conus; the approximately symmetrical annular ridge is sunk into the cup; the foraminal ring has a dorsal and a ventral cusp; there appears to be a ridge close inside the annular ridge on each side representing a caestus (difficult to see because this region is deeply recessed). Segment 3 (Fig. 116) resembles that of the Psilidae particularly in the long basal stem bearing the ventrally directed symmetrical foramen on a ventral prominence.

The Syringogastridae have been regarded as the sister group of the Diopsidae s.l. (Griffiths, 1972; D. McAlpine, 1997), despite their greater resemblance to the Psilidae in antennal structure. The view of Feijen (1983) that the Syringogastridae form the sister group of the “Centrioncidae” (as distinct from the Diopsidae s.str.) was rejected by D. McAlpine (1997), and the present study seems to provide further evidence against Feijen’s viewpoint. However, I am not at present inclined to abandon the theory of close relationship between Syringogastridae and Diopsidae s.l. solely on antennal characters. Of the six distinctive apomorphies shared by Syringogastridae and Diopsidae (D. McAlpine, 1997: table 1) none is present in the Psilidae. In addition, the small, transverse basal articular foramen of the syringogastrid fore coxa is like that of typical diopsids, in contrast to the longer, oblique foramen of the Gobryidae and Psilidae; and the complex, crazed cuticle of the central part of the face in Syringogastridae somewhat resembles that of various diopsid genera (see Figs 20, 22, 24 in D. McAlpine, 1997), while the Psilidae have the face with continuous, unbroken sclerotization.

The Nothybidae and Gobryidae

These two families were referred to the superfamily Diopsoidea by D. McAlpine (1997), and each is only known from its type genus (respectively *Nothybus* and *Gobrya*). They show agreement in many aspects of antennal morphology (Figs 117–121).

The rim of segment 2 is developed into a pair of large hood-like lobes (approximately as in Ephydroidea and other groups), but the distal articular surface, though concave, has no defined cup containing the annular ridge and foramen; the conus is reduced to a low but distinct prominence on the medial side of the foramen, but is obsolete on the lateral side, and as a result the irregularly and asymmetrically developed annular ridge and the foramen face laterally; there are no caesti. Segment 3 (Figs 117, 118) has the strongly produced basal stem bilaterally compressed, and the basal foramen on its medial surface faces medially in *Nothybus*, ventromedially in *Gobrya*; the medial surface of the basal stem has a scabrous zone which extends into the small sub-basal caecum near where the basal stem adjoins the disc of the segment. Segments 4 and 5 of the arista are short but separately sclerotized in *Nothybus*, absent in *Gobrya*; in both groups the arista arises dorsally on segment 3, instead of in the usual dorsolateral position.



Figures 119–121. Antennae of Nothybidae and Gobryidae. (119) *Nothybus decorus* de Meijere, left seg. 2, distolateral view, seg. 3 removed. (120) *Gobrya cyanea* (Enderlein), right seg. 2, distolateral view, seg. 3 removed. (121) The same, detail of conus and adjacent parts. *bu*, pedicellar button; *c*, medial prominence of reduced conus.

The Diopsidae

The broad classification of the Diopsidae given by Hennig (1965: 62) is still preferred. This gives two subfamilies: Centrioncinae, including *Centrioncus* (synonym *Teloglabus*, since added; D. McAlpine, 1997); and Diopsinae, including all other genera. I have examined details of antennal structure in *Centrioncus decoronotus* Feijen, *Sphyracephala* (*Hexechopsis*) *beccarii* (Rondani), and *Cyrtodiopsis* sp. (West Malaysia). Feijen (1983: figs 4–6) has illustrated the general features of some diopsid antennae.

The antennae of Diopsidae differ from those of the four diopsoid families treated above in the following conditions: segment 2, though having the rim well developed and encircling the distal articular surface, is not produced into a pair of dorsal lobes; the conus is relatively large, well removed from the medial margin of the distal articular surface, and the armature of the annular ridge is relatively slightly developed; caesti are absent; segment 3 has a large basal hollow, into which the conus is inserted, and has no basal stem—two features sharply distinguishing it from that of all other diopsoid families, including the Syringogastridae.

In *Centrioncus* (Fig. 122) the conus is deep, somewhat bilaterally compressed, and asymmetrical, with laterally facing preapical foramen; segment 3 (Fig. 124) has its basal foramen inside the basal hollow on its lateral wall; the arista is inserted slightly laterally to the dorsal margin of segment 3.

In *Sphyracephala* segment 2 (Fig. 123) is more nearly radially symmetrical (only slightly bilaterally compressed), with the conus erect, elongate, slightly clavate, arising from near the centre of the distal articular surface, and possessing a terminal foramen; the button is located preapically on the mediodorsal part of the conus (a most unusual location in the Cyclorrhapha); segment 3 (Fig. 125) has the basal hollow deep, almost symmetrical, with the basal foramen located

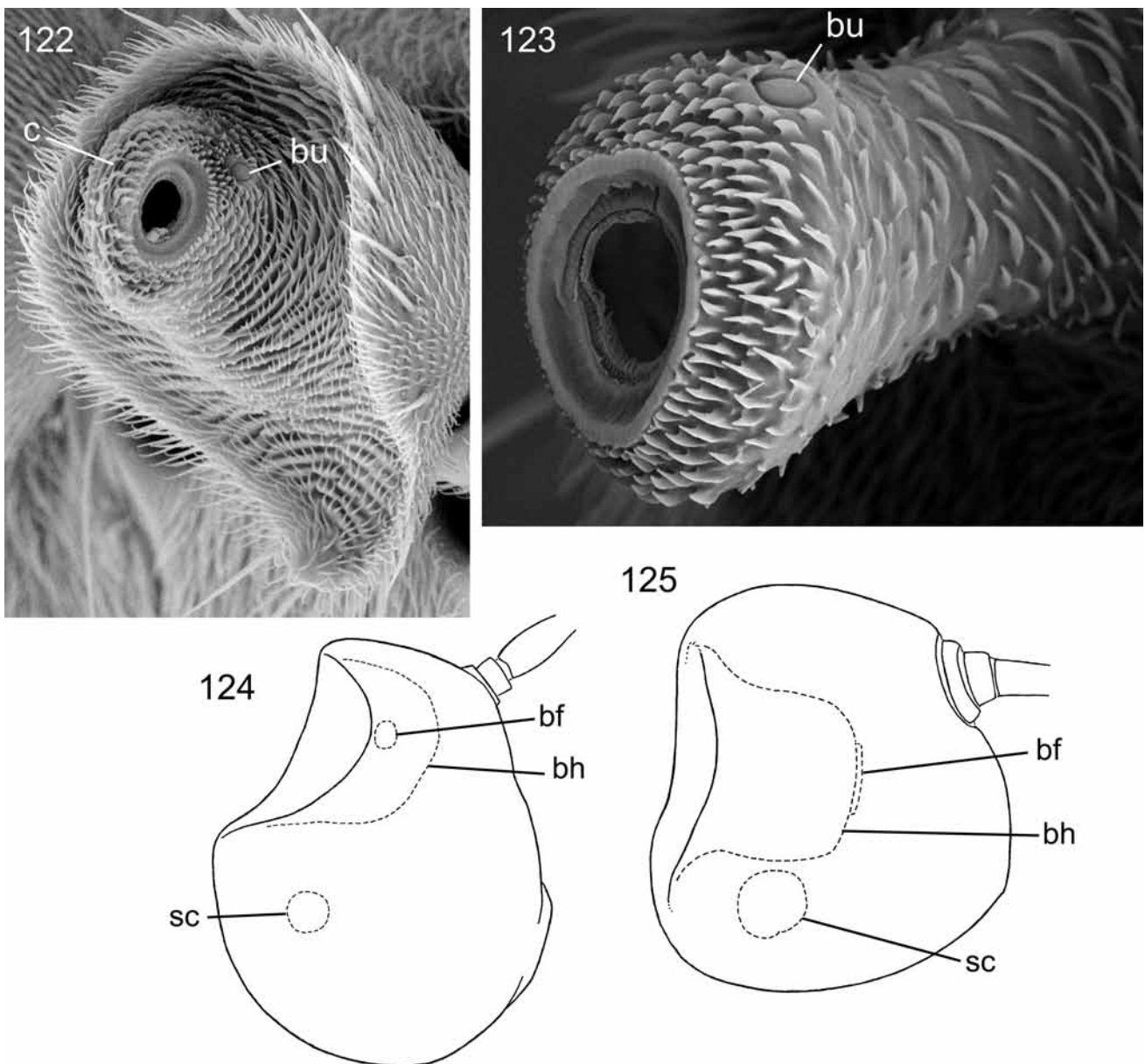
on its floor; the arista is placed symmetrically on its dorsal margin. In *Cyrtodiopsis* the conus is even longer than in *Sphyracephala*, with the button on the dorsal surface at *c*, the distal quarter of its length. The form of segment 2 and its conus in these more advanced diopsids is remarkably convergent with that of the lower cyclorrhaphous family Lonchopteridae.

Other genera of Diopsinae (e.g., *Diopsis*) appear similar to the above examples in most details. The antenna of *Centrioncus* is more like that of various basal schizophoran types found in the Sciomyzoidea and Heteromyzoidea than is that of the Diopsinae, though it may partly retain the plesiomorphic structure from which that of the Diopsinae was derived.

The lower tephritoid families

In this informal category I include the families Lonchaeidae, Pallopteridae, Piophilidae, Richardiidae, and Ulidiidae (syn. Otitidae) as distinct from the higher tephritoid families Pyrgotidae, Platystomatidae, and Tephritidae. I have examined in at least moderate detail the antenna of one species of each family, viz. *Lonchaea* sp. (Lonchaeidae), *Palloptera muliebris* (Harris) (Pallopteridae), *Piophila vitrea* McAlpine (Piophilidae), *Richardia tephritina* Enderlein (Richardiidae), and *Herina macalpinei* Kameneva (Ulidiidae); see Figs 126–133.

Wiegmann *et al.* (2011) in their phylogenetic study of dipterous families remove the Pallopteridae far from the tephritoid families, with which they are usually associated, and place the family as the sister group of the Neurochaetidae. I find antennal segment 2 of *Palloptera* to be exceedingly similar structurally to that of the tephritoid genus *Richardia* Fig. 129) and without the distinctive characters of the Neurochaetidae. This fact, together with the distinctive tephritoid synapomorphies of the pallopterid female postabdomen, not approached



Figures 122–125. Antennae of Diopsidae. (122) *Centrioncus decoronotus* Feijen, left seg. 2, distolateral view, seg. 3 removed. (123) *Sphyracephala beccarii* (Rondani), conus of right seg. 2, distomedial view. (124) *C. decoronotus*, left seg. 3, medial view. (125) *S. beccarii*, the same. *bf*, basal foramen of seg. 3; *bh*, basal hollow; *bu*, pedicellar button; *c*, conus; *sc*, sacculus.

