

AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

McAlpine, David K., 1997. Gobryidae, a new family of acalyptrate flies (Diptera: Diopsoidea), and a discussion of relationships of the diopsoid families. *Records of the Australian Museum* 49(2): 167–194. [15 October 1997].

doi:10.3853/j.0067-1975.49.1997.1264

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

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Gobryidae, a New Family of Acalyptrate Flies (Diptera: Diopsoidea), and a Discussion of Relationships of the Diopsoid Families

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ABSTRACT. Relationships among families referred to the superfamily Diopsoidea (or Nothyboidea) are discussed from the evidence of comparative morphology, particular attention being given to the Nothybidae, Psilidae, Syringogastridae, and Diopsidae. Some comments are made on selection of autapomorphies in cladistic methodology. The Tanypezidae and Somatiidae are removed from the Diopsoidea to *incertae sedis*. The new diopsoid family Gobryidae, or hinge flies, is established for the Oriental-Australasian genus *Gobrya* Walker, previously variously associated with the families Megamerinidae, Nothybidae, and Syringogastridae. A key to the families which have been included in Diopsoidea is given. A systematic arrangement of taxa mentioned in the discussion is appended.

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The genus *Gobrya* was described by Walker (1860) in the “Subfam. Psilides” of the family Muscidae. Walker’s only originally included species of *Gobrya* was *G. bacchoides* Walker, from Celebes, Indonesia (type species by monotypy).

Hendel (1913) treated *Gobrya* and his newly described genus *Syrittomyia* in the “Megamerininae”, later raised to family rank as Megamerinidae. He separated *Syrittomyia* from *Gobrya* because of the supposed reduction of the subcosta in the wing of the latter. This, however, was an error, as *Gobrya* consistently has a complete subcosta, and the two names were synonymised by Steyskal (1977). The Megamerinidae have commonly been referred to the superfamily Diopsoidea (subjective synonym Nothyboidea) following Hennig (1958), but D.

McAlpine (1997) transferred the Megamerinidae, excluding *Gobrya*, to the Nerioidae.

Gobrya is known from Taiwan, the Philippines, Malaysia, Indonesia, and New Guinea (Steyskal, 1977; and author’s observations). Steyskal listed five described species of *Gobrya* (loc. cit.), but has generously supplied me with a copy (dated 1967) of a preliminary manuscript key to seven species, two of them undescribed. I have on hand material of four species, at least one of which is not in Steyskal’s key. Hence, there are at least eight species of *Gobrya* in collections. I introduce the common name hinge flies for these insects, in reference to the hinge-like articulation between the thorax and abdomen (compare base of abdomen of *Gobrya*, Fig. 1, with that of *Nothybus*, Fig. 3).

I have collected several specimens of *Gobrya*, including both sexes, on foliage in or at the margin of lowland rainforests in West Malaysia and Papua New Guinea. The immature stages are unknown.

The morphology of *Gobrya* is largely undescribed, and it is the aim of this paper to make known aspects of the adult morphology of this genus, together with that of other taxa that have been referred to the superfamily Diopsoidea or Nothyboidea, in order to throw some light on its phylogenetic relationships.

Morphological terms here used are explained by Colless & D. McAlpine (1991), D. McAlpine (1973), and Harrison (1959). I have tended, where possible, to use traditional terms in preference to terms that suggest doubtful, disputed, or imprecise homologies. Authors of all genera mentioned are given in Table 2.

Notes on cladistic methods

In my discussions of classification systems I have rarely mentioned work published before that of Hennig (1958), because this work, which initiated a modern cladistic approach to classification of Schizophora, superseded nearly everything previously published on the subject. On the other hand, conclusions reached by Hennig in that paper have often subsequently been revised, both by Hennig and other dipterists.

My own treatment of the comparative data does not always lead to the formulation of detailed cladistic hypotheses. Because it is intrinsically improbable that the available morphological data are adequate for or relevant to answering every question in cladistic reconstruction (D. McAlpine, 1996), one should not feel forced to produce a solution to the relationships of every taxon, e.g., by identification of its sister group. I have, however, often indicated where an existing hypothesis rests on a basis which I consider to be scientifically inadequate.

In cladistic analysis, I consider it necessary to apply stringent criteria for the selection of autapomorphies to be cited as the primal evidence for postulating monophyletic taxa. The most reliable apomorphies for this purpose possess the qualities of infrequent arising, a degree of complexity, and relative stability, as indicated by a broad study of related taxa. An apomorphic character state which does not go some way to meeting these criteria, while not providing primal evidence for monophyly of a taxon, may sometimes be deduced to be an autapomorphy of the taxon as a corollary to a theory of monophyly. If secondarily deduced autapomorphies are added to lists of autapomorphies for a hypothetically monophyletic taxon, their inclusion in the evidence for its monophyly leads to circular reasoning and an unjustified degree of confidence in the cladistic hypothesis. The above distinctions are made because of numbers of difficulties with cladistic logic encountered in the literature on higher Diptera. It sometimes appears, where studies have included lists of secondarily deduced autapomorphies in accordance with a particular cladistic hypothesis, that an alternative cladistic hypothesis could

be made to appear equally credible simply by reversing the polarities of selected character sequences (i.e. rededucing them to fit another hypothesis).

The superfamily Diopsoidea (syn. Nothyboidea)

The Nothybidae and Psilidae

Aczél (1955) placed the Nothybidae in a separate superfamily, Nothyboidea, from all other Schizophora, because he thought it was the only schizophoran group with the male postabdomen symmetrical and therefore not circumverted. In this he was mistaken, for in many schizophoran families the male postabdomen (particularly in the more or less reduced protandrial segments 6–8) is symmetrical (e.g., Conopidae, Drosophilidae, Ephydriidae, Lauxaniidae, Psilidae, Teratomyzidae, etc.). The Dolichopodidae, in which the protandrium possesses groundplan asymmetry, includes also forms with secondary symmetry (D. Bickel, pers. comm.). This is no longer taken as evidence of lack of circumversion of the genital segment, at least historically, in these taxa (see Hennig, 1958; Griffiths, 1972).

Hennig (1958) employed the superfamily Nothyboidea to include the families Diopsidae, Nothybidae, Megamerinidae, Tanypezidae, Strongylophthalmyiidae, and Psilidae, although he was unable to find a single apomorphy to establish monophyly of the superfamily. J. McAlpine (1989) recognised the same superfamily concept as Diopsoidea (on grounds of nomenclatural priority), with the addition of Somatiidae and Syringogastridae. J. McAlpine (1989) considered the Diopsoidea and Neriioidea to be sister groups, but I have found no validity in the evidence presented (D. McAlpine, 1996).

Griffiths (1972) used a revised concept of the Nothyboidea to include only the families Nothybidae, Psilidae, Teratomyzidae, and Periscelididae (the last including *Somatia* but not *Cyamops* and *Stenomicro*). I do not find the four stated groundplan apomorphies at all convincing as support for his superfamily concept. Among such a diverse lot of taxa, only unusually distinctive apomorphies can provide acceptable evidence for interrelationships, and these four are very widely distributed among acalyptrate families and undoubtedly subject to convergence.

Griffiths also suggested, but simultaneously queried, a sister group relationship between Nothybidae and Teratomyzidae (1972, fig. 16, and accompanying table), supported by the following three apomorphies (from his more extensive listing for nothyboid families): 1, postvertical bristles reduced; 5, axillary lobe and alula reduced; 7, lower basal cell (bm) open anterodistally. These do not appear to provide a set of primal synapomorphies, because the postvertical bristles, though absent in Nothybidae, are well developed but rather short in the groundplan of Teratomyzidae; the alula is not as much reduced in the groundplan of Teratomyzidae as it is in many other taxa of elongate acalyptrate flies; the cell bm is not open anterodistally in the Teratomyzidae, but

vein 4 has a flexure or weak point in this region. I find such a weakening or flexure in the basal section of vein 4 to be manifested to a variable degree in some taxa of Agromyzidae, Coelopidae, Heleomyzidae, Helosciomyzidae, Pallopteridae, Platystomatidae, Psilidae, Sepsidae, Tephritidae, and Tethinidae. The Teratomyzidae, which have been the subject of a recent study (D. McAlpine & de Keyser, 1994), are widely different from the Nothybidae in their morphology, except for the simplified, symmetrical protandrium; also the aedeagal characters, which Griffiths considered significant for placement in the Nothyboidea, are quite diverse among the teratomyzids and their groundplan conditions for the family are uncertain. I consider that there is no case for considering the Nothybidae and Teratomyzidae to be closely related.

The Nothybidae and Psilidae show some interesting points of morphological resemblance. There is an enlarged postocular bristle laterad of the outer vertical in *Nothybus* and in several psilid genera (so that it may be present in the groundplan of both families). There are, however, some difficulties in establishing homologies of bristles on the upper part of the head in both families, as indicated by Hennig (1958). There is a general resemblance in antennal structure between Nothybidae and Psilidae, but a more detailed resemblance between Nothybidae and *Gobrya*, as indicated below. The anterior notopleural bristle is absent in Nothybidae and Psilidae, as in many other elongate flies (see D. McAlpine, 1997). The apparent groundplan for both Nothybidae and Psilidae includes a secondarily symmetrical male abdominal segment 6 with ventrally placed sternite. The groundplan for both families probably includes a largely membranous distiphallus which is ribbon-like and almost symmetrical.

The most likely synapomorphies for Nothybidae and Psilidae would seem to be in the male postabdominal conditions indicated, the subcircular prothoracic spiracle not largely closed over by intermeshed hairs on its outer lips, and the enlarged postocular bristle. As indications of relationship these seem to conflict with the evidence for relationship between *Gobrya* and Nothybidae reviewed below.

Some of the numerous character states of Nothybidae which differ from those of Psilidae (the latter bracketed) are as follows: (1) distal articular surface of antennal segment 2 facing forwards (facing downwards); (2) lateral arms of ptilinal fissure much abbreviated (moderately long and decurrent on parafacial); (3) prothoracic precoxal bridge extremely broad (absent); (4) subscutellum hypertrophied (not prominent, sometimes vestigial); (5) mesopleural bristle present (absent); (6) pleurotergite setulose, without noticeable pubescence (pubescent, without setulae); (7) tibiae with setulae all aligned in several longitudinal series (tibial setulae irregularly placed); (8) subcosta completely sclerotised distally, terminating in costa close to termination of vein 1 (subcosta desclerotised distally, terminating well before end of vein 1); (9) first and second basal cells partly confluent (completely separated); (10) alula absent

(present); (11) female with spermathecal vesicles (spermathecal vesicles absent, ?consistently). In many of these characters the Nothybid state is apomorphic relative to the psilid state, but the psilids are apomorphic in characters 8 (at least partly) and 11. In characters 1, 5, and 6, polarity is uncertain, and, if Nothybidae and Psilidae are not sister-groups, it may not be reasonable to regard a character state present in one family as necessarily directly derived from that of the other.

An intriguing possibility, which I cannot at present regard as a probability, is the following: the Nothybidae are not closely related to any of the families here placed in the Diopsoidea, but are derived from near the Curtonotidae in the superfamily Ephydroidea (syn. Drosophiloidea). Because I cannot completely refute this idea, I point out some evidence for and against it. The Curtonotidae are considered to include the genera *Curtonotum*, *Cyrtona*, and *Axinota*. The following 13 conditions (a–m) could be considered to give some support to this hypothesis.

(a) The antennal structure of Nothybidae, described above, agrees with that of *Curtonotum* in most details, as it does with most diopsoids (other than Diopsidae).

(b) In Nothybidae and Curtonotidae the external opening of the prothoracic spiracle is subcircular, instead of having the usual narrowly two-lipped conformation. This feature does not, however, give a separation from Psilidae, as mentioned above.