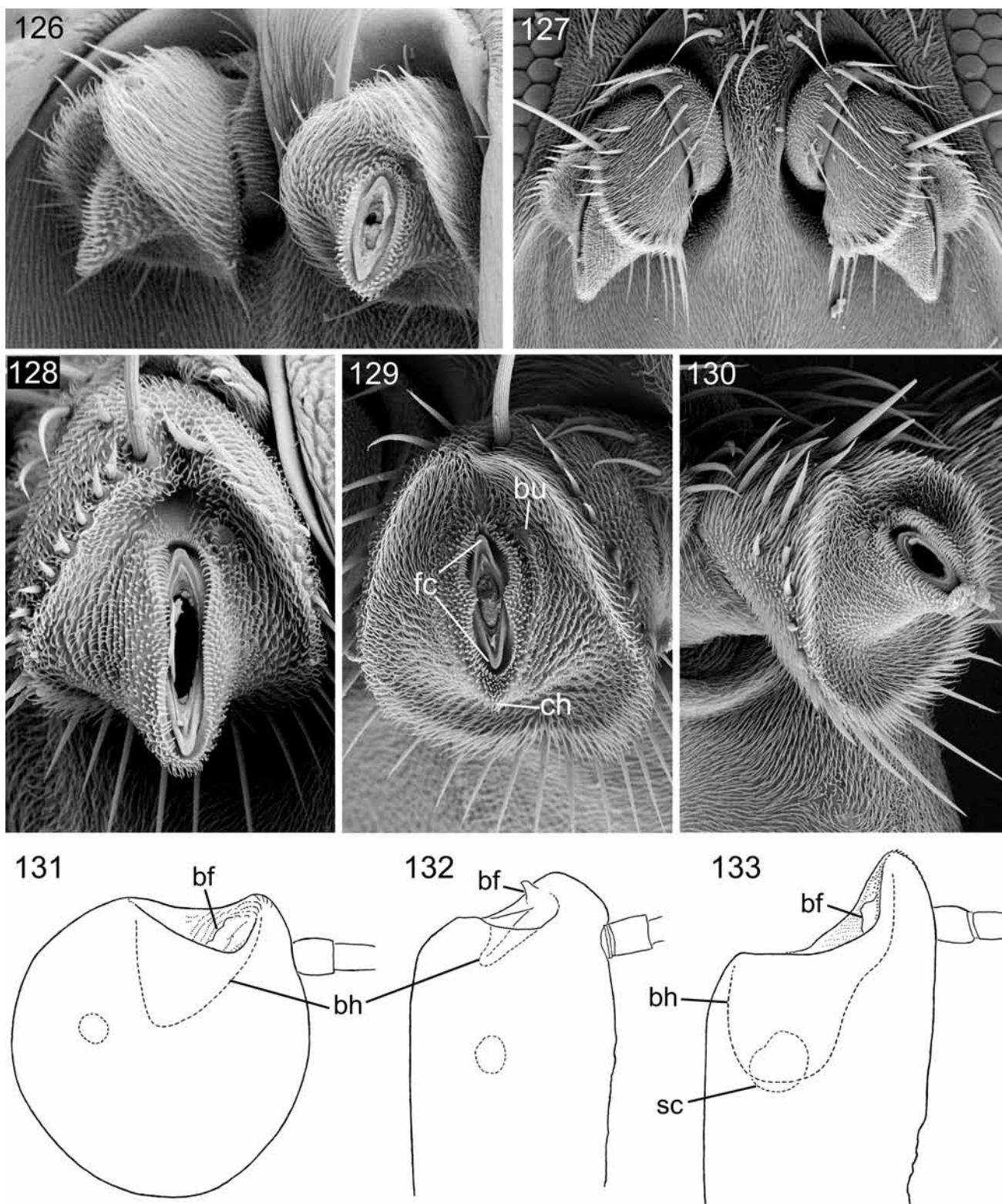
in the Neurochaetidae (see J. McAlpine, 1987: figs 5, 6; D. McAlpine, 1978: fig. 19), and the general lack of morphological and behavioural resemblances between the two families render the placement indicated by Wiegmann *et al.* very improbable. Also, the plesiomorphic Eocene neurochaetid genus *Anthoclusia* shows no significant points of resemblance to the Pallopteridae (Hennig, 1965, and author's unpublished study).

The lower tephritoid taxa show the general features of segments 2 and 3 somewhat as in the Sciomyzoidea, but with some modifications. The distal articular surface of segment 2 is generally somewhat concave and encircled or almost so by the prominent rim, but the latter is often interrupted by a slight mid-dorsal notch, not by a long cleft as in most platystomatids and calyptrates. The conus is broad, almost uniformly sclerotized, rather short, and, with a little variation, more nearly bilaterally symmetrical than in most sciomyzoid

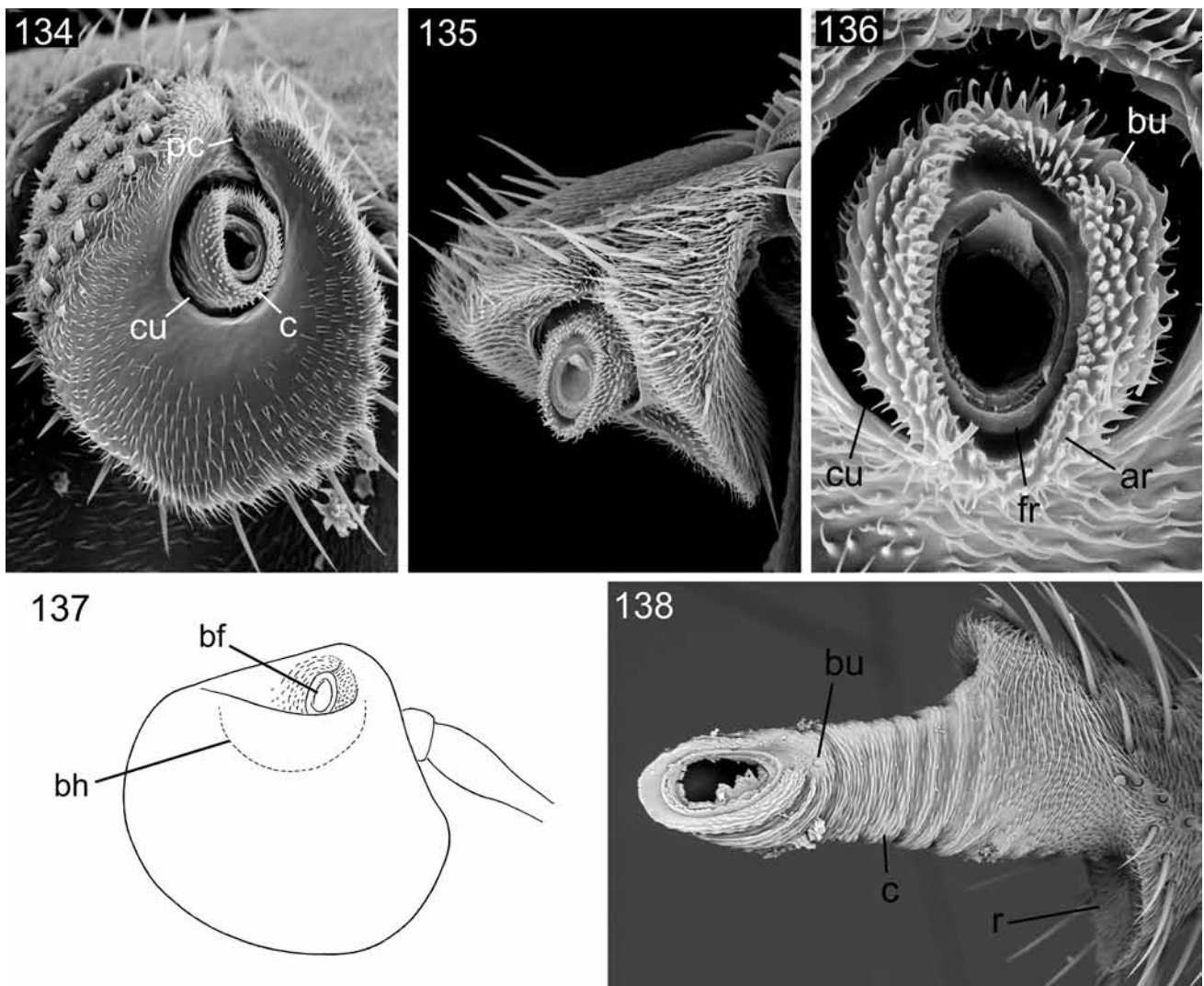
taxa; it is tilted so as to retain its ventral prominence, often with a slight chin, but dorsally it is often scarcely raised above the general level of the articular surface. The distal foramen is vertically more or less elongate and tilted dorsally but not or only slightly laterally (as in *Piophilila*). The foraminal ring usually bears a dorsal and a ventral cusp (except in *Herina*). The button occupies a dorsolateral position rather near the annular ridge. No taxon in this group is known to possess an encircling furrow (round the base of the conus) or caesti between the foraminal ring and annular ridge.

Segment 3 has usually a capacious basal hollow, but in *Lonchaea* it is reduced and divided by a ridge (Fig. 132). The basal stem is generally absent or only slightly indicated. The basal foramen is on a very slightly developed prominence near the margin of the basal hollow and usually faces ventrally, almost symmetrically.

The examples studied all have a three-segmented arista.



Figures 126–133. Antennae of lower tephritoids. (126) *Piophila vitrea* McAlpine (fam. Piophilidae), antennae, each with seg. 3 removed to expose conus. (127) *Lonchaea* sp. (Willoughby East, N.S.W.; fam. Lonchaeidae), the same. (128) *Lonchaea* sp., left antennal seg. 2, seg. 3 removed. (129) *Richardia tephritina* Enderlein (fam. Richardiidae), the same. (130) *Herina macalpinei* Kameneva (fam. Ulidiidae or Otitidae), right antennal seg. 2, seg. 3 removed. (131) *Piophila vitrea*, left antennal seg. 3, medial view. (132) *Lonchaea* sp., the same. (133) *Richardia tephritina*, the same. *bf*, basal foramen of seg. 3; *bh*, basal hollow of seg. 3; *bu*, pedicellar button; *ch*, chin; *fc*, foraminal cusps; *sc*, sacculus.