(c) The scutellum in Nothybidae has two pairs of large bristles on its margins. This agrees with Curtonotidae and most other ephydroid taxa, but in the typical diopsoid taxa there is only one large pair of scutellar bristles, the apical pair, and any others are much smaller.

(d) While Nothybidae are noted for the prominently hypertrophied subscutellum, that of *Curtonotum* more nearly approaches the nothybid condition than any other taxon included in the Diopsoidea.

(e) The presence of a mesopleural bristle in Nothybidae is in disagreement with other taxa here placed in Diopsoidea, but one or two mesopleurals are present in many taxa of Ephydroidea, including the Curtonotidae, but not the Drosophilidae. A mesopleural bristle is so widely present among schizophoran taxa, that its presence does not constitute a very particular point of agreement for the above families.

(f) The setulae on the tibiae in Nothybidae and Curtonotidae are arranged in longitudinal rows, a condition present in many other ephydroids. However, this character does not give a good separation from other taxa of Diopsoidea, many of which show a tendency for these setulae to become seriate.

(g) The tarsi of Curtonotidae (least so in *Cyrtona*) are, like those of Nothybidae, remarkably long, slender and subcylindrical. In most other diopsoids the tarsi are either somewhat shorter, in relation to the tibiae, or somewhat more depressed.

(h) The subcosta in Nothybidae, as in *Curtonotum*, is fully developed to its distal termination in the costa very near but quite separate from the end of vein 1. The variations in subcostal development in other diopsoid

taxa do not include these precise features.

(i) In both the Nothybidae and Curtonotidae the anal region of the wing, immediately beyond the alular region, is narrowed, the margin here showing more or less concave curvature, and the much shortened but sclerotised distal section of vein 6 ends at or near the margin. Although basal wing-narrowing occurs in other diopsoid families, it does not follow this pattern. I note here that J. McAlpine (1989) was mistaken in considering vein 7 (A_2) to be visible in this region in both Curtonotidae and Cryptochetidae. The correct identities of the anal veins in these flies, as given by Hennig (1958), become apparent when the curtonotid genera are carefully compared with the less reduced forms of Drosophilidae. The structure in *Cyrtoneura* illustrates the true position of vein 6 and also shows how a secondary spur is liable to misidentification as vein 6 in the Cryptochetidae. I affirm that there is no trace of vein 7 beyond the alular region in any taxon of either Diopsoidea or Ephydroidea.

(j) In both Nothybidae and Curtonotidae there is a convex longitudinal crease of the wing membrane arising just beyond the origin of the distal section of vein 6. This crease is not the homologue of any true vein, and is not known to me in other taxa of Diopsoidea, though there is a trace of it in a few other ephydroid taxa, e.g., Diastatidae.

(k) In the male postabdomen of Nothybidae and Curtonotidae there is a somewhat similar degree of reduction of sclerites of segments 6 to 8, in contrast to the large tergite and sternite 5, with a tendency towards symmetry.

(l) The male genital segment of Nothybidae and Curtonotidae is directed posteriorly, in contrast to that of most taxa of Diopsoidea and Ephydroidea, in which the genital segment is directed ventrally. In the diopsoid family Psilidae there is also a strong tendency for the genital segment to be directed posteriorly.

(m) Pollock (1996) has recorded ovoviviparity in the curtonotid *Cyrtoneura*, a condition which it shares with *Nothybus longithorax* Rondani. This is apparently an infrequently derived condition in acalyptrate taxa, the few other known cases being listed by Pollock. However, it is not known if it is a groundplan condition for either Nothybidae or Curtonotidae.

Of the above arguments, (a), (b), (f), (k), (l), (m) may be seen as rendering relationships of Nothybidae to Ephydroidea as feasible as to Diopsoidea, while (c), (d), (e), (g), (h), (i), (j) may, to varying degrees, be seen as favouring the hypothesis of ephydroid relationships (with particular reference to the Curtonotidae) over that of diopsoid relationships.

The above indications of possible relationship between Nothybidae and Curtonotidae seem to be countered by the following points, (n) to (s), which are more in accordance with diopsoid relationships for the Nothybidae.

(n) The Nothybidae lack the postvertical bristle, vibrissa, and seriate postocular setulae, as in *Gobrya*, Syringogastridae, and Diopsidae. Such a degree of reduction of cephalic bristles is unusual in the

Ephydroidea and not found in the Curtonotidae.

(o) The Nothybidae lack the humeral, anterior notopleural, presutural, and sternopleural bristles. This reduction of thoracic bristles is in disagreement with Curtonotidae and most less reduced ephydroids, but is typical of the Diopsoidea.

(p) The Nothybidae lack the preapical dorsal tibial bristle, characteristic of the Curtonotidae, Diastatidae and many drosophilids, but uniformly absent in Diopsoidea.

(q) The costa in Nothybidae lacks the break at the subcostal position. This condition disagrees with probably all macropterous Ephydroidea, but agrees with the diopsoid taxa other than Psilidae.

(r) In the Nothybidae the basal end of the discal cell is strongly enclosed, but the second basal cell is confluent with the first basal cell because of an extensive break in vein 4. This condition contrasts with that in Curtonotidae, where vein 4 is complete but the basal end of the discal cell is confluent with the second basal cell. In those ephydroids with discal and second basal cells visibly separated, the basal crossvein separating them is generally weakly sclerotised. This difference between Nothybidae and typical ephydroids is most readily explained as an independent derivation of each condition from a plesiomorphic condition with both basal cells completely enclosed by well sclerotised veins, as in the Psilidae. A similar pattern of variation in these cells at a lower taxonomic level occurs in the family Neurochaetidae, where the two different apomorphic conditions distinguishing the genera *Neurotaxis* and *Neurochaeta* have been separately derived from the plesiomorphic condition found in *Anthoclusia* and *Neurocytta* (D. McAlpine, 1993).

(s) the Nothybidae lack the incomplete suture between abdominal tergites 1 and 2, present in the Curtonotidae and other less reduced forms of Ephydroidea. This suture is absent in all typical families of Diopsoidea.

For the above reasons I leave the Nothybidae in the provisional superfamily Diopsoidea. The problem of relationships between Nothybidae and *Gobrya* will be discussed below.

The Syringogastridae and Diopsidae

The neotropical genus *Syringogaster* was generally placed in the Megamerinidae until Prado (1969) erected for it the family Syringogastridae in a detailed taxonomic review. Griffiths (1972) regarded the Syringogastridae as the sister group of the Diopsidae (including Centroncinae), the two families together forming his "prefamily Diopsoinea". J. McAlpine (1989) accepted family status for Syringogastridae, but placed it as a sister group of Megamerinidae (including *Gobrya*), a classification I consider too improbable for further consideration (see D. McAlpine, 1997).

I accept that Syringogastridae and Diopsidae (including Centroncinae) are sister groups on the basis of a different set of synapomorphies from those

given by Griffiths. I review the eight autapomorphies listed by Griffiths (1972) in support of monophyly of the Diopsoinea as follows, drawing comparisons with other families (numbering as given by Griffiths except that characters (2) and (4) are separated into their components):

(1) *Postvertical bristles absent*. This is an apomorphy relative to the plesiomorphic state of Psilidae, but, because the apomorphic state is present in the groundplan of outgroups Nothybidae and *Gobrya*, it cannot be claimed as a primal autapomorphy for Diopsoinea (synapomorphy for Syringogastridae and Diopsidae *sensu* Hennig, 1965).

(2a) *Only one fronto-orbital (ors)... present*. This is perhaps an apomorphy relative to the presence of two pairs of fronto-orbital bristles, which is perhaps a groundplan plesiomorphy for the Psilidae. The outgroup Nothybidae is subject to interpretation as having one, two, or three fronto-orbitals. Doubt as to whether the foremost frontal bristle of Nothybidae is the homologue of a fronto-orbital (supraorbital) bristle arises from its unusual position, but the doubtfully inferred presence of three fronto-orbitals (Hennig, 1958: fig. 54) seems not to rest on any firm evidence. *Syringogaster* has no fronto-orbital bristles, like *Gobrya*, but there is no evidence as to whether the condition in the former was attained by loss of a single such bristle or by simultaneous reduction of two bristles. For these reasons I am doubtful if the inferred presence of one pair of fronto-orbitals in the groundplan of Diopsoinea is an autapomorphy.

(2b) *Only... one vertical bristle (vte) present*. This could be a valid autapomorphy, though its interpretation is disputed by Feijen (1989) on improbable grounds.

(3) *Only one postalar bristle present*. As this condition is present in the outgroups Nothybidae, Psilidae, and *Gobrya*, it cannot be claimed as a primal autapomorphy for Diopsoinea.

(4a) *First and second abdominal terga fused, forming syntergum which is the largest sclerite of the abdomen*. Partial fusion of tergites 1 and 2 is evidently present in the groundplan of the Schizophora. As complete fusion is present in all likely diopsoid outgroups (Somatiidae excluded) this cannot be claimed as an autapomorphy for Diopsoinea.

(4b) *Basal segments of abdomen (especially the second segment) elongate, but distal segments becoming short and wide, so that the abdomen has a petiolate appearance*. This condition is present in the outgroup *Gobrya* and to a varying extent in many elongate acalyptrate flies of various families. In several primitive diopsid genera the condition is only slightly developed. Hence its status as an autapomorphy for Diopsoinea is unconvincing.

(5) *Seventh sternum (male) forming complete ventral band of sclerotisation, fused with inverted eighth sternum on right side...* This may be a genuine autapomorphy but it needs more investigation within the Diopsidae where sternite 7 is variable. The fusion of a ventrally placed sternite 7 with sternite 8 on the right side does not occur in outgroups.

(6) *Seventh and eighth tergum vestiges (male) lost*. This is the condition in all diopsoid families and most other families of Schizophora. It is therefore illogical to give it as an autapomorphy for Diopsoinea.

(7) *Seventh left spiracle (male) lying within seventh sternum*. While this condition may be in the groundplan of Diopsoinea, its presence in *Gobrya*, which otherwise has a rather different protandrium (Fig. 8), precludes its recognition as a primal autapomorphy for Diopsoinea.

(8) *Aedeagus (male) rather short, with a complex distal section which bears lobes or processes*. There is a strong resemblance between the aedeagi of *Syringogaster* and certain diopsids (compare figs 79 and 80 of Griffiths, 1972, and the figures of *Sphyracephala* spp. of Feijen, 1989), even though homology of individual lobes has not been demonstrated. This condition, according to the above general description, occurs also in *Gobrya* (Fig. 12), but not in the investigated taxa of Nothybidae and Psilidae. The evidence suggests that this condition of the aedeagus may be a synapomorphy for *Gobrya* and Diopsoinea, rather than an autapomorphy for Diopsoinea.

Despite the above arguments, I believe that the taxa constituting Griffiths' Diopsoinea together form a monophyletic group as indicated by the synapomorphies for Syringogastridae and Diopsidae set out in Table 1. Four of these, (a) the presence of a supra-alar carina, (b) the cylindrical extension of metathorax, (c) the presence of tarsal sawlines, and (d) the reduction of the inner vertical bristles (together with general cephalic chaetotaxy) call for special comment.

(a) The supra-alar carina (Figs 34–36) is a structure which, within my experience, is peculiar to the Syringogastridae and Diopsidae. It is probably at its most primitive condition in *Centrioncus* (including *Teloglabyrus*, Fig. 35), where it consists of a well-defined ridge on the surface of the mesoscutum passing posterodorsally from the postnotopleural ridge (as defined by D. McAlpine, 1991: 32–33) to the base of the supra-alar bristle. In the Syringogastridae and most Diopsinae the supra-alar bristle is vestigial or absent (probably as a convergent apomorphy in the two groups), but the carina remains. In the Diopsinae (*sensu* Hennig), other than the *Teleopsis* complex (Fig. 36), the supra-alar carina is more extended posteriorly than in the Syringogastridae, so that in these forms which possess a supra-alar bristle (or a secondary hair at the summit of the carina) it lies only slightly in advance of the dorsomedially displaced postalar bristle.