Figures 134–138. Antennae of Pyrgotidae. (134) *Cardiacera carnei* (Paramonov), left seg. 2, distal view, seg. 3 removed. (135) *Prodalmania variabilis* Bezzi, left seg. 2, lateral view, seg. 3 removed. (136) *P. variabilis*, left conus and associated parts, distal view. (137) *P. variabilis*, left seg. 3, medial view. (138) *Adapsilia* sp. (Kuranda, Qld), male, part of left seg. 2, lateral view, seg. 3 removed to expose conus. *ar*, annular ridge; *bf*, basal foramen of seg. 3; *bh*, basal hollow; *bu*, pedicellar button; *c*, conus; *cu*, pedicellar cup; *fr*, foraminal ring of seg. 2; *pc*, pedicellar cleft; *r*, pedicellar rim.

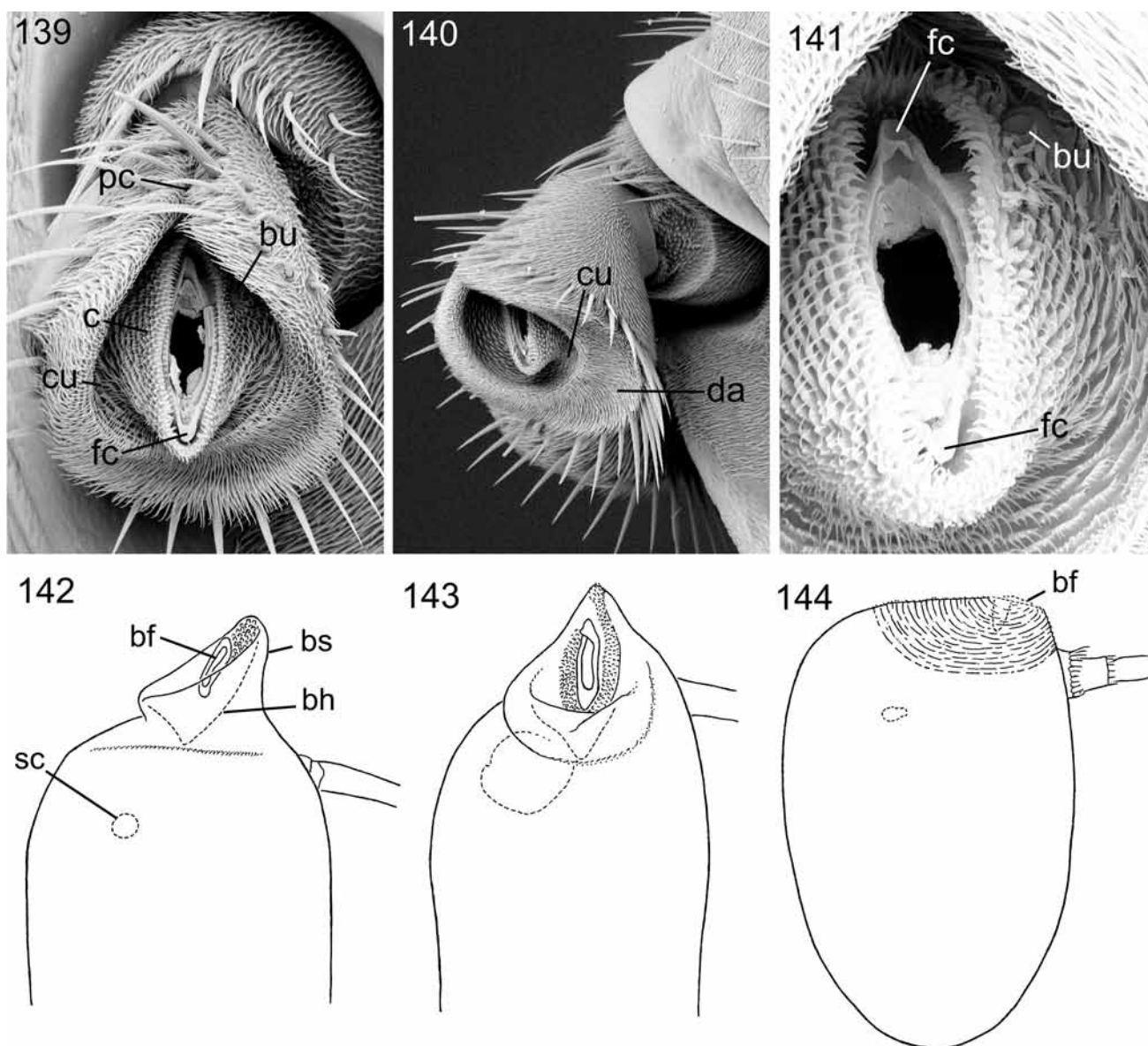
The Pyrgotidae

I have examined antennal structure in the following species: *Cardiacera carnei* (Paramonov), *Maenomenus ensifer* Bezzi, *Prodalmania variabilis* Bezzi, *Adapsilia* sp. (Kuranda, Queensland). The first three of these have fairly uniform antennal structure, but *Adapsilia* has some unusual features and will be described separately.

In the more typical genera segment 2 has a broad encircling rim, often interrupted by a dorsal notch or incipient cleft. The distal articular surface is more or less concave. The conus is moderately short, not markedly receding dorsally, arising from within a deep cup lined by largely membranous cuticle. This condition apparently confers considerable flexibility on the conus which therefore has the property of an additional articulated antennal segment (Figs 134–136). The foraminal ring is simple, rounded but not quite circular and only slightly tilted dorsally to dorsolaterally; caesti and cusps are absent. The button is located dorsolaterally near or on the annular ridge. This condition somewhat resembles that

in the Chloropidae, but there is no chin and the collar is less developed; the chloropids studied have no cleft in the rim. Segment 3 (Fig. 137) is without a typical basal stem, though sometimes it may be more basally prominent dorsally than ventrally. The basal hollow is broad, but only of moderate depth. The basal foramen is located on the lateral wall of the hollow on a slight gibbosity, which is probably flexible. The sacculus of *Maenomenus* has a relatively large external pore. The external pore could not be detected in the other pyrgotid genera, but a sacculus is presumably present (certainly present in *Cardiacera*). The arista in these examples is three-segmented with strongly marked articulation between segments 5 and 6. Segment 4 is relatively large in *Cardiacera*, in some species almost as long as segment 5; in the other genera it is short but sclerotized.

In *Adapsilia* sp. (Fig. 138) the antenna is longer than in the above examples. The rim lacks the dorsal notch and the distal articular surface is only partly concave. There is no cup or encircling furrow. The conus is remarkably large, elongate, and apparently flexible over most of its length,



Figures 139–144. Antennae of Platystomatidae. (139) *Duomyia curta* McAlpine, left seg. 2, distodorsal view, seg. 3 removed. (140) *Lamprogaster stenoparia* Hendel, left seg. 2, lateral view, seg. 3 removed. (141) The same, parts contained in cup of seg. 2. (142) *Loxonevra* sp. (West Sumatra), part of left seg. 3, medial view. (143) *Euprosopia armipes* McAlpine, the same. (144) *Peltacanthina* sp. (Karen, Kenya), left seg. 3, medial view. *bf*, basal foramen of seg. 3; *bh*, basal hollow; *bs*, incipient basal stem; *bu*, pedicellar button; *c*, conus; *cu*, pedicellar cup; *da*, distal articular surface of seg. 2; *fc*, foraminal cusp; *pc*, pedicellar cleft; *sc*, sacculus.

but less so basally; its cuticle is thrown into many encircling folds and the surface has finer transverse ridging; the foramen is strongly tilted laterally. This structure is apparently derived from that of *Cardiacera* etc., but differs markedly in the great prolongation of the conus and extension of the flexibility of the cuticle over much of the length of the conus. Segment 3 has a deep, capacious basal hollow. Segment 4 is reduced to a minute vestige, so that the arista appears to be two-segmented. Korneyev (2004) drew attention to the numbers of arisal segments in the key to Palaearctic genera of Pyrgotidae.

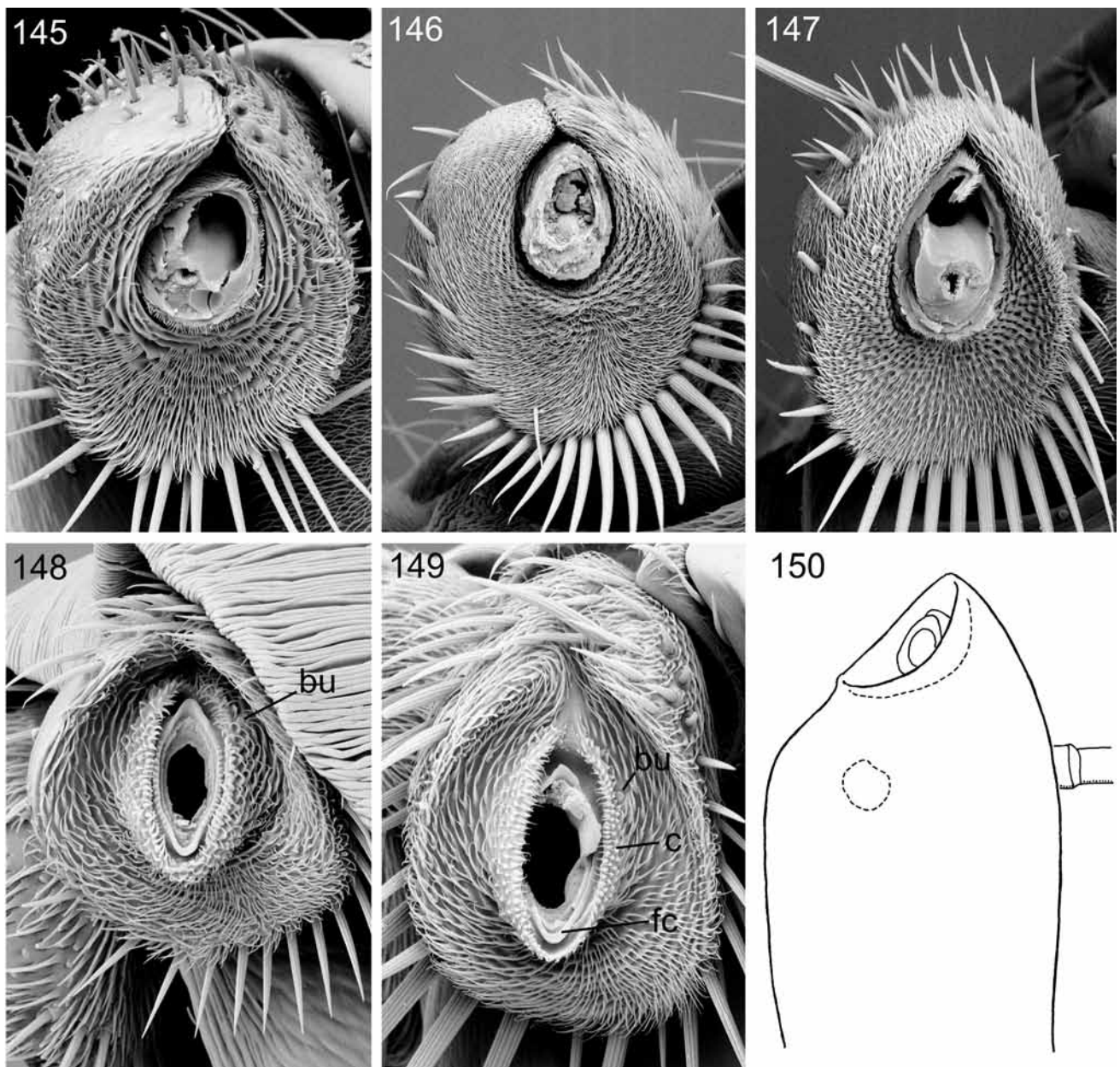
The convergent resemblance in some characters between certain taxa of Conopidae and Pyrgotidae has been mentioned before (e.g., Hennig, 1952: 195). The structure of antennal segment 2 and the conus in *Adapsilia* provides an additional example (compare Figs 138 and 43). As

these conditions differ from those in the groundplans of both families, the structural similarities are perhaps to be interpreted as due to similarities in habits of the adult flies.

In addition to the condition of antennal segment 4, possibly useful taxonomic characters in the Pyrgotidae include the structure and position of the prelabrum (“clypeus” in error) and various features of the proboscis.

The Platystomatidae and Tephritidae

Antennal structure in the Platystomatidae reflects some of the general diversity occurring in the family. I therefore divide the selection of taxa examined for antennal morphology into four categories for descriptive purposes. These categories (types A to D) are not necessarily sharply defined, nor do they consistently follow a natural classification.

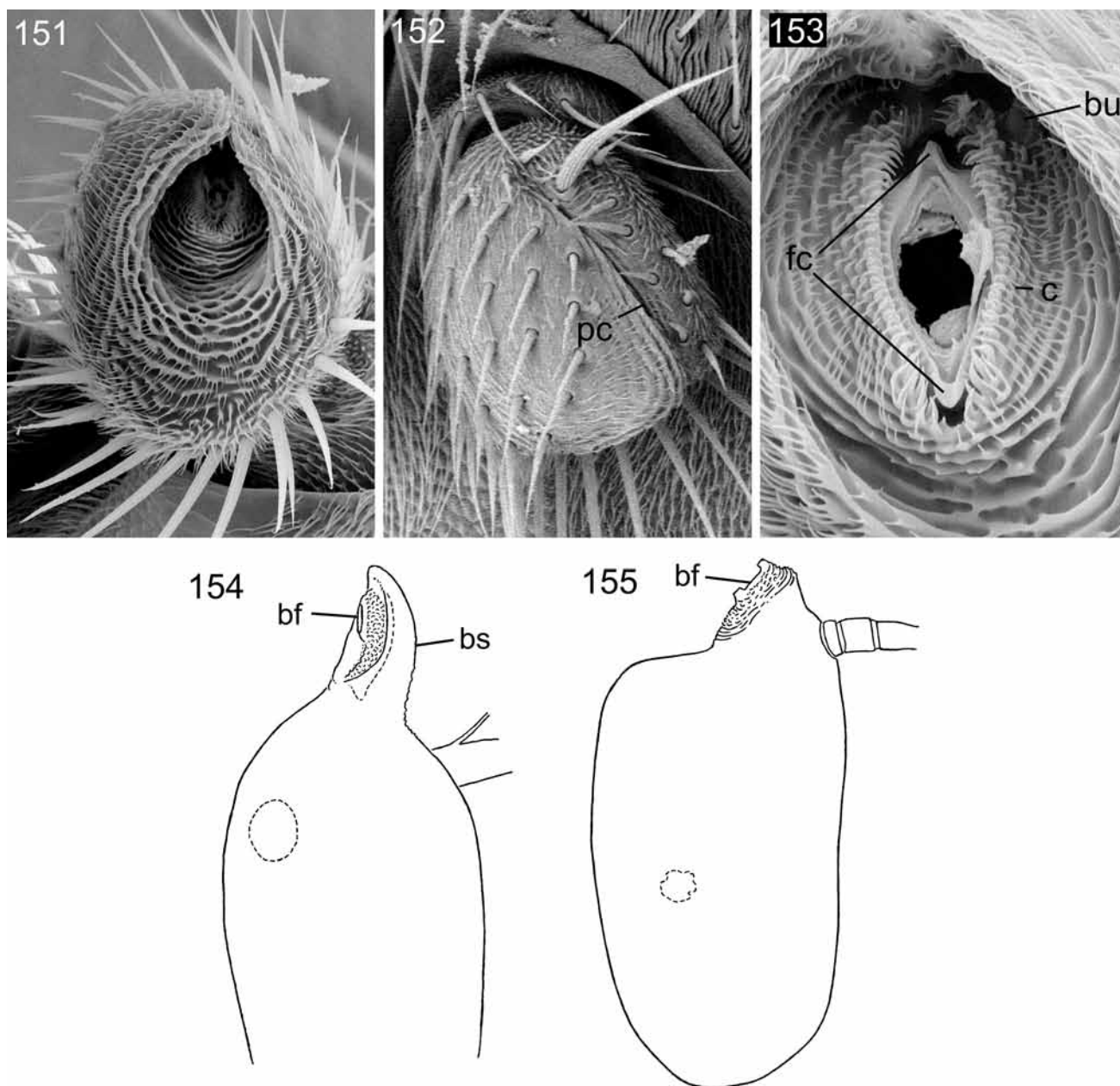


Figures 145–150. Antennae of Platystomatidae. (145) *Peltacanthina* sp. (Karen, Kenya), left seg. 2, distal view, seg. 3 removed. (146) *Cleitamia astrolabei* (Macquart), the same. (147) *Scholastes cinctus* (Guérin-Méneville), the same. (148) *Microepicausta* “sp. 1” (in AM), the same. (149) *Rhytidortalis averni* McAlpine, the same. (150) The same sp., part of left seg. 3, medial view. *bu*, pedicellar button; *c*, conus; *fc*, foraminal cusp.

Type A (Figs 139–143). Examples studied: *Achias kurandanus* Hennig, *Duomyia* spp., *Euprosopia vitrea* McAlpine, *E. armipes* McAlpine, *Lamprogaster stenoparia* Hendel, *Lenophila achilles* McAlpine & Kim, *Loxonevra* sp. (western Sumatra), *Plagiostenopterina* sp. (near *enderleini* Hendel), *Platystoma gemmationis* (Rondani). This is the most frequent type in the family, particularly in the subfamily Platystomatinae, and is perhaps the groundplan condition for the Platystomatidae, the other types being derived from it. It resembles the condition commonly found in the Tephritidae.

Segment 2 has a long dorsal cleft extending near its base (Figs 139, 152, pc). The distal articular surface immediately within the rim is flattened to slightly concave, but centrally it abruptly gives way to a capacious cup (Fig. 140). The collar separating the distal articular surface from the cup (as seen

in the Chloropidae) is here at most slightly developed and dorsally interrupted. In some species of *Duomyia* it is almost obsolete, so that the surface of the cup is not so sharply differentiated from that of the surrounding articular surface. The short conus is often almost bilaterally symmetrical and almost symmetrically placed on the segment, but is tilted so that the annular ridge and distal foram face somewhat dorsally. Thus there is often a slight ventral chin and the dorsal extremity of the annular ridge is scarcely raised above the floor of the cup. Because of its small size, the conus does not nearly fill the cavity of the cup. The annular ridge and foraminal ring are vertically elongate, the latter usually with a dorsal and a ventral cusp. The button is located near the dorsolateral part of the annular ridge, virtually on the floor of the cup. Segment 3 is most often elongate, with both sacculus and arista located



Figures 151–155. Antennae of Platystomatidae. (151) *Atopognathus complens* (Walker), left seg. 2, distal view, seg. 3 removed. (152) The same, dorsal view of left seg. 2. (153) *Mesanopin biplexum* Whittington, pedicellar cup and contents. (154) *A. complens*, part of left seg. 3, medial view. (155) *M. biplexum*, the same parts. *bf*, basal foramen of seg. 3; *bs*, basal stem of seg. 3; *bu*, pedicellar button; *c*, conus; *fc*, foraminal cusps; *pc*, pedicellar cleft.