In the genus *Teleopsis* the summit of the supra-alar carina is produced as a large spinous process (the supra-alar spine) and the lower part of the carina is more or less obsolete. This highly apomorphic condition is the only modification known to me in the Diopsoinea involving significant reduction of the supra-alar carina. The supra-alar carina is a quite distinct development from the horizontal lamina formed by the postnotopleural ridge in the Megamerinidae, some Coelopidae (genus *Coelopa*, see D. McAlpine 1991, fig. 7), Curtonotidae (especially *Curtonotum*), some Psilidae (genus *Loxocera*),

and some Platystomatidae (e.g., genus *Giraffomyia*).

(b) The cylindrical posterior extension of the metathorax is found only in the Diopsoinea among the taxa of Diopsoidea and is usually quite short (Figs 38, 39). As a prerequisite to the cylindrical extension, there must be a well sclerotised metathoracic postcoxal bridge to provide support for its lower part. Such a postcoxal bridge is present in all available taxa of Diopsoinea, as in a number of other schizophoran taxa. The upper part of the cylindrical extension is developed from the margin of the metanotum, a sclerite which occurs in most schizophorans as an inconspicuous transversely attenuated rim on the posterior margin of the postscutellum. In the Diopsoinea the metanotum is always somewhat better developed, and in *Syringogaster papaveri* Prado it is remarkably large (Fig. 38). A cylindrical extension of the metathorax similar to that of the Diopsoinea occurs in the platystomatid subfamily Angitulinae.

(c) A tarsal sawline consists of a well defined linear longitudinal series of short, compressed cuneate setulae situated on either the anterior or posterior side of a tarsal segment. The sawline is well differentiated from any other longitudinal series of tarsal setulae, its component setulae being typically shorter and more closely placed, so that it may look like a continuous line under low magnification (Fig. 40). Its setulae usually consist of two kinds, which alternate along its length (Figs 41–43), the larger being longitudinally grooved with the basal socket usually evident, the smaller being almost smooth, arising at a different angle to the larger ones, and without evident basal sockets. However, it should be remembered that the electron micrographs may sometimes fail to show existing basal sockets as they do not indicate more transparent zones of cuticle. Often a larger setula and its distally adjacent smaller setula are set on a common basal prominence as in Fig. 43.

A sawline is present on the mid basitarsus (mid tarsal segment 1) of all diopsidea examined except *Sphyracephala* (*Sphyracephala*) *brevicornis* (Say) and even in the latter there is a loose posterior series of less specialised setulae which are probably homologous with the sawline of other genera. In *Sphyracephala* (*Hexechopsis*) *beccarii* (Rondani) the sawline is identifiable on the posterior surfaces of mid tarsal segments 1 and 2, but is somewhat atypical in consisting of longer, less crowded setulae than in most diopsidea. *Sphyracephala* and *Pseudodiopsis* differ from other diopsidea in the absence of sawlines on the hind tarsus, whereas other genera examined have at least the anterior side of hind tarsal segment 1 with a sawline, except *Centrioncus*, which has well developed sawlines only on the posterior surfaces of hind tarsal segments 1–4. A sawline is present on the fore tarsus (posterior surface of segment 1 only) only in the advanced diopside genera (e.g., *Diasemopsis*, *Cyrtodiopsis*, *Teleopsis*, and *Diopsis*). In *Centrioncus* well developed sawlines are present on the posterior surfaces of mid tarsal segments 1–4 and also extend for most of the length of the mid tibia on the posterior surface.

In the two presently available somewhat morphologically divergent species of *Syringogaster* (*S. papaveri* Prado, Brazil, and *Syringogaster* sp., Costa Rica, see Fig. 40), both anterior and posterior sawlines are present on segments 1–4 of the mid tarsus and anterior ones on the hind tarsus in both sexes, but sawlines are absent from the fore tarsus.

From the distribution of tarsal sawlines in diopsidea it can only be confidently stated that the groundplan for the family includes the presence of a posterior sawline on mid tarsal segment 1. There is a possibility, however, that the groundplan includes a more extensive presence of tarsal sawlines, and, in view of their presence in Syringogastridae, Centrioncinae, and Diopsinae, the reduction of sawlines in *Sphyracephala* is apparently a derived state.

In a non-exhaustive survey of cyclorrhaphous families I have found tarsal structures resembling diopside sawlines to a varying extent only in the Platypezoidea (syn. Phoroidea; families Ironomyiidae, Sciadoceridae, Phoridae, Platypezidae, but not Lonchopteridae; Opetiidae not examined), certain Ephydroidea (syn. Drosophiloidae sensu Hennig, 1958), and in the Glossinidae (superfamily Muscoidea = Calyptrata). The survey revealed some diversity in setation and spination of the tarsi. In some groups there are very loose series of spaced spines. In others the setulae of the basitarsus have a tendency to form several longitudinal series, most conspicuous in Neriidae, Nothybidae, and some calyptrates, but, outside the previously mentioned groups, none shows such a distinct, dense, anterior and posterior series as do the Diopsidae and Syringogastridae.

In the Ephydroidea typical basitarsal sawlines occur apparently only in the Curtonotidae and a number of genera of Drosophilidae. In the Drosophilidae they are not restricted, as has been sometimes supposed, to the subfamily Steganinae but occur also in some species of *Drosophila* (Castro, 1953, and author's observations). They commonly consist of two kinds of processes alternating in each series, as in the Diopsoinea. The tarsal sex-combs present in males of some *Drosophila* species are quite different from sawlines. Other ephydroids (e.g., Diastatidae, Camillidae) have loose longitudinal combs of setulae on the basitarsi, but no sawlines.

The distribution of presence of tarsal sawlines in the Cyclorrhapha suggests that their presence is an apomorphy of infrequent arisal, having probably arisen as few as three times in the Schizophora. Their presence in the groundplans of Diopsidae and Syringogastridae is significant evidence for the monophyly of the Diopsoinea and emphasises its morphological distance from other diopside groups.

(d) The genera *Diopsina* and *Cyrtodiopsis* include several remarkably hirsute diopside species (some well illustrated by Feijen, 1981), having many long setulae on the head, legs, scutellum, and other parts of the thorax and abdomen, some of those on the head and thorax tending to a symmetrical arrangement. Also, in *Pseudodiopsis* there is a linear fringe of setulae on the frontal orbits. In many taxa of Schizophora there are

minor setulae on the orbital plates and elsewhere on the head, but these, for the most part, do not intergrade with true fronto-orbital bristles. In those diopsids with setulae or hairs on the ocellar tubercle their size is similar to and dependent on that of the other frontal setulae, and in *Cyrtodiopsis* they show the same modified apices. However, Feijen (1983) supposes that those setulae which appear to be in the position of ocellar and fronto-orbital bristles are in fact the homologues of these bristles in other dipterous families. On this basis he attributes the presence of a pair of ocellar bristles and of "several" fronto-orbital bristles to the groundplan of both the Diopsoinea and the "Diopsidae" (s.str., i.e. the subfamily Diopsinae of Hennig, 1965), and declines to recognise the two really distinct pairs of cephalic bristles present in many diopsines as homologous with the two pairs present in centricines. The two pairs of cephalic bristles present in the groundplan of the Diopsidae are most logically treated as outer vertical (vte) and fronto-orbital (ors) bristles as indicated by Hennig (1965: figs. 45, 46). Also, it can be stated that, in the groundplan of the Diopsidae, the ocellar bristles are undifferentiated from frontal setulae, though well differentiated proclinate, divergent ocellar bristles are present in the groundplan of Syringogastridae. As the ocellar bristles of Syringogastridae appear to be homologous with those of Psilidae and more remote outgroups, it is probable that their presence is a groundplan plesiomorphy for the Diopsoinea.

In addition to the autapomorphies for the Diopsoinea given in Table 1, the presence of densely microtrichose crazed cuticle on the face is almost certainly a groundplan condition for Diopsoinea, and may be an autapomorphy. It is present, with some variation, in *Centrioncus*, *Sphyracephala*, and *Syringogaster* (Figs 20, 22, 24), i.e. in all major clades of Diopsoinea, or at least in their more "basal" taxa (*Sphyracephala* being a remarkably primitive genus of Diopsinae). The crazed appearance of this cuticle is produced by numerous fine but apparently deep suture-like grooves, with a mainly almost vertical orientation. Some of the grooves appear to widen in an irregular manner, probably through shrinkage of the cuticle in drying. The grooves divide the surface of the cuticle into many vertically elongate plates, most of which bear a single microtrichium each. The scale-like structures on the face of *Syringogaster* are homologised with microtrichia, or at least with their dilated bases, because of their similarity to the facial microtrichia of *Centrioncus* (compare Figs 20, 22).

Because of lack of knowledge of ultrastructure of the face in other acalyptate families, I hesitate to class the presence of densely microtrichose crazed cuticle on the face as a definite autapomorphy of the Diopsoinea, though it may be so.

The parafacial of *Centrioncus*, *Sphyracephala*, and *Syringogaster* has a dense covering of "pubescence", in the first two of similar size to that on the face. However, these parafacial hair-elements differ from those on the face in being wholly or partly socket-based macrotrichia (Fig. 23). (Electron microscopy does not always enable

ready discrimination of macrotrichia from microtrichia as the membranous rings surrounding the bases of the former are distinguishable only if somewhat sunken). I therefore regard the presence of dense, minute parafacial macrotrichia as a groundplan condition of Diopsoinea, but I cannot determine if it is an autapomorphy for Diopsoinea, because it has not yet been demonstrated if the condition is also present in outgroups.

The absence of any dorsocentral bristle is a groundplan apomorphy for the Diopsoinea, judging from the universal absence of such a bristle among the included taxa. I do not, however, treat the condition as an autapomorphy, as it is shared with the outgroup *Gobrya*. Presence of a dorsocentral has been claimed for some diopsids, but this is an error. The large bristle that looks like a dorsocentral in some taxa (e.g., in fig. 61.1 of Peterson, 1987) is the medially displaced postalar bristle, as discussed below.

The pitting along the median ventral suture of the sternopleura in some taxa of Diopsoinea shows some interesting diversity. In *Syringogaster* sp. (Fig. 26), there is a single median series of relatively few, spaced, deep pits, of which the foremost is the largest. The suture is apparent as a dark internal line (therefore not visible in the electron micrograph). The condition in *Centrioncus* spp. is very similar, but the pits are more numerous and crowded. In most Diopsinae the median sternopleural suture is externally apparent as a groove or ridge, sometimes as a narrow ridge lying within a groove. In most diopsine taxa there are no pits associated with this suture, but in *Sphyracephala* sp. (Fig. 27), a somewhat primitive diopsine, there is a series of pits on each side of a slight median ridge.

A possible evolutionary sequence for these structures is as follows. The uniform median groove, representing the median ventral suture in such outgroups as the Psilidae, has become sunken in such a way that it is represented on the surface only by a series of pits (as in *Syringogaster* and *Centrioncus*). A further strengthening of the suture brought about emergence of the suture as a surface ridge dividing the originally uniseriate pits in two (as in *Sphyracephala*). Further modification of the thorax brought about loss of the pits (as in *Cyrtodiopsis*, *Diopsis* etc). In *Gobrya cyanea* there is weak transverse rugosity on the posteroventral parts of the sternopleura (Fig. 25), but this condition cannot form part of the above series, as *Gobrya* lies outside the Diopsoinea phylogenetically.

Because the above sequence is inferred partly from a particular interpretation of phylogeny within the Diopsoinea, it cannot be classed as primal evidence for inferring phylogenetic relationships among the included taxa. It is reasonably certain from their taxonomic distribution that median sternopleural pits occur in some form in the groundplan of the Diopsoinea. Because what appear to be rudimentary sternopleural pits occur in *Gobrya*, I do not list the presence of these pits as an autapomorphy of Diopsoinea.