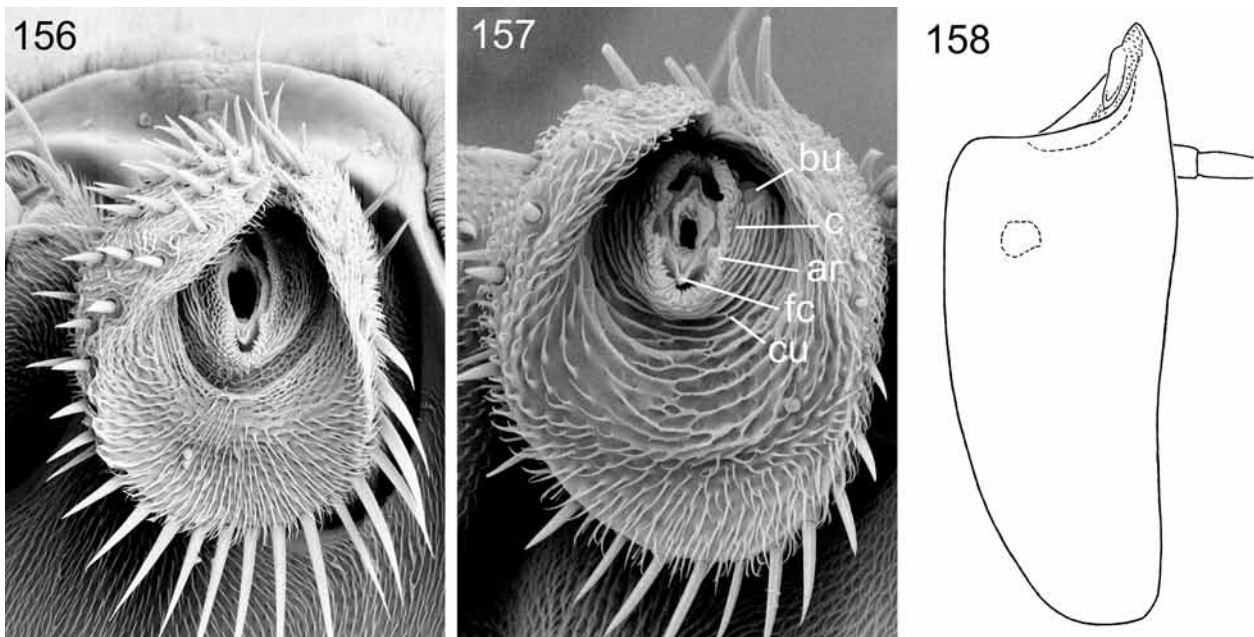
not far from its base. The basal hollow is generally present but small and there may be slight development of the basal stem. The basal foramen is asymmetrically placed at or near the margin of the hollow. The arista is commonly three-segmented, but in numerous species of *Euprosopia* and some of other genera segments 5 and 6 are fused.

Type B (Figs 144–147). Examples studied: *Cleitamia astrolabei* (Macquart), *Peltacanthina* sp. (Karen, Kenya), *Scholastes cinctus* (Guérin-Méneville). The morphology of this group may not be well understood but a more detailed study should be completed by future students.

The most distinctive apparent feature is the deep, narrow cup of segment 2, which is almost plugged by the stout, apparently subcylindrical conus with distal foramen of

greater area than usual. However, in all disarticulated specimens the conus has snapped or crumbled so that the features of its distal surface cannot be accurately ascertained. The tendency of the conus to break up may indicate that its distal part is flexible and incompletely sclerotized, as in the pyrgotid genus *Adapsilia*. Segment 3 appears not to have a typical hollow or sub-basal stem, but there is a narrow caecum next to the basal foramen, at least in *Peltacanthina* sp. (Fig. 144), and the cuticle of the convex basal zone of the segment is covered with a dense set of fine encircling ridges.

Mezonia sp. (Sokoke Forest, Kenya, in AM) appears to have several sacculi on segment 3, but available material is too limited for detailed study. This genus is perhaps closely related to *Peltacanthina*.



Figures 156–158. Antennae of Tephritidae. (156) *Euphranta marina* Permkam & Hancock, left seg. 2, distal view, seg. 3 removed. (157) *Spathulina acroleuca* (Schiner), the same parts. (158) *E. marina*, left seg. 3, medial view. *ar*, annular ridge; *bu*, pedicellar button; *c*, conus; *cu*, pedicellar cup; *fc*, foraminal cusp.

Type C (Figs 148–150). Examples studied: *Microepicausta* “sp. 1” (New South Wales, in AM), *Rhytidortalis averni* McAlpine.

These taxa resemble those listed under type A, but the cup is absent or incompletely differentiated from the surrounding articular surface of segment 2. The condition of the base of the conus is therefore not very different from that of such lower tephritoid families as Piophilidae and Ulidiidae, though the resemblance is probably secondary.

Type D (Figs 151–155). Examples studied: *Atopognathus complens* (Walker), *Mesanopin biplexum* Whittington, *Xiria* sp. (West Malaysia, in AM).

The cup is deep and capacious but not very sharply demarcated at its periphery. The conus is much reduced or shortened, but in *Mesanopin* it retains a degree of ventral prominence. In *Atopognathus* and *Xiria* the annular ridge is only slightly raised above the floor of the cup. In all three genera the basal hollow of segment 3 is absent and the basal stem is well developed, with the foramen near its extremity. *Mesanopin* is unusual in having the sacculus located beyond mid-length of segment 3. *Atopognathus* differs from the other two examples in having segments 5 and 6 fused (arista two-segmented as in some *Euprosopia* spp.).

Examples of the family Tephritidae examined for this study include the following: *Bactrocera tryoni* (Froggatt), *Euphranta marina* Permkam & Hancock, *Spathulina acroleuca* (Schiner) (see Figs 156–158). It is a family of great taxonomic diversity and these taxa are unlikely to show the full range of variation.

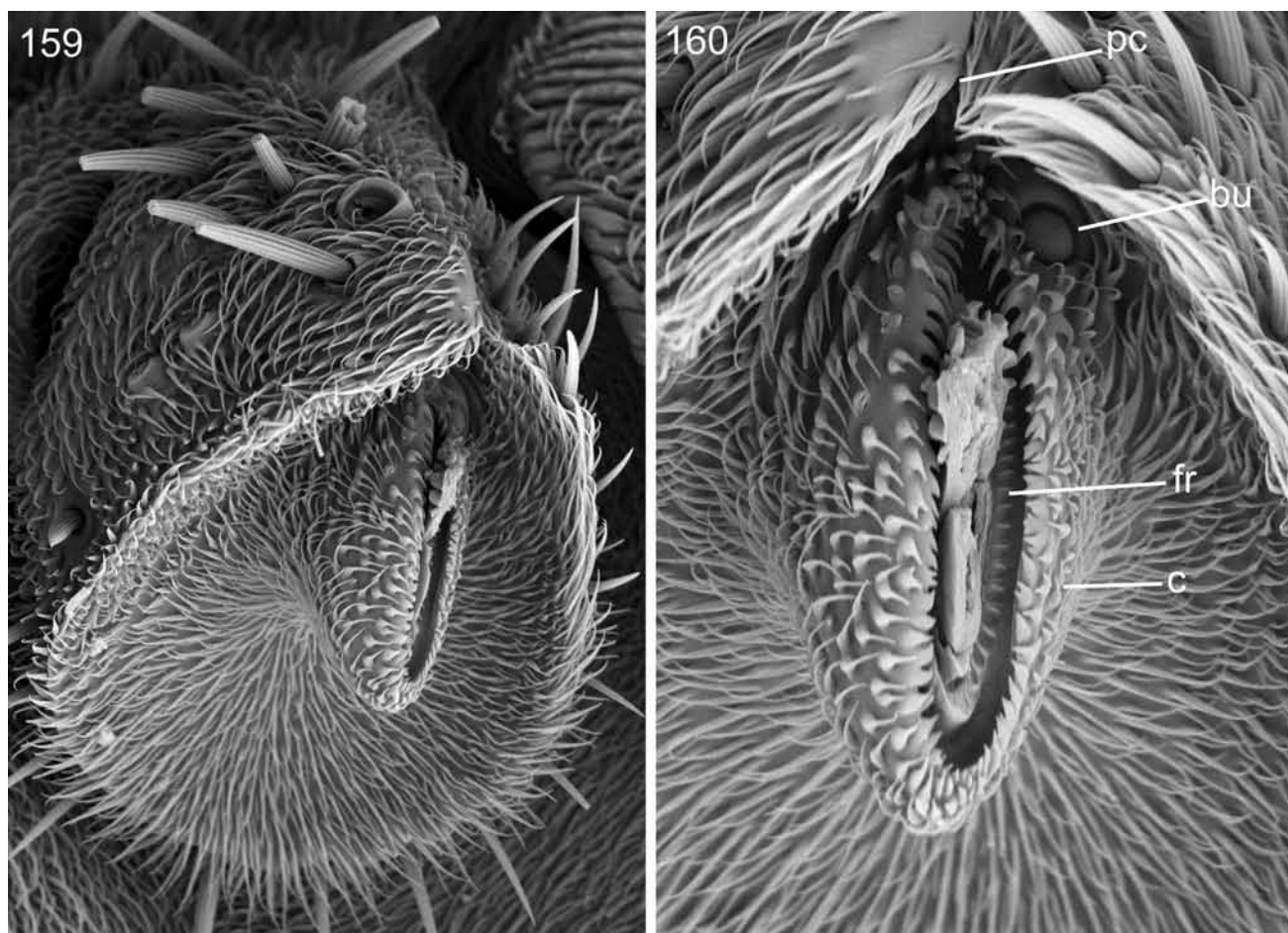
Segment 2 shows the main features described above for platystomatid type A. The conus is short in *Euphranta* and *Spathulina*, longer and more ventrally prominent in *Bactrocera*. Segment 3 has a small basal hollow, broader and shallower in *Euphranta* than in the other two genera. There is a short subacute basal stem, with the foramen on its ventral surface. The arista is three-segmented, with segment 4 very short.

The Calyptratae (Muscoidea s.l.)

Probably the most generally utilized recent superfamily and family classification for the calyptrates is still that of J. McAlpine (1989), though Hennig (1973) recognized a larger number of families. However, the phylogenetic study of Kutty *et al.* (2010) indicated that some major changes in superfamily and family classification are needed. Possibly the treatment of the calyptrates as a single superfamily (termed Muscoidea by Richards & Davies, 1977, Crosskey [ed.], 1980, and by Colless & D. McAlpine, 1991), is the best system, and is in accord with the analyses by Roback (1951), Griffiths (1972), Kutty *et al.* (2010), and Wiegmann *et al.* (2011), though Roback did not consider the pupiparous families.

The calyptrates show a general uniformity of antennal structure, particularly in details of segment 2, over the majority of included taxa. The main exceptions appear, from my limited selection of taxa, to be the highly derived Hippoboscidae and related so-called families (i.e. the Streblidae and Nycteribiidae, perhaps better not afforded separate family rank from the Hippoboscidae, if results of the phylogenetic study by Kutty *et al.*, 2010, gain general acceptance). These latter taxa (but not the related Glossinidae) have proved difficult for SEM work, but this need not affect the interpretation of morphology in the vast majority of calyptrate flies. Examples of Glossinidae, Hippoboscidae, and Nycteribiidae, previously studied by me, differ from other calyptrates and most other schizophorans (except for certain periscelidids) in having the rays (or primary branches) of the arista (segment 6) with secondary branching (see Fig. 167 and Theodor, 1967).

Calyptrate taxa which I have used for SEM study include: *Australofannia* sp. (family Fanniidae, Fig. 163), *Hydrotaea* sp. and *Musca vetustissima* Walker (family Muscidae, Figs 161, 162, 169), *Delia urbana* (Malloch) (family Anthomyiidae, Figs 159, 160), *Stomorhina discolor* (Fabricius) (family Rhiniidae, formerly in Calliphoridae, Fig.



Figures 159, 160. Left antenna of *Delia urbana* (Malloch) (fam. Anthomyiidae), female. (159) Seg. 2, seg. 3 removed, distomedial view. (160) The same, upper part of distal articular surface. *bu*, pedicellar button; *c*, conus; *fr*, foraminal ring; *pc*, pedicellar cleft.

172), *Chrysomya* sp. and *Amenia chrysame* (Walker) (family Calliphoridae, Figs 164, 171), *Axinia lucaris* Colless (family Axiniidae or Rhinophoridae, Fig. 165), *Senostoma mcalpinei* Barraclough (family Tachinidae), “McAlpine’s fly” (near family Anthomyiidae according to Ferrar, 1979; near family Mystacinobiidae according to Kutty *et al.*, 2010; Figs 170, 173), *Glossina* sp. (family Glossinidae, Figs 166–168). Several other taxa have been examined with CLM.

The following description applies, with little deviation, to segment 2 of the many typical examples studied (see Figs 159–166). The rim has a deep dorsal cleft, the margins of which remain in contact or almost so. The distal articular surface is broadly moderately concave, but recedes, often deeply and narrowly, on its central dorsal part between the dorsal extremity of the conus and the cleft. The conus is almost bilaterally symmetrical in shape and position on the mid-dorsal region of the articular surface, little raised from this surface at the dorsal end of the vertically elongate annular ridge, but always prominent at its ventral extremity (or chin) so that the annular ridge and distal foramen face dorsally rather than distally. The annular ridge generally does not have strongly differentiated armature, but is usually interrupted mid-dorsally below the cleft. The chin becomes particularly elongate and sharp apically in some examples of Calliphoridae and Tachinidae (though a broad representation of these families has not yet been examined), but is broadly rounded in *Stomorhina*. As in many other schizophorans with narrowly elongate distal foramen, the foraminal ring often

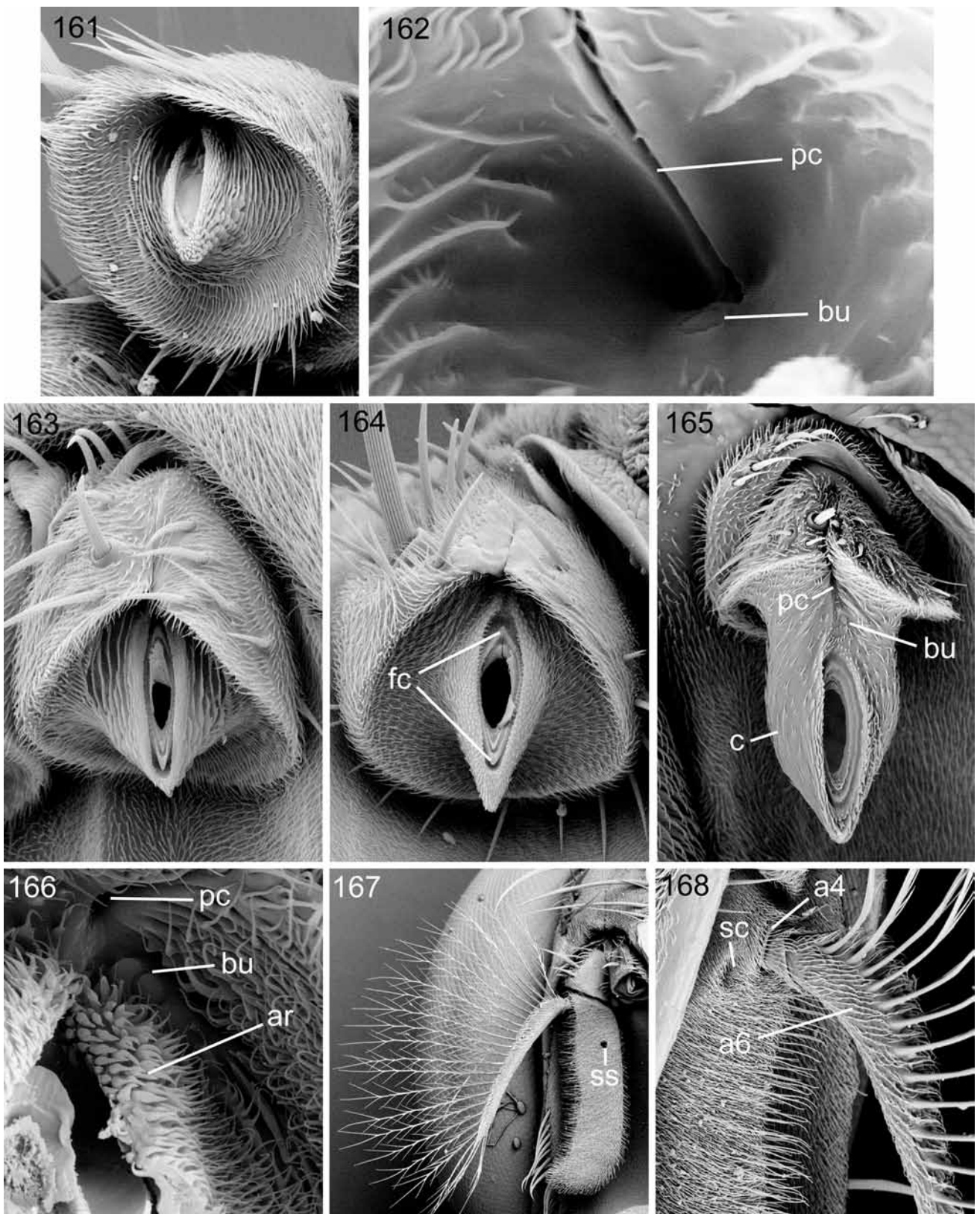
has a distinct dorsal and ventral foraminal cusp (Fig. 164).

The conus of the examined calyptrate taxa does not arise from a cup or any recessed zone surrounding its base, described above in several acalyptrate groups. It is possible in such examples as *Australofannia* (Fig. 163) and *Musca* (Fig. 161), that the surrounding cuticular surface consisting of sclerotized ridges alternating with bands of thinner cuticle allows some side-to-side movement of the conus and of segment 3 which it supports. The conus of *Axinia* (Fig. 165) is much larger than in other calyptrate taxa studied, and, when exposed, projects beyond the distal articular surface for a distance greater than the length of the main body of segment 2.

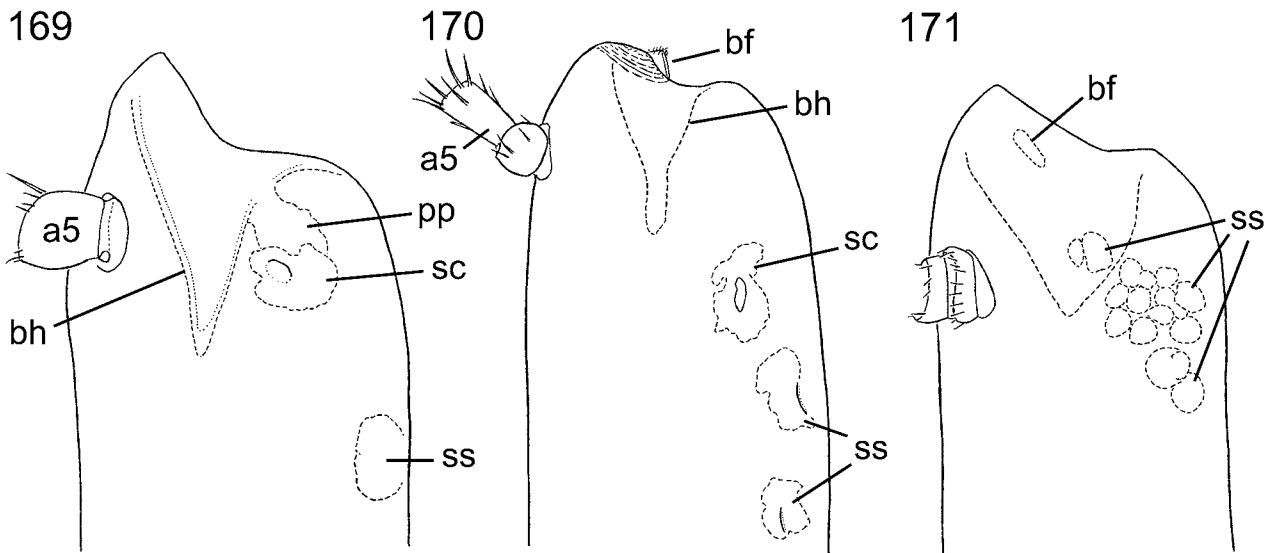
The pedicellar button of calyptrates is generally located dorsolaterally to the annular ridge, often within the dorsal recess and near the pedicellar cleft. In *Musca* (Fig. 162) it is particularly deeply recessed and faces dorsally towards the cleft.

In the Calyptratae the number of sacculi in segment 3 is variable, but I have had time to examine very few taxa, especially as the usually darkly pigmented and rough cuticle makes study difficult with CLM.