The assertions of Feijen (1983; 1989), that the (probably upper Eocene) fossil *Prospyracephala* was

a true sphyracephaline contemporary with true diopsines, and that Syringogastridae and Centrioncinae (Centrioncidae in Feijen's classification) are sister groups which separated from each other before the end of the Cretaceous, do not arise from a logical treatment of the available data. In my view, the primary groupings of Diopsidae given by Hennig (1965) are more likely to be phylogenetically valid than either those of Feijen or those of Steyskal (1972).

The family Syringogastridae was well characterised by Prado (1969) and treated as a monophyletic group by Griffiths (1972). J. McAlpine (1989: table 116.2) gave several autapomorphies for the Syringogastridae, but unfortunately treated the remotely related Megamerinidae as the relevant outgroup. Therefore the majority of given character states, though apomorphic in the broader field, are not autapomorphies for Syringogastridae. The following four conditions (a–d) would appear to be distinctive syringogastrid autapomorphies, if they can be confirmed for more species than are at present available to me.

(a) *Pleurotergite, without convex callus*. In outgroups of various levels in the Schizophora there is a convex callus on the pleurotergite, which, in the Diopsinae, bears a cuticular spine, unfortunately termed "metapleural spine" by Feijen (1983).

(b) *Anterior margin of metathoracic spiracle with blunt cuticular spine* (Fig. 29). This is a distinctive syringogastrid condition, not encountered in outgroups.

(c) *Median panel of face with dense covering of scales* (Figs 19, 20). These are probably modified microtrichia (pruinescence) as suggested by comparison with the corresponding surface in *Centrioncus* (Fig. 22), but I have not encountered a similar facial vestiture in my limited studies of other flies under the scanning electron microscope.

(d) *Subscutellum vestigial* (Fig. 31). In most taxa of Diopsoidea there is a distinguishable subscutellum between the scutellum and postscutellum, which forms a convexity separate from that of the latter. A convex subscutellum of variable size is present in the Diopsidae and in *Gobrya* (Fig. 30), but in the available syringogastrids it can be detected only as a linear rim on the dorsal margin of the postscutellum bordering the subscutellar membrane.

As the family Syringogastridae includes a single genus, *Syringogaster*, of limited morphological diversity (Prado, 1969), its monophyletic status seems very probable, though I cannot yet prove that all the above conditions are in its groundplan.

The family Diopsidae has been characterised as a monophyletic group by Hennig (1958) and Griffiths (1972). Because some of the character states given as evidence for monophyly, particularly in the list of Hennig, are not demonstrably groundplan autapomorphies for Diopsidae, I would base my argument for monophyly principally on the following six autapomorphies (a–f).

(a) *Antenna porrect; segment 2 not cap-like, without dorsal slit or seam; segment 3 short, not deflexed, without dorsobasal process fitting into cavity of segment*

2, with arisal insertion not closer to basal than to distal extremity (see Feijen, 1983: figs 4–6). The antenna of Syringogastridae (Figs 17, 18) has much the same complex structure as that of the Psilidae as described below among groundplan characters of Diopsoidea. Also, the arista is bipectinate. These features, with the possible exception of the bipectinate condition of the arista, which is variable in the Psilidae though a consistent condition of Nothybidae and *Gobrya*, are plesiomorphic compared with the contrasting features of the Diopsidae, in which the antenna has more simplified articulation between segments 2 and 3, and more nearly dorsoventrally symmetrical segment 3.

Feijen has reversed the evolutionary polarity of most of these antennal features in the Diopsoidea so far as he has described them, but it must be pointed out that the condition in the most acceptable outgroups to the Diopsoidea is similar to that of Syringogastridae. The strongly dorsoventrally asymmetrical segment 3 with arista inserted dorsally well before mid-length, is very probably a groundplan condition of the Schizophora (and perhaps a synapomorphy for Syrphoidea and Schizophora, Cumming et al. 1995). The condition present (to variable degrees) in typical representatives of the Pseudopomyzidae, Neriidae, Clusiidae, and Diopsinae is almost certainly apomorphic.

(b) *Postalar bristle displaced dorsomedially* (Fig. 35). The Syringogastridae retain the probably plesiomorphic position of the postalar bristle on the lateral surface of the mesoscutum, no higher than the summit of the supralar carina (Fig. 34), as in the outgroups Psilidae, Nothybidae, and *Gobrya*. In the Diopsidae the postalar bristle has moved to a more dorsomedial position and in some taxa has subsequently lost its distinction from the mesoscutal setulae (as in Fig. 36). The degree of displacement of the postalar in *Centrioncus*, though quite noticeable, is less extreme than in other diopsids (subfamily Diopsinae).

(c) *Sockets of major pair of scutellar bristles situated at apices of elongate horn-like processes*. This condition is present in all taxa of Diopsidae, but is absent in all out-groups (e.g., Syringogastridae, *Gobrya*, Figs 30, 31). Setiferous scutellar horns have arisen independently in several families of Schizophora (e.g., Chloropidae, Ephydriidae), but only in the platystomatid subfamily (? or tribe) Angitulinae do they closely resemble those of Diopsidae. This is interesting, because the Angitulinae are also convergent with Diopsoidea in metathoracic structure and the nature of the articulation between thorax and abdomen.

(d) *Fore coxa and femur enlarged (fore leg raptorial)*. This condition in the Diopsidae is accompanied by the presence of short, incrassate, seriate ventral fore femoral bristles of variable distribution. Such bristles are present in outgroups of two different degrees of removal, viz. Syringogastridae and *Gobrya*, but these groups, as well as all other families of Diopsoidea, lack the enlargement and raptorial modification of the foreleg: hence the deduction that lack of the raptorial modification is the plesiomorphic state for Diopsoidea. Somewhat similar

raptorial enlargement of the foreleg to that of Diopsidae has evolved infrequently in other schizophoran taxa, e.g., in *Ochthera* and *Stratiothyrea* (Ephydriidae), *Aragara* (Chloropidae), *Rhinotora* and allied genera (Heleomyzidae), and to a less marked extent in certain sepsids and other taxa.

(e) *Basal crossvein* (*tb*, *bm-cu*, or base of M_{3+4}) *absent*. Among families referred to the Diopsoidea this condition is present only in the Diopsidae. The condition has arisen several times in the Schizophora, mainly in taxa of small body size. Its occurrence is rarer in groups with the size range of Diopsidae, e.g., certain curtonotids, which have probably undergone an increase in size, as evidenced by the smaller body-size in their outgroups.

It is not an aim of this paper to elucidate in detail the internal phylogeny of the Diopsidae, but I note that the characters which are used by Steyskal (1972) and Feijen (1989) to characterise the Sphyracephalini or Sphyracephalinae include no likely apomorphies. *Pseudodiopsis* therefore remains a possibly distinct genus from *Sphyracephala* in my view, as in that of Hennig (1965) and others, because I can find no demonstrable synapomorphies uniting it with *Sphyracephala*. Also, the phylogenetic diagram of Shillito (1971) is not based on principles of Hennigian cladistics.

Feijen (1983) has demonstrated that *Centrioncus* is a polytypic genus, though previously entomologists determined all specimens from many African countries as *C. prodiopsis* Speiser (e.g., Steyskal, 1970a). Feijen has further grouped these *prodiopsis*-like species into two genera, *Centrioncus* s.str. and *Teloglabus*, though the slight differences given in his key, some of them admittedly inconsistent, would hardly seem to justify generic segregation. However, he states that: "*Centrioncus* [s.str.] are characterized as a monophyletic group by the following groundplan conditions, which are apomorphous with respect to the groundplan of the Centrioncidae: (1) Costal cell partly or wholly glabrous. (2) Subcostal cell absent." These character states are also given in his table 4. I have checked these characters for my available specimens of *Centrioncus* (s.str.) *decoronotus* Feijen and three "*Teloglabus*" spp. (from South Africa and Zimbabwe, not readily identifiable from Feijen's key). Among the numerous specimens of *C. decoronotus* there is a little variation in the microtrichiation of the costal cells, but the range of variation among the "*Teloglabus*" spp. is extreme, as indicated in Feijen's own key. These centrioncine flies have a much reduced subcostal cell because of the close proximity of the subcosta to vein 1 over most of its length, and separation of the two veins is best appreciated in anterodorsal aspect. The subcosta touches or almost touches vein 1 on part of the extent of the second costal cell, but has distinct and complete sclerotisation, and, though there is a distal divergence at the pterostigma, the intervening space is partly sclerotised. I am unable to demonstrate a significant degree of difference in my material of the centrioncine taxa in the separation of these two veins. Feijen's study is based on a much larger range of centrioncine taxa than is my present one, but, even with this reservation,

it is apparent that neither of his two stated apomorphies can be logically treated as evidence for accepting a monophyletic group *Centrioncus* sensu Feijen. I therefore recommend that *Teloglabus* Feijen be treated as a synonym of *Centrioncus* Speiser.

Shillito (1971) and Feijen (1989) refer to a median suture-like groove of the facial region of some diopsids as the facial sulcus. A comparison between various diopsid taxa, commencing with the less apomorphic *Centrioncus*, shows that the facial sulcus does not divide the face medially as has been assumed, but that the facial sulcus is actually the face, which has become greatly narrowed in more advanced diopsids (e.g., *Diopsis*, *Teleopsis*) by the encroachment of the more strongly sclerotised parafacial. The supposed absence of the sulcus in species of *Sphyracephala* and *Pseudodiopsis* (Feijen, 1989: p. 68) is due to smaller difference in degree of sclerotisation between parafacial and face and less narrowing of the face in these taxa (see Fig. 23). Differences in degree of development of the facial sulcus among the groups within the genus *Sphyracephala* may have been exaggerated. Among the diverse *Sphyracephala* material available to me, the specimen with the seemingly most distinct facial sulcus is one of *S. brevicornis* (Say) in which the face has collapsed slightly in drying. The distinction between face and parafacial in *Sphyracephala* is demonstrated by the presence of microtrichia on the crazed cuticle of the former (Fig. 24), compared with minute socket-based macrotrichia on the smooth cuticle of the latter (Fig. 23), though this is hard to appreciate without electron microscopy.

The so-called facial teeth of certain diopsids are lobes on the ventral margin of the genoparafacial sclerite, not of the face.

The Tanypezidae

Except in the classification of Griffiths (1972), the Tanypezidae have generally been referred to the superfamily Diopsoidea (or its equivalent under other names). The alternative association between Tanypezidae and "Heteromyzidae" proposed by Griffiths has been discarded (D. McAlpine, 1985) as based on convergent character states or on apomorphies which may date too far back in the phylogenetic history of the Schizophora to be classed as synapomorphies for this particular association. *Heteromyza* and allied genera almost certainly represent a particular development within the tribe Heleomyzini (sensu D. McAlpine) of the Heleomyzidae. Modern authors, following Hennig (1958), have generally considered that the genus *Strongylophthalmyia* forms a monophyletic group with the more typical tanypezids. Following Colless & D. McAlpine (1970) and Griffiths (1972), I prefer to include *Strongylophthalmyia* in the Tanypezidae, despite the obvious differences, because of their close agreement in many structures. Some differences between Tanypezidae and Strongylophthalmyiidae given by J. McAlpine (1989) apply for the separation of New

World forms, but not or less accurately for separation of some Old World species of *Strongylophthalmyia*, which are more morphologically diverse.