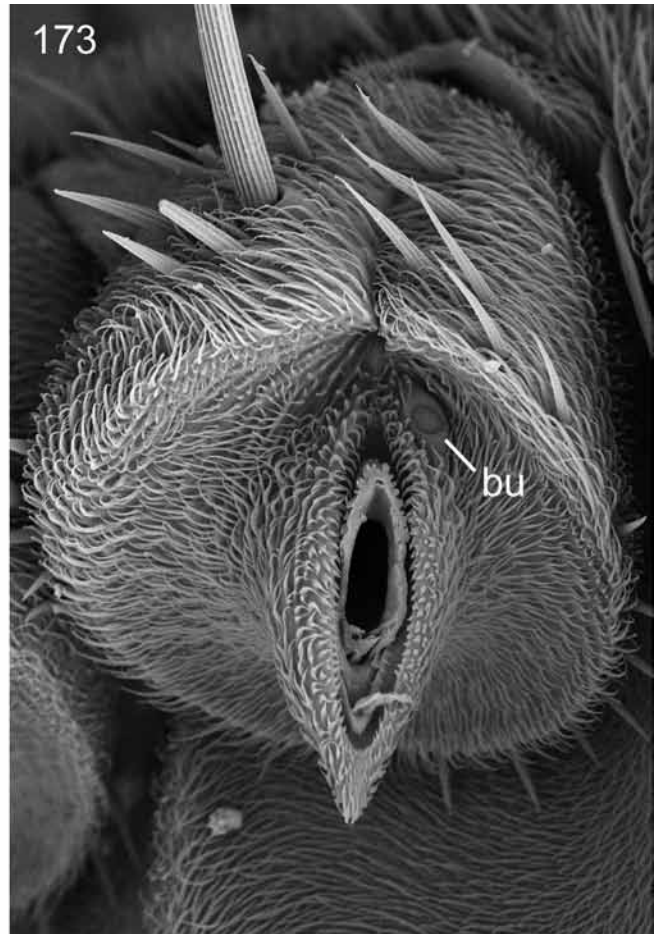
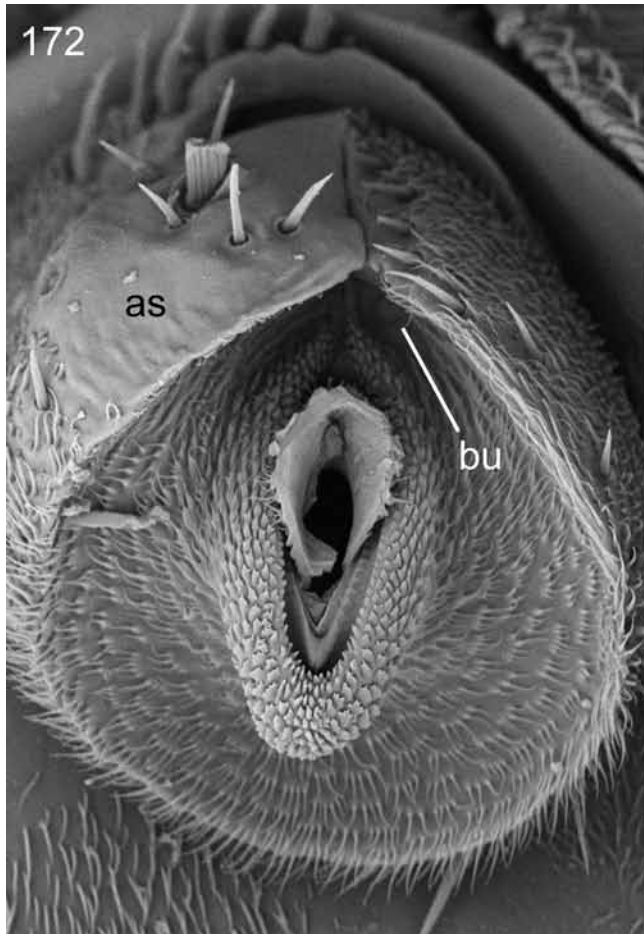
Glossina has a sacculus on the more basal part of the lateral surface of segment 3 (Fig. 168, *sc*), and this appears to be the homologue of the one sacculus in most acalyptrate taxa; but there is also an apparent sacculus (presumably a secondary structure) on the medial surface of this segment a little further from the base (Fig. 167, *ss*).



Figures 161–168. Antennae of Calyptratae. (161) *Musca vetustissima* Walker (fam. Muscidae), female, left seg. 2, distal view. (162) The same, dorsal recess of right seg. 2. (163) *Australofannia* sp. (fam. Fanniidae), female, left seg. 2, distodorsal view. (164) *Amenia chrysame* (Walker) (fam. Calliphoridae), female, left seg. 2, distodorsal view. (165) *Axinia lucaris* Colless (fam. Axiniidae or Rhinophoridae), male, left seg. 2, dorsal view. (166) *Glossina* sp. (fam. Glossinidae), male, part of recess of left seg. 2. (167) The same, right antenna, medial view. (168) The same, part of right antenna, lateral view, showing base of arista. *a4*, *a6*, antennal segments 4 and 6 (arista); *ar*, annular ridge; *bu*, pedicellar button; *c*, conus; *fc*, foraminal cusp; *pc*, pedicellar cleft; *sc*, opening of sacculus; *ss*, secondary sacculus.



Figures 169–171. Basal part of left seg. 3, lateral view, of Calyptroteae. (169) *Musca vetustissima* Walker (fam. Muscidae), male. (170) McAlpine's fly (fam. near Anthomyiidae or Mystacinobiidae), female. (171) *Amenia chrysame* (Walker) (fam. Calliphoridae), female. *a5*, antennal segment 5; *bf*, basal foramen, not visible in Fig. 169; *bh*, basal hollow; *pp*, postpedicellar pouch; *sc*, sacculus; *ss*, secondary sacculi.

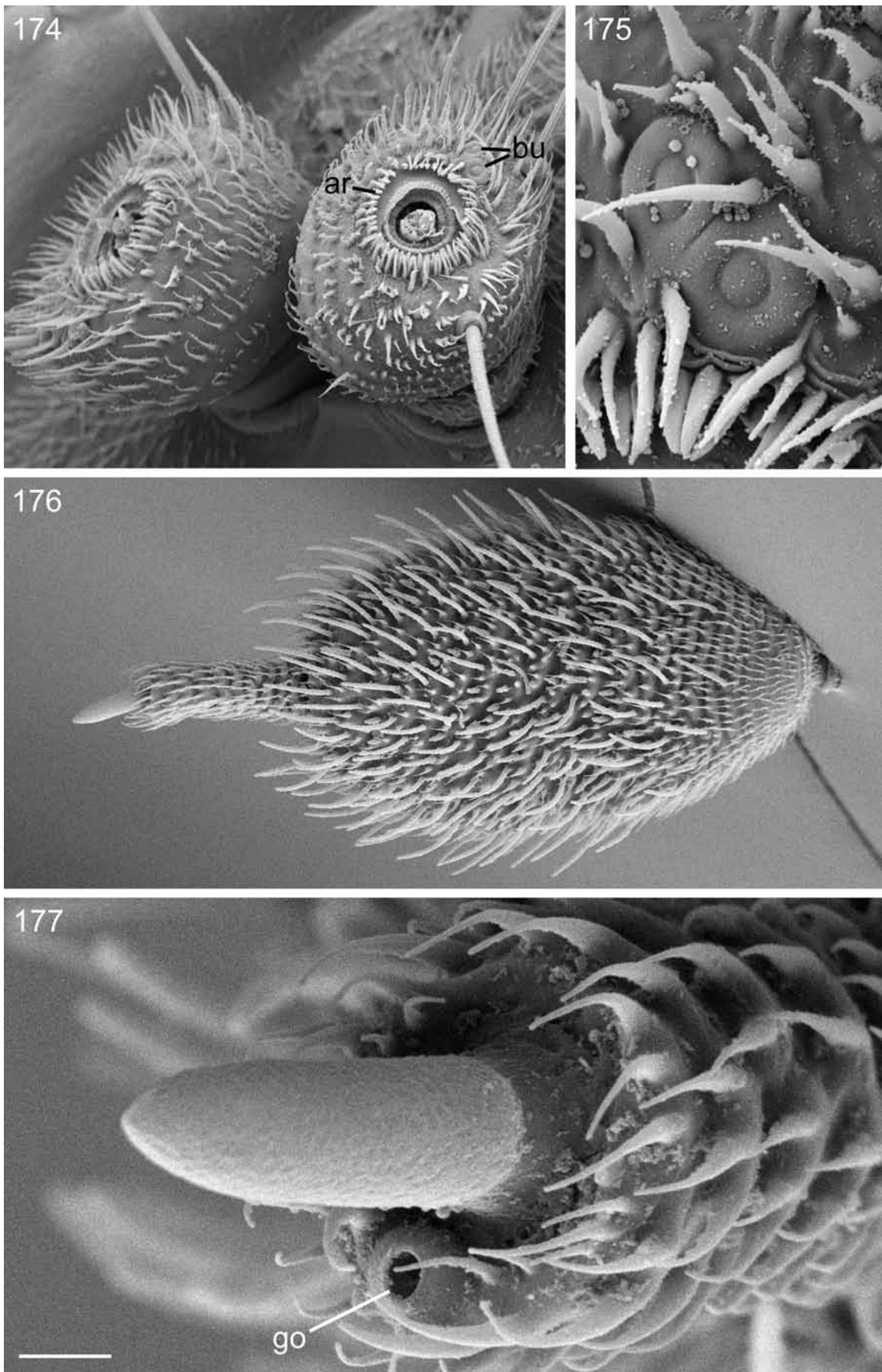


Figures 172–173. Antennal segment 2 of Calyptroteae, distodorsal view. (172) *Stomorhina discolor* (Fabricius) (fam. Rhiniidae), male. (173) McAlpine's fly (? fam.), female. *as*, abraded surface; *bu*, pedicellar button.

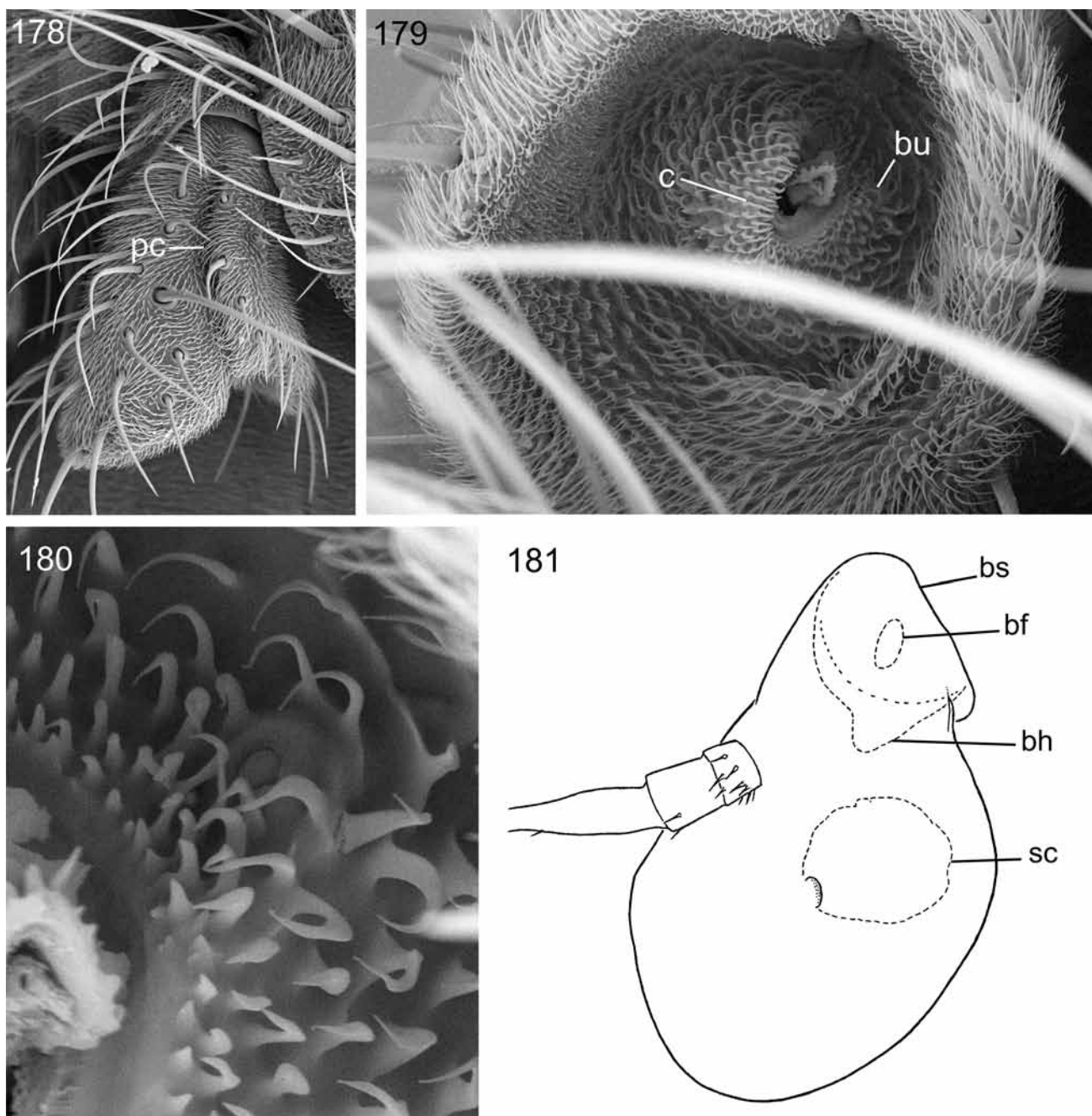
As *Glossina* represents the morphologically most basal clade of the Pupipara—the sister group to the rest of the Calyptroteae—it may be that it resembles the basal condition for the Calyptroteae in these features (despite its apomorphic life history and arisal structure). In a sense, it typifies the

common calyptrote condition of possession of a primary sacculus, with one or more secondary sacculi.

In *Fannia canicularis* (Linné) segment 3 has one major sacculus near the middle of the lateral surface, but there are also numerous smaller pit-like structures, some of



Figures 174–177. Antenna of *Apystomyia elinguis* Melander (fam. Apystomyiidae), male. (174) Both antennae, segs 3 removed. (175) Buttons of left seg. 2. (176) Right flagellum, medial view. (177) Distal part of right stylus, distomedial view; scale = 4 μ m. *ar*, annular ridge; *bu*, pedicellar buttons; *go*, stylar goblet.



Figures 178–181. Antenna of *Mormotomyia hirsuta* Austen (fam. Mormotomyiidae), male. (178) Segs 1 and 2, dorsolateral view. (179) Distal articular surface of seg. 2, seg. 3 removed. (180) Part of distal articular surface, showing button. (181) Left seg. 3, lateral view. *bf*, basal foramen; *bh*, basal hollow; *bs*, basal stem; *bu*, pedicellar button; *c*, conus; *pc*, pedicellar cleft; *sc*, sacculus.

which contain several sensilla. In *Scathophaga* sp. (family Anthomyiidae or Scathophagidae) segment 3 has a sacculus on the lateral surface and another on the medial surface near the base. This condition resembles that of *Glossina*. In *Musca vetustissima* (Fig. 169) segment 3 carries a normal sacculus on the lateral surface rather close to the base and a secondary sacculus-like ventral organ more removed from the base, which may be divided in two in some individuals. There is also a postpedicellar pouch opening into the ventral side of the basal hollow, not seen by me in other calyptrate taxa. This is reminiscent of the pouch in *Australoconops* (family Conopidae), but in the latter the pouch opens to the exterior ventrally to the hollow (Fig. 44), not into the hollow. The

phylogenetic distance between *Musca* and *Australoconops* renders it improbable that this pouch is homologous in the two taxa. In McAlpine's fly (Fig. 170), segment 3 resembles that of *Musca*. A large sacculus is located at *c*. the basal quarter of its length and there are *c.* three ventral secondary sacculi near mid-length and beyond. In the calliphorid *Amenia* (Fig. 171), segment 3 has *c.* 14 sacculus-like organs of various sizes on the lateral surface ventrad of the arisal socket. I cannot identify any one of these as the primary sacculus seen in other families. Some of these contain rounded internal bodies (as seen with CLM), but the internal structure needs interpretation by ultramicroscopic technique. Also in *Chrysomya* and some other calliphorid

taxa there are numerous sacculus-like structures. By contrast *Stomorhina*, now placed in the separate family Rhiniidae, clearly has only one sacculus. Among the tachinids, *Chetogaster* and *Senostoma* have one large sacculus only. In the “axiniids” (family Axiniidae or Rhinophoridae; see Colless, 1994) there is commonly one sacculus (“sensory pore”), but it is multiple or absent in various taxa.

As the Calypratae form an apparent clade derived from among the acalyprate groupings, it may be profitable to ascertain which acalyprate groups conform most closely to basal calyprates in antennal morphology.

The features of the distal surface of segment 2 in typical calyprates (e.g., *Delia*, Figs 159, 160; *Amenia*, Fig. 164) conform in some detail with those of such lower tephritoid families as Piophilidae (see Fig. 126), Lonchaeidae (Figs 127, 128), and Richardiidae (Fig. 129). Main common features include: segment 2 approaching bilateral symmetry, with conus centred on mid-line of distal articular surface, strongly tilted so that dorsal part of its distal surface is scarcely raised above level of distal articular surface, while the ventral part is produced as a prominent chin; foraminal ring and distal foramen narrowly elongate, former produced as an upper and a lower foraminal cusp; button located at lateral side of dorsal extremity of foraminal ring. These examples of Tephritoidea differ from my calyprate examples in that the pedicellar cleft is absent or represented by a shallow notch in the rim. However, a more distinct cleft is present in numerous taxa of Tephritidae and Platystomatidae (classed as “higher tephritoids”), and in the latter family the cleft is often as long and distinct as in typical calyprates (Fig. 152). This is of interest because numerous platystomatid taxa show the squama (lower calypter) larger than in any other acalyprate family (“calyprate” condition). In the past this character combination has occasionally caused species of the platystomatid genera *Achias* and *Euprosopia* to be classed erroneously as calyprates.

Some comparative molecular studies (Vossbrinck & Friedman, 1989; Cameron *et al.*, 2007) have suggested an affinity of the Calypratae to the Ephydroidea (Drosophiloidea). In antennal structure the most marked resemblance between these two groups is the well-developed pedicellar cleft. Otherwise the ephydroid pedicel is very unlike that encountered in the Calypratae. In more plesiomorphic ephydroid forms (e.g., *Campichoeta*, Fig. 74; *Cyrtona*, Fig. 77; *Ephydrella*, Fig. 84) the conus is situated towards the medial part of the rim and is very bilaterally asymmetrical, so that the foramen faces laterally (without any dorsal inclination) and is not narrowly elongate, the chin and foraminal cusps are absent, and the button is less dorsally located. More apomorphic forms (e.g., *Drosophila* s.str., Fig. 80; *Tambourella*, Fig. 81; *Stratiothyrea*, Fig. 88) have the conus sunk into a deep pedicellar cup (scarcely resembling the dorsal recess of calyprates) and remaining asymmetrical in form, a condition very unlike that of any calyprates that I have observed.

For the above reasons it appears that antennal morphology is likely to support an origin of the Calypratae nearer to the Tephritoidea than to the Ephydroidea, but certainly the problem of calyprate origin must ultimately depend on a much broader analysis of evidence.

Greenberg’s plaques and abrasive surfaces on segment 2

Greenberg (1970) and Greenberg & Ash (1972) described small button-like cuticular structures or “plaques” on the external surface of the dorsomedial lobe of the pedicellar rim of some taxa in several calyprate families, including Calliphoridae, Sarcophagidae, Tachinidae, Muscidae, Fanniidae, and Scathophagidae. He also recorded their absence in examined material of *Stomoxys calcitrans* (Linné) (Muscidae), *Nemorilla maculosa* (Meigen) (Tachinidae), and *Drosophila melanogaster* Meigen (Drosophilidae). In their typical form in the Calliphoridae and Sarcophagidae each Greenberg’s plaque bears a minute bulbous setula, which is liable to wear in older flies, and is overlapped by a group of fine microtrichia. I also noted these plaques in *Musca vetustissima* Walker and *Hydrotaea* sp. (Muscidae), but they are apparently absent in *Glossina* sp. (Glossinidae), *Australofannia* sp. (Fanniidae), *Axinia lucaris* Colless (Axiniidae or Rhinophoridae), and *Amenia chrysame* (Walker) (Calliphoridae, Ameniinae). Greenberg & Ash found the plaques apparently not to have an olfactory function, and they appear to be modified macrotrichia in which the membranous socket has become more conspicuous than the reduced setula.

I consider these modifications in the same broad category as the specialized abrasive dorsomedial surface of segment 2 observed in numerous taxa of acalyprate schizophorans. Specially developed spination on this surface, often showing signs of abrasion under high magnification, occurs in *Myopa* sp. (family Conopidae), *Cardiacera carnei* (Paramonov) (family Pyrgotidae, see Fig. 134), in several tephritid genera (Figs 156, 157), in some *Rhytidortalis* spp. (family Platystomatidae, see D. McAlpine 2000), *Dayomyia molens* McAlpine (family Platystomatidae, see D. McAlpine, 2007b), and in *Tethinosoma fulvifrons* Malloch (family Canacidae, formerly in Tethinidae, see D. McAlpine 2007a). Also specimens of *Stratiothyrea* (family Ephydriidae, Fig. 87), *Chyliza* (family Psilidae, Fig. 112), *Senostoma* (family Tachinidae), *Stomorhina* (family Rhiniidae, Fig. 172), and *Syringogaster* (family Syringogastridae, Fig. 114) show signs of abrasion on this surface, though without obvious morphological adaptation.

It is likely that a more thorough survey of schizophoran antennae would reveal evidence of such specialized usage in many additional taxa. The biological significance of the abrasive antennal surface remains unknown.

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