The Tanypezidae do not show clear morphological evidence of close relationships to any other family of Diopsoidea, though they provide a mixture of features of several of these families; e.g., the presence of a mesopleural bristle is shared only with Nothybidae, and the presence of a subcostal break in the costa and of divergent postvertical bristles agrees with the groundplan of the Psilidae. The presence of prothoracic precoxal bridges agrees with taxa of several diopsoid families, but the details of shape and contour of the prosternum, with its broad, ventrally exposed bridges, can be very like those of *Gobrya*, particularly in some *Strongylophthalmyia* species. However, as I can find no other significant points of resemblance between *Gobrya* and Tanypezidae, I interpret the resemblance as probably due to convergence.

The tanypezid *Neotanypeza dallasi* (Shannon) and several *Strongylophthalmyia* species have a well differentiated presutural bristle, and the former also has a posterior intra-alar ("inner postalar") and some well developed posteroventral bristles on the distal part of the fore femur. These look like the homologues of the bristles so named in certain taxa of Heleomyzoidea, Neriioidea, Tephritoidea, and other superfamilies, but such bristles do not occur in more typical diopsoid flies. (The true postalar bristle in the Diopsidae approximates in position to the intra-alar in other taxa. See autapomorphy (c) for that family).

The structure and relations of antennal segments 2 and 3 in Tanypezidae are much more like those of many taxa of Neriioidea than of any other Diopsoidea (except for the almost certainly derived condition in Diopsidae). The facial structure is unlike that of any other Diopsoidea and typical of the Neriioidea (e.g., certain Pseudopomyzidae, Neriidae, etc., see D. McAlpine, 1996). The strongly recurved anal crossvein (transverse section of CuA₂ or of CuA) is unlike that of any other diopsoid fly, but is similar to that of the pseudopomyzid genera *Heloclusia* and *Latheticomyia*, which I have regarded as somewhat primitive taxa of Neriioidea. However, no undoubted nerioid fly known to me has a prosternal structure remotely resembling that of Tanypezidae.

In *Strongylophthalmyia* spp. segment 7 of the female has the tergite and sternite fused by elimination of the pleural membrane, but the segment becomes desclerotised posteriorly. In *Tanypeza* (see Steyskal, 1987a: fig. 4) sclerotisation of segment 7 is represented by two pairs of longitudinal strips. Neither of the above conditions is typical of the Diopsoidea, but that of *Strongylophthalmyia* is not far from that of the Neriioidea, in which the tergite and sternite are fused to form an oviscape. The condition in *Tanypeza* may be derived either from that of *Strongylophthalmyia* or from a more plesiomorphic condition in which a separately sclerotised tergite and sternite have each been divided longitudinally.

While I do not claim to understand the relationships of the Tanypezidae to other taxa of Schizophora, were I to make an arbitrary superfamily assignment of the family on the basis of least improbability, this assignment should probably be to the Neriioidea.

The Somatiidae

The Somatiidae are a small probably very uniform family of flies, including only the genus *Somatia* restricted to the Neotropical Region. The species are listed by Steyskal (1970b). Steyskal (1958) made a case for their close relationship to the tephritoid family Richardiidae. J. McAlpine (1989) and Colless & D. McAlpine (1991) treated the Somatiidae as a family of Diopsoidea, and a relationship to the diopsoid family Psilidae has sometimes been accepted (e.g., by Hennig, 1971). Griffiths (1972), however, included *Somatia* in the Periscelididae, and rejected some further historical attempts at determining somatiid relationships. This diversity of opinion is indicative of the difficulty in deciding the systematic position of the Somatiidae within the Schizophora.

The antenna of Somatiidae has the essential features described above for the diopsoid families Syringogastridae and Psilidae. Taxa with these antennal features occur also in the superfamilies Tephritoidea, Asteioidea, Ephydroidea, and Muscoidea (= Calyptrata), as used in the classification of Colless & D. McAlpine (1991), so that further consideration of somatiid relationships will focus only on these superfamilies. The Somatiidae have none of the more distinctive features of Muscoidea so that relationships with this superfamily need not be further considered. The Ephydroidea (syn. Drosophiloidea) probably have as groundplan apomorphies distinct prothoracic precoxal bridges and symmetrical protandrial sclerites. In these features the Somatiidae are too plesiomorphic to have been derived from within the limits of the Ephydroidea, and wide divergence in other characters provides no grounds for suspecting any unusual homoplasy in these characters.

My study of comparative morphology indicates that, in the groundplan of the Schizophora, tergites 1 and 2 are imperfectly separated, that there is a linear transverse membranous zone between these tergites centrally, and a separate visible suture on each side running to the lateral margin where there is a notch or incision. This condition exists in at least some taxa of numerous schizophoran families. Also an oblique internal ridge on each side, running from the lateral suture towards the anterior margin of tergite 1, is present either in the groundplan of the Schizophora or of a substantial part thereof. In *Somatia* there is a long, sharply defined, impressed suture separating tergites 1 and 2 in the medial region, though the membranous line is indistinct; laterally the suture is obsolete, but there is a sclerotised oblique internal ridge on each side. From the relatively few taxa of the family Richardiidae at present available to me (representatives of subfamilies

Epiplateinae and Richardiinae) it appears that total absence of the suture between tergites 1 and 2 is probably a groundplan apomorphy for the family. Therefore *Somatia*, which retains a well marked suture, would not seem to belong within the Richardiidae.

The female postabdomen of *Somatia* (Steyskal, 1958: fig. 3) includes a definite free sternite behind segment 7, and the terminal parts are not fused into an aculeus. These conditions probably provide sufficient evidence for excluding *Somatia* from the superfamily Tephritoidea, to which the Richardiidae belong, even though some richardiids have apparently a (? secondarily) divided aculeus (Steyskal, 1987b). The presence of a large male tergite 6 (Steyskal, 1958; Griffiths, 1972) alone would negate any close relationship to the Richardiidae and allied tephritoid families. The very elongate distiphallus in the male and annular tergosternite 7 in the female of *Somatia* are conditions so frequently acquired in the Schizophora that they can no longer be considered to indicate an affinity with the Tephritoidea. The above considerations induce me to discard any hypothesis of close relationship between the Somatiidae and the tephritoid families.

Returning to a comparison of Somatiidae and the Diopsoidea, the unusually large, neck-like pronotum of *Somatia* is reminiscent of the Diopsidae and Syringogastridae, though detail of the articulation with the occipital part of the head is different. The deeply sclerotised metathoracic postcoxal bridge resembles that of Diopsidae, Syringogastridae, *Gobrya*, and some psilids, but such a postcoxal bridge has been derived many times in the Schizophora, e.g., several times in each of the families Platystomatidae and Tephritidae. It is particularly frequent in elongate flies with deep thorax and often wasp-like form, and is an element of the megamerinoid character set (D. McAlpine, 1997).

The glabrous arista (apart from its long, bipectinate rays) of the Somatiidae (see Fig. 7) contrasts with that of typical diopsoid taxa, which have pubescence on the basal part of segment 6, and on segments 4 and 5 when present. Among the typical diopsoids, only some of the more advanced diopsids show reduction (usually not complete absence) of this pubescence.

The apomorphic loss of the suture between abdominal tergites 1 and 2, apparently in the groundplan of the Diopsoidea, provides a difficulty for inclusion of Somatiidae in this superfamily, just as it does for its placement in the Richardiidae, as mentioned above. The Somatiidae also differ from all more typical diopsoids in the presence of strongly convergent postvertical bristles and a well differentiated cheek bristle (perhaps even to be identified as a vibrissa). The presence of a mesopleural bristle is shared with the Nothybidae and the doubtfully diopsoid family Tanypezidae, but not the Psilidae, the diopsoid family with which the Somatiidae have sometimes been closely associated.

Because the possible synapomorphies of Somatiidae and Diopsoidea are not very persuasive, and because of the above disagreements with the hypothetical groundplan of the Diopsoidea, I think that the

hypothesis of close relationship between the Somatiidae and the Diopsoidea should be discarded.

Of the previously floated hypotheses on somatiid relationship, there remains only the question of affinity with the family Periscelididae. The Periscelididae are placed in the superfamily Asteioidea by Colless & D. McAlpine (1991) and in the suprafamily Asteioinea of the superfamily Opomyzoidea by J. McAlpine (1989). The former authors' Asteioidea and the latter's rather similar Asteioinea are not very strongly supported by cladistic evidence, and each should be regarded as a provisional grouping. There is lack of evidence that the diverse family-group taxa included in Opomyzoidea by J. McAlpine cohere in even a few of the postulated groundplan apomorphies (including three autapomorphies) listed by him. A critical analysis of this grouping is beyond the scope of this paper, but I know of no convincing evidence that these taxa of Opomyzoidea (sensu J. McAlpine) share a common ancestral state of, for instance, "face membranized along vertical midline," or "wing contrastingly patterned." Also, the fate of tergite 7 is unknown for these taxa (it is generally absent in likely outgroups to the Opomyzoidea), and, in the groundplan of some included families, sternite 7 is no more reduced and no more closely fused with sternite 8 than it is in likely outgroups. I therefore cannot recognise any validity in the broad superfamily Opomyzoidea of J. McAlpine, and I adhere provisionally to the separate superfamilies Asteioidea and Opomyzoidea of Colless & D. McAlpine.

Griffiths (1972) regarded the Periscelididae as consisting of the subfamily Periscelidinae (with approximately the same limits as used by Mathis, 1993) plus the genus *Somatia*. His case for monophyly of this family concept relies on five apomorphic conditions (by inference autapomorphies), numbered (1) to (5), which I review as follows:

(1) Anal vein ($cu_{1b}+1a$) abruptly cut off apically, not reaching margin.

This condition occurs in the groundplans of most families of Asteioidea, as well as Psilidae, Syringogastridae, Diopsinae, *Gobrya*, and a very large number of other schizophoran taxa.

(2a) Only one fronto-orbital bristle present.

This is the usual condition for Periscelidinae. The absence of such bristles in *Somatia* could have been achieved either by reduction of a single fronto-orbital or by simultaneous reduction of members of a series. We have no means of deciding which process was the relevant one, unless we first assume derivation from the periscelidine condition, adopting a circular argument.

(2b) ... ocellar bristles standing near ocellar prominence, not between ocelli.

This description seems to refer to the greater distance between the sockets of the ocellar bristles than that between the posterior ocelli. This condition applies to both Periscelidinae and *Somatia*, but is less marked in *Somatia* than in some species of Periscelidinae, in which subfamily there is some variability in the distance between the ocellars. I do not find this degree of

resemblance so distinctive, as compared with that in hypothetically related taxa that retain the ocellar pair of bristles, to convince one of synapomorphy. Most of the more diverse acalyprate families in which ocellar bristles are commonly present show diversity in their placement, and this instability must often result in similarity which is not related to phylogenetic proximity.

(3) 7th abdominal tergum and sternum (female) fused, forming ring which includes the 7th pair of spiracles.

As mentioned above, this condition could be cited to support various relationship hypotheses for *Somatia*. Fusion of tergite 7 with sternite 7 has arisen many times in the Schizophora, and the superfamilies Neriioidea and Tephritoidea are the only major groups with the condition consistently present.

(4) Pregenital sclerite (male) extending ventrally on either side; 7th abdominal spiracles lying within this sclerite.

Actually, in *Somatia* the dorsal pregenital sclerite (apparently fused sternites 7 and 8) extends further downwards on the left side than on the right, because of inclusion of the laterally placed sternite 7. Such a condition is frequently found in the Schizophora as a stage in an often repeated reduction series (see D. McAlpine, 1985; 1988). In *Gobrya* and in numerous similarly reduced taxa the condition occurs with inclusion of one or more spiracles enclosed in the compound sclerite (Fig. 8).

(5) Aedeagus (male) slender and ribbon-like, supported by broad strip of flexible sclerotisation.

The "ribbon-like" or tubular aedeagus of the Periscelidinae is now known to show some diversity (e.g., Mathis, 1993; Mathis & Papp, 1992). As an elongate, flexible tubular or strap-like aedeagus occurs in many families of acalyprate Schizophora (in addition to most tephritoid families), this is not a very particular point of resemblance between Periscelidinae and *Somatia*. Some groups containing species with flexible, strap-like aedeagus also include others with quite different aedeagal structure (e.g., Clusiidae, Teratomyzidae, the heleomyzid tribes Allophylipsini and Gephyromyzini).

I consider that, viewed in the broader field of schizophoran morphology, the supposed evidence for monophyly of the taxon Periscelidinae + *Somatia* does not hold up well.

In the broader concept of Periscelididae accepted by D. McAlpine (1983) and Mathis (1993) there is a distinctive apomorphy of the arista. Segment 5 (primitively the middle segment of the arista) is rather short, very asymmetrical, and reduced on the outer side, and the base of segment 6 is asymmetrically oblique. This structure can be traced through the periscelidid genera *Scutops*, *Periscelis*, *Cyamops*, and *Stenomicroa*. In examined material of *Stenomicroa*, segment 5 has disappeared, but the oblique base of segment 6 is retained. The aristal structure of *Somatia* (Fig. 7) does not fit into this sequence. Segment 5 is more elongate, ovoid, and almost symmetrical; segment 6 is not noticeably oblique at the base and lacks the general tendency seen in periscelidids (also in Nothybidae but

not in Syringogastridae) for the dorsal rays to be crowded towards the base of the segment.

For these reasons I believe that the Somatiidae should not be merged with the Periscelididae. The Somatiidae have several strongly developed apomorphies, which have had a transforming effect on their general morphology, so that it is difficult to establish what the morphology of its lineage must have been before it reached such a degree of specialisation. I am unable at present to adduce a superfamily placement for this family.

The status of the Diopsoidea (Nothyboidea)

As deduced by Hennig (1958), there appears to be a morphologically coherent group of families, which may be termed the Diopsoidea, on the evidence of numerous cross-resemblances between the included families. Included taxa are the Psilidae, Nothybidae, Syringogastridae, Diopsidae, and *Gobrya*, but this coherence does not extend to the Megamerinidae, Tanypezidae, and Somatiidae, as indicated above and by D. McAlpine (1997).

J. McAlpine (1989) gave a list of seven groundplan autapomorphies for the Diopsoidea. I reject this set of character states as conditions that are too widely distributed through major schizophoran taxa to have any value as indicators of particular relationships among the Diopsoidea. Thus, they do not possess the attributes of primal autapomorphies discussed above. I note that the whole set occurs also in the families Pallopteridae, Lauxaniidae, Anthomyzidae, and Drosophilidae, *inter alia*, except that the fate of sternite 7 in the two latter is sometimes unclear (as it is in many diopsoid taxa).

Though the most certain morphological basis for monophyletic taxa is a set of rigorously tested autapomorphies (except where there is a fossil record of extraordinary completeness), I contend that this is an ideal scenario that may be frequently unattainable (D. McAlpine, 1996). It is therefore possible that a group of families may be or may approximate to a monophyletic group without providing clearly indicated groundplan autapomorphies. I suggest that the superfamily Diopsoidea is possibly such a group. It is also a useful category for classifying the component families and data concerning them, especially as strong evidence for relating any of them to families placed outside the Diopsoidea has not been discovered. Two of its component families (Psilidae and Diopsidae) are represented unambiguously in Baltic amber (Hennig, 1965), which is mainly of Upper Eocene origin. The superfamily, if really monophyletic, must therefore have originated very early in the Tertiary, i.e. very early in the history of the Schizophora. Also the comparative morphology of the diopsoid families seems to confirm that the Diopsoidea are a fairly "basal" group of Schizophora, i.e. their earliest members possessed an overall relatively primitive morphology, despite the later acquisition of striking apomorphies among the derived taxa.

The following is a list of groundplan conditions (a–r) for the hypothetical clade Diopsoidea, derived from my study of the included taxa. As they are generally not demonstrable autapomorphies, they do not prove the monophyly of the superfamily. They can have some value as diagnostic characters in so far as included taxa should have a morphology derivable from this character set, rather than in complete agreement with it.

(a) *Body and legs elongate*. This condition is not to be precisely defined, but is more noticeable in the diopsoid families than in most representatives of such other superfamilies as Sciomyzoidea, Ephydroidea etc. Its use as a primal synapomorphy for uniting the Neriioidea and Diopsoidea (J. McAlpine, 1989) cannot be accepted because the elongate habitus has arisen many times in various schizophoran groups, and because it is not well developed in the nerioid groundplan.

(b) *Differentiated frontal triangle (ocellar plate) present*. This is probably a plesiomorphy shared with several other schizophoran superfamilies.

(c) *Face sclerotised*. This is a probable plesiomorphy, and contrasts with the condition in the nerioid groundplan, where the face is desclerotised on its lower median part (D. McAlpine, 1996).

(d) *Vibrissa absent*. Hennig (1958) regarded the presence of a vibrissa as an apomorphy relative to the groundplan of the Schizophora. However, its status may vary in different schizophoran taxa, and present lack of understanding of outgroups for the Diopsoidea makes its status indeterminate.

(e) *Differentiated series of postocular setulae or bristles absent*. In certain representatives of all schizophoran superfamilies recognised by Colless & D. McAlpine (1991), except the highly autapomorphic Brauloidea, there is a linear series of postocular setulae differentiated from other hairs or setulae on the postocular surface of the head. These tend to lose their identity in certain taxa when there is general reduction of cephalic macrotrichia, or when this region becomes covered with long, dense hairs or mollisetae from which the postocular setulae are not differentiated. The taxonomic distribution of uniseriate postocular setulae suggests that their presence is in the groundplan of the Schizophora. I have failed to find a series of postocular setulae in any taxon here referred to the Diopsoidea (after removal of the Tanypezidae and Somatiidae), so that its loss may be a groundplan condition of this superfamily, if it is monophyletic. (*Psila rosae* [Fabricius] has one or two distinct bristles behind each outer vertical bristle, but these are not members of a particular series, and are absent in other available psilids.) The frequency of arisal of loss of the postocular series in the Schizophora, including its loss or reduction in certain taxa of Neriioidea, which have paralleled the morphological tendencies of the Diopsoidea in a number of ways, leads me to doubt its value as an indicator of monophyly for the Diopsoidea.

(f) *Antennal segments 2 and 3 with psilid-like structure, including the following elements: segment 2 has a distodorsal longitudinal slit, and deeply concave*

terminal surface; segment 3 is variably elongate, deflexed at an angle to the axis of the two basal segments, and has a dorsobasal prolongation that fits into the cavity of segment 2; the arista is attached dorsobasally on segment 3. Presence of the structure in outgroups, as discussed above, virtually precludes its interpretation as an autapomorphy for Diopsoidea. The psilid-like antenna occurs in all families here retained in the Diopsoidea except the Diopsidae, where its loss is evidently an autapomorphy from comparison with other diopsoid families, particularly the sister group Syringogastridae.

(g) *Anterior notopleural bristle reduced*. All taxa of Diopsoidea known to me are without the anterior notopleural bristle, except for some species of *Gobrya*, which have a small but well differentiated bristle.

(h) *Presutural bristle (sometimes termed "posthumeral") absent*. This is a consistent condition in the Diopsoidea, but Feijen (1989) misidentifies the posterior notopleural of diopsids as a "presutural bristle".

(i) *Posterior intra-alar bristle (or "inner postalar") absent*. This is a consistent condition in the Diopsoidea.

(j) *Sternopleural bristle absent*. This is a consistent condition in the Diopsoidea, and contrasts with the groundplan condition of Neriioidea (D. McAlpine, 1996).

(k) *Fore femur without series of elongate posteroventral bristles*. In the superfamilies Sciomyzoidea, Heleomyzoidea, Opomyzoidea, Asteioidea, Ephydroidea, Tephritoidea, and Muscoidea (sensibus Colless & D. McAlpine, 1991), also in the primitive nerioid family Pseudopomyzidae, there is commonly a series of long, strong posteroventral bristles on the fore femur. The nearest approach to this condition in Diopsoidea occurs in some Diopsinae, where their degree of development together with outgroup comparison does not convince me of their homology with similarly placed bristles in the above-mentioned superfamilies.

(l) *Preapical dorsal tibial bristle absent*. A single well differentiated preapical dorsal bristle is commonly present on all or some tibiae in the superfamilies Sciomyzoidea, Heleomyzoidea, Ephydroidea, Muscoidea, and much less frequently in the Opomyzoidea. The Diopsoidea are one of the schizophoran superfamilies in which the preapical dorsal bristle is uniformly absent.

(m) *Fore basitarsus without male-restricted terminal ventral process* (see D. McAlpine, 1991: fig. 42; 1996). I have inferred that this process is probably present in the groundplans of the Sciomyzoidea, Heleomyzoidea, and Neriioidea, but I know of no instances of its presence in any other schizophoran superfamily, including the Diopsoidea.

(n) *Second basal and anal cells relatively long, but latter not markedly produced posterodistally*. This condition is a little variable in the superfamily and its range may well include the groundplan condition for the Schizophora. It contrasts with that of numerous families in other superfamilies.

(o) *Vein 7 (2A or A₂) absent without trace beyond alular region*. This condition, consistent within the Diopsoidea, is of fairly frequent arisal in the Schizophora. J. McAlpine (1989) gives it as a synapomorphy for

Diopsoidea and Neriioidea, but the presence of vein 7 in representatives of two subfamilies of the nerioid family Micropezidae negates this interpretation.

(p) *Abdominal tergites 1 and 2 fused, with total loss of intervening suture.* This character is discussed above in connection with the Somatiidae.

(q) *Male tergite 6 relatively large.* This condition may be a plesiomorphy, but distinguishes most taxa of Diopsoidea from many other schizophoran taxa in which tergite 6 is markedly reduced or absent in the male.

(r) *Female abdominal segment 7 with separately sclerotised tergite and sternite.* This plesiomorphic condition contrasts with that of the groundplans of the superfamilies Neriioidea and Tephritoidea.

Relationships of *Gobrya*

The megamerinid hypothesis

Hendel (1913), in including *Syrittomyia* and *Gobrya* in the Megamerininae, defined the latter group on a number of superficial characters, particularly on several of those that I have listed (D. McAlpine, 1997) as the "megamerinoid character set". All seven elements of this set can be identified to some extent in *Gobrya*, as follows: (1) the body form is very elongate; (2) bristling on the thorax is greatly reduced, though some species have both pairs of notopleurals; (3) the base of the wing is much narrowed; (4) the metapleuron and metasternum together form a prominence for insertion of the hind coxae; (5) the metathorax has a deep postcoxal bridge; (6) the hind femur is ventrally spinose and somewhat larger than other femora; (7) the abdomen has a narrow, hinge-like junction with the thorax. Evidence has been provided (D. McAlpine, 1997) that this whole set of apomorphies is subject to simultaneous convergence in numbers of phylogenetically remote taxa, and cannot be relied upon in deducing monophyly.

Hennig (1958) indicated a set of five groundplan apomorphies for Megamerinidae s.l. These included four particular bristle losses, one of them considered doubtful, and the thickened, spinose condition of the hind femur. Of these, loss of the ocellar bristle is not present in some taxa he included in Megamerinidae s.l., and the thickening of the hind femur of *Gobrya* is not nearly as marked as in some other taxa sharing the megamerinoid character set.

Recently (D. McAlpine, 1997) I reviewed a set of characters occurring in Megamerinidae s.str. which suggest relationship to the superfamily Neriioidea. None of these nerioid-like conditions occurs in *Gobrya*. To be specific, *Gobrya* differs from true megamerinids in having a completely sclerotised face, simple, quite short ptilinal fissure, simple antennal socket, reduced and virtually concealed frontal lunule, nothybid- or psilid-like antenna, very extensively sclerotised prosternal region with precoxal bridge, and relatively short female postabdomen. Also the hypandrium and

aedeagus of *Gobrya* is of such completely different structure from that of true megamerinids that none of the distinctive component parts present in the latter can be homologised with any part in *Gobrya*. The one notable feature they have in common, loss of the aedeagal apodeme, does not, therefore, provide a plausible synapomorphy.

I conclude that *Gobrya*, like several other genera of diverse relationships, shows remarkable morphological convergence with the Megamerinidae, but shares no likely synapomorphies with the latter. In view of the numerous significant differences, it is improbable that they are referable to the same superfamily.

The syringogastrid hypothesis

Colless & D. McAlpine (1975) suggested that *Gobrya* "may be related" to the Syringogastridae, and Ferrar (1987) mentioned *Gobrya* under that family without further discussion. As shown above, I consider that the Diopsidae represent the sister group of the Syringogastridae (these two families constituting the prefamily Diopsoinea), but *Gobrya* does not share their distinctive set of synapomorphies (Table 1). This comparison demonstrates that the closest conceivable relationship between *Gobrya* and Syringogastridae would be a sister group relationship between *Gobrya* on one hand and the Diopsoinea on the other, but it does not in itself provide support for such a relationship.

Evidence for relationship between *Gobrya* and Syringogastridae-Diopsidae is difficult to substantiate. The loss of the postvertical and dorsocentral bristles is perhaps such evidence, but loss of the former is shared with Nothybidae, and, in view of the loss of the supra-alar and usual reduction of the postalar bristle also in *Gobrya*, absence of the dorsocentral therein could be interpreted as part of an independent process of general bristle reduction on this region of the thorax. Acquisition of the megamerinoid character set (or most of its elements) is another apomorphy common to both groups, though not necessarily a valid synapomorphy.

Gobrya differs from the Syringogastridae in having the following attributes: ptilinal fissure shortened; parafacial suture obsolete; facial cuticle smooth; upper occiput concave; subcranial region small; antennal segment 2 with recessed terminal surface facing forwards (instead of downwards); arista unsegmented (three-segmented in Syringogastridae, see Figs 16, 18), its series of dorsal rays extending almost to base; precoxal bridge of prothorax very broad, its surface largely facing ventrally; fore coxa not much longer than hind coxa; subcosta complete, distally meeting costa; spiracle of abdominal segment 1 in pleural membrane (not in tergite).

I conclude that evidence for close relationship between *Gobrya* and Syringogastridae-Diopsidae is weak and ambiguous.

The nothybid hypothesis

D. McAlpine (1982) placed *Gobrya* tentatively in the Nothybidae. There are several interesting points of similarity between *Gobrya* and *Nothybus*.

There is remarkably detailed similarity between *Gobrya* and *Nothybus* in antennal structure. In addition to the generally psilid-like features present in the possible groundplan of the Diopsoidea, the arista (strictly antennal segment 6) is bipectinate, with the series of dorsal rays (but not the ventral series) extending almost to its base. The rather similar antenna of the Psilidae and Syringogastridae differs in having the pedicel more cap-like, with terminal articular surface facing ventrally, and no long dorsal rays of segment 6 arising near base of the latter. However, the above conditions of the antenna in *Gobrya* and *Nothybus* exist also in the Periscolidae, and, with a little variation, in Neurochaetidae, Drosophilidae, and other families. In *Nothybus* segment 6 is much more thickened basally than in *Gobrya*, and segments 4 and 5 are well sclerotised but quite short and annular. The latter condition could be an approach towards loss of segments 4 and 5 as in *Gobrya*. For these reasons, I cannot feel certain that the antennal structure of *Gobrya* and *Nothybus* includes synapomorphies.

The facial region of both *Gobrya* and *Nothybus* is well sclerotised and convex, but the contour and proportions are so different in the two genera that it is doubtful if any synapomorphy can be inferred. Again, both genera have the upper occiput concave, but the disagreement in contour of the vertex and arrangement of the bristles of this region renders any synapomorphy uncertain.

Gobrya and *Nothybus* have a large prosternal plate bordered laterally by unusually broad precoxal bridges with extensive ventral exposure. Though there seems a possibility of synapomorphy here, there is a little difference in detail. The posterior part of the sternal plate is raised and medially grooved in *Gobrya*, but almost flat in *Nothybus*. The precoxal bridge of *Nothybus* is even broader than that of *Gobrya*.

Both genera have the ptilinal fissure shortened, without descending lateral arms (Fig. 15). Though there is some variation in the ptilinal fissure among families referred to the Diopsoidea, I can find no other examples where it is as reduced as in *Gobrya* and *Nothybus*. The condition could therefore be a synapomorphy.

Gobrya differs from *Nothybus*, notably, but not exclusively, in having the following morphological conditions: head very broadly depressed; all frontal bristles absent except those at vertex; face and cheek region with extensive ventrally facing surface; ocelli located near vertex; arista unsegmented; prothoracic spiracle vertically elongate; posterior notopleural callus absent; scutellum and subscutellum short; pleurotergite without setulae; the following thoracic bristles much reduced or absent: supra-alar, postalar, dorsocentral, lateral scutellar, anepisternal; metathorax and base of abdomen as in megamerinoid character set; femora not attenuated, with variably developed ventral spines; tarsi

not longer than their respective tibiae; wing with only one (anterodorsal) costagial bristle; male postabdomen strongly asymmetrical in almost all parts; male tergite 6 fused with sternite 8; distiphallus not strap-like; female with fused, annular tergite 6 and sternite 6.

I conclude that, while *Gobrya* and *Nothybus* share several apomorphies (possible synapomorphies), the morphological difference between them is very substantial. Apart from the possible connection between Nothybidae and Psilidae, these differences do not, however, seem to indicate synapomorphies of either genus with any other taxon. While it is conceivable that *Gobrya* and *Nothybus* may be sister groups, any such relationship must be due to a very ancient common ancestry, for which much evidence has been obscured by subsequent morphological change.

Some plesiomorphies of *Gobrya*

In *Gobrya* there is a well differentiated oblique katepimeral sclerite (barette) between the posteroventral margin of the pteropleuron and the anterodorsal part (meron or meropleurite) of the hypopleuron, but separated from the latter by a sharply defined, tympanum-like membranous panel along its entire length (Fig. 28). This panel I designate the katepimeral membrane. Apart from *Gobrya*, no taxon here referred to the Diopsoidea possesses a katepimeral membrane, but it shows a varying degree of development in several other schizophoran superfamilies, including Conopoidea, Sciomyzoidea, Heleomyzoidea, Neriodea, Tephritoidea, and Muscoidea. It is particularly well developed in the Tanypezidae, and narrow but defined in the Somatiidae. I have not detected it in any representative of Aschiza.

This character distribution suggests that the katepimeral membrane may have been acquired early in the evolution of the Schizophora, perhaps even in the stem-group, but has become reduced or lost in many lineages. On this basis the well defined katepisternal membrane in *Gobrya* is probably a plesiomorphy. The absence of the membrane in the other families of Diopsoidea would therefore be an apomorphy, but because the monophyly of the Diopsoidea is uncertain, and because there is variation of development of the membrane in those superfamilies in which it has been detected, this condition may not be a groundplan condition of the superfamily, even supposing that *Gobrya* does not belong here.

At least two undetermined *Gobrya* species (West Malaysia, Australian Museum) have a well-differentiated anterior notopleural bristle. In the other available species (including *G. cyanea* [Enderlein]) there is only the usual posterior notopleural bristle, the anterior one being undifferentiated from the few fine hairs of the region (the 0+1 condition). The 1+1 condition of the notopleural bristles occurs in the groundplans of probably all superfamilies of Schizophora, with the possible exception noted below, and it is probable that this is a homologous condition preserved in the groundplan of *Gobrya*. However, as far as I can ascertain, no other taxon here

considered to belong in the Diopsoidea possesses an anterior notopleural bristle, the 0+1 condition being usual. The consistency of this apomorphic condition in the Diopsoidea would suggest it to be an autapomorphy for the superfamily, but for the difficulty imposed by the apparently plesiomorphic condition in *Gobrya*. Exclusion of *Gobrya* from the Diopsoidea would seem to smooth out this difficulty. On the other hand, reduction of the anterior notopleural is an element of the frequently acquired megamerinoid character set (D. McAlpine, 1997), and, as the various component taxa of Diopsoidea have a strong tendency towards the kind of habitus associated with this character set, convergence in the 0+1 notopleural condition is not deemed highly improbable. Hence exclusion of *Gobrya* from the Diopsoidea on the above grounds seems not to be justified.

While the presence in *Gobrya* of these two plesiomorphies, otherwise uniformly replaced by their corresponding apomorphies in diopsoid taxa, is not regarded as disproof of its postulated diopsoid affinities, it emphasises the distinctness of *Gobrya* from other diopsoid taxa.

Groundplan autapomorphies of *Gobrya* (AA),
contrasted with plesiomorphic states in other
diopsoid families (P)

These are selected as apomorphies not present in the groundplans of the two most plausible outgroups, Nothybidae and Syringogastridae + Diopsidae. Even if these are not the nearest outgroups, and the relationships of *Gobrya* lie elsewhere in the Schizophora, these character states remain as very probable autapomorphies.

(a) Head not broader than high (P)/ head broadly depressed (AA).

(b) One or two fronto-orbital bristles present (P)/ fronto-orbital bristles absent (AA).

(c) Parafacial suture distinct (P)/ parafacial suture obsolete (AA).

(d) Arista 3-segmented (P)/ arista unsegmented (AA).

(e) Postalar bristle (on summit of postalar callus) present (P)/ postalar bristle absent (AA).

(f) Abdominal tergite 1 completely sclerotised anteriorly (P)/ abdominal tergite 1 with deep membranous sinuation in anterior margin (AA).

(g) Male abdominal tergite 6 separately sclerotised (P)/ male abdominal tergite 6 fused with sternite 8 (AA).

(h) Epandrium and surstyli approximately symmetrical (P)/ epandrium and surstyli very asymmetrical (AA).

(i) Aedeagus not fused with hypandrium, at least its basal part approximately symmetrical (P)/ aedeagus rigidly fused with hypandrium, very asymmetrical (AA).

(j) Aedeagal apodeme present (P)/ aedeagal apodeme absent (AA).

(k) Female abdominal segment 6 with separate tergite and sternite (P)/ female abdominal segment 6 with tergite and sternite fused into a complete annulus (AA).

Taxonomic conclusions

Taking into consideration degrees of difference between acalyptrate families in general, the evidence for wide phylogenetic isolation of *Gobrya* from other taxa, and the likelihood of future stability in classification, I consider that the most appropriate course is to place *Gobrya* in a separate monogeneric family. The Gobryidae n.fam. are well supported as a monophyletic group by eleven identified autapomorphies and a low degree of morphological diversity among the included species. The family may be placed in the provisional superfamily Diopsoidea, and, if there is particular (sister-group) relationship to a single diopsoid family, this may be to the Nothybidae, though the evidence for this is ambiguous.

Because of the apparently low morphological diversity and incomplete taxonomic knowledge of the only included genus, a cladistic treatment of the family is not warranted at present.

Gobryidae n.fam.

Type genus: *Gobrya* Walker

Diagnostic description. Fully winged, moderately small, elongate flies, with reduced chaetotaxy and somewhat braconid-like habitus. Head large, somewhat depressed, much broader than thorax; postfrons oblong, its surface entirely occupied by a uniformly sclerotised plate apparently derived from ocellar plate or triangle, with fine setulae at orbital margins; frontal lunule largely concealed; ptilinal fissure short, its descending lateral arms undeveloped; facial region broad, uniformly sclerotised, convex in profile, its lower part extensively facing ventrally; parafacial suture obsolete; upper occiput concave; supracervical region with compact, convex setulose callosity; eye large, much broader than postfrons in dorsal view; ocelli well developed, posterior ones on ridge of vertex; inner and outer vertical bristles present, the former much, the latter slightly behind ridge of vertex; other cephalic bristles absent; membranous subcranial region small, broadly oval. Antenna: segment 1 short; segment 2 short, deeply slit dorsally, with distal surface facing forwards; segment 3 elongate, deflexed at angle to rest of antenna, with dorsobasal process inserted into cavity of segment 2; arista unsegmented, probably through desclerotisation of segments 4 and 5, so that segment 6 appears to arise from a gibbosity on segment 3 a little beyond basal process of latter; segment 6 irregularly bipectinate, with dorsal rays more numerous than ventral ones densely pubescent on basal part. Prelabrum (postclypeus) short and deep; palpus and proboscis moderately developed; labella well developed, reflexed.

Thorax elongate, without neck-like anterior extension; pronotum very short; prosternal region with large basisternal plate, raised and medially grooved posteriorly, with very broad, largely ventrally facing precoxal bridges anteriorly; scutellum short; subscutellum distinct, convex,

but not very prominent; prothoracic spiracle vertically elongate; narrow oblique sclerite (remnant of katepimeron) sharply demarcated from upper part of meron (meropleurite) by a well defined membranous strip; metathorax forming a prominent base for hind coxae, not cylindrically produced at attachment of abdomen (in contrast to Syringogastridae and Diopsidae); postcoxal bridge deep, but deeply sinuate on dorsal side; apical scutellar, posterior notopleural (not on callosity), and sometimes anterior notopleural bristles present; postalar bristle either undifferentiated or small but distinct, located on angle of postalar callus and not dorsomedially displaced (i.e. located as in Syringogastridae, not as in Diopsidae); scutellar bristle inserted on very slight tubercle; other thoracic bristles absent or scarcely differentiated from setulae. Legs of moderate proportions, but markedly increasing in length in the order fore, mid, hind; fore coxa slightly longer than hind coxa, inserted far from anterior end of thorax (but less far than in Nothybidae); hind femur with thickened, spinescent seriate anteroventral and posteroventral bristles; other femora often with less developed ventral spinescent bristles; mid tibia with large apical ventral spur; tibiae otherwise without bristles; fore and mid tarsi much more slender than hind one; basitarsi cylindrical, without series of short cuneate setulae (in contrast to Syringogastridae and Diopsidae). Wing narrow, attenuated basally; tegula very small; anterodorsal costagial bristle usually present but weak; costa extending to vein 4, without break or visible weakening at either humeral or subcostal position, with numerous fine setulae, but no stouter spines or spinules; subcosta complete, well sclerotised, terminating well before end of vein 1 so as to leave a clear subtriangular area of subcostal cell between the two veins; second basal, discal, and anal cells all elongate and complete; distal section of vein 6 well sclerotised but rather short, sometimes reaching approximately to wing margin;

vein 7 indistinguishable beyond alular incision; alula much reduced, with incomplete marginal fringe; squama (lower calypter) quite undeveloped.

Abdomen very slender, with anterior segments forming a slender petiole which is more pronounced in male; abdomen dorsoventrally compressed at its hinge-like articulation with thorax; tergite 1 and sternite 1 with deep membranous sinuation in anterior margin (as component of hinge mechanism, in contrast to that of Syringogastridae and Diopsidae); tergites 1 and 2 quite fused; other preabdominal tergites well separated by intersegmental membrane (in contrast to Syringogastridae); sternites 1 to 5 all separate and well sclerotised; spiracles of segments 1 to 5 all located in pleural membrane, that of segment 1 well removed from margin of tergite.

Male postabdomen. Protandrium with single asymmetrical sclerite, apparently consisting of fused tergite 6 and sternites 6, 7, and 8, enclosing two pairs of spiracles (6 and 7). Epandrium large, asymmetrically subspherical; surstyli separated from margin of epandrium by membrane, very asymmetrical and of unequal size; a separate, undivided, plate-like subepandrial sclerite present between bases of surstyli; hypandrium desclerotised; aedeagus short and broad, with very complex, irregular, asymmetrical sclerotization; aedeagal apodeme absent; ejaculatory sclerite rather small, slender, bent near middle; cerci well developed, separate but attached to sides of proctiger, only slightly asymmetrical.

Female postabdomen short, not markedly extensile. Segment 6 large, with tergite and sternite fused into a complete ring (its form suggesting that it consists very largely of tergite), enclosing spiracle laterally; segment 7 shorter, with separate tergite and sternite and spiracle enclosed in tergite; cerci separate, very broad; spermathecae 3, with pigmented cuticular lining to vesicles (at least in *G. cyanea*).

Key to families which have been associated with the Diopsoidea

1. Antennal segment 2 without narrow dorsal slit in distal margin; segment 3 not deflexed at an angle to basal segments, usually not much longer than deep 2
 - Antennal segment 2 with narrow dorsal slit in distal margin; segment 3 deflexed at an angle to basal segments, usually markedly longer than deep 4
2. Scutellum with pair of setiferous horns; fore leg generally raptorial with enlarged coxa and incrassate femur; second basal and discal cells confluent Diopsidae
 - Scutellum without setiferous horns; fore leg not thus modified; second basal and discal cells separated 3
3. Mesopleural bristle absent; costa not broken or incised at end of subcosta; prothoracic precoxal bridge absent; hind femur incrassate, ventrally spinose Megamerinidae
 - Mesopleural bristle present; costa broken or incised at end of subcosta or its distal vestige; prothoracic precoxal bridge well developed; hind femur neither incrassate nor spinose Tanypezidae
4. Pronotum enlarged and prominent, holding head away from mesothorax 5
 - Pronotum very short, so that head can be held close to mesothorax 6
5. Convergent postvertical bristles present; arista glabrous basally; hind femur neither incrassate nor spinose; abdomen broadly oval; abdominal tergites 1 and 2 partly separated by an impressed suture Somatiidae
 - Postvertical bristles absent; arista pubescent basally; hind femur incrassate and ventrally spinose; abdomen slender; tergites 1 and 2 fused, without visible suture Syringogastridae
6. Ptilinal fissure well developed, with descending lateral arms; prothoracic precoxal bridge absent; postvertical bristles usually present, divergent Psilidae
 - Ptilinal fissure short, without descending lateral arms; prothoracic precoxal bridge broad; postvertical bristles absent 7
7. Fronto-orbital bristles large; arista 3-segmented; hind femur not thicker than mid femur; metathorax without postcoxal bridge Nothybidae
 - Fronto-orbital bristles absent; arista unsegmented; hind femur thicker than mid femur; metathorax with deep postcoxal bridge Gobryidae

ACKNOWLEDGMENTS. I am indebted to the following for help with material, literature and information: A.R. Baptista, P.S. Cranston, N.L. Evenhuis, D. Grimaldi, G.C. Steyskal. D. Bickel constructively reviewed the manuscript. G. Avern produced the electron micrographs. J. Bowley assisted with the illustrations. S. Cowan processed the words. M.R. Gray, Head of Division of Invertebrate Zoology Australian Museum, gave general support to this project.

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Accepted 4 August, 1997

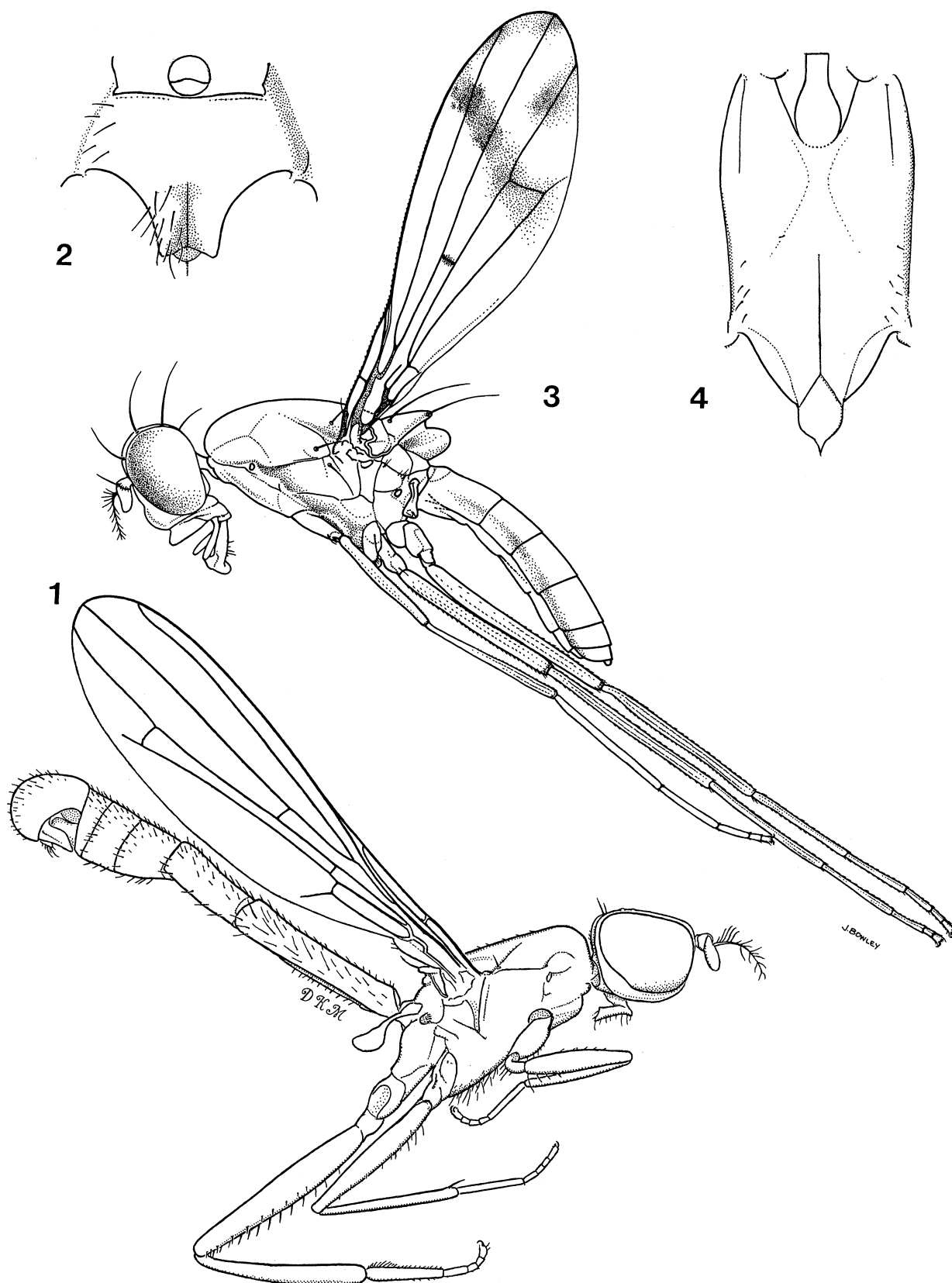
Table 1. Synapomorphies for Syringogastridae and Diopsidae compared with character states of *Gobrya*.

Syringogastridae + Diopsidae	<i>Gobrya</i>
Inner vertical bristle vestigial (though outer vertical retained)	Inner vertical bristle present
Pronotum well developed, projecting well beyond margin of mesoscutum in dorsal view	Pronotum undeveloped (as in most schizophorans)
Supra-alar carina strongly developed	Supra-alar carina absent
Metathorax produced into a short posterior cylinder, articulating with abdominal segment 1; tergite 1 ensheathing cylinder when abdomen is raised	Metathorax not cylindrically produced, tergite 1 with deeply sinuate, non-ensheathing anterior margin
Tarsal sawline present at least on posterior side of mid basitarsus	Tarsi without sawlines
Intersegmental membrane between abdominal tergites 2 and 3 reduced	Intersegmental membrane between tergites 2 and 3 normally developed, enabling overlap of tergites and articulation between segments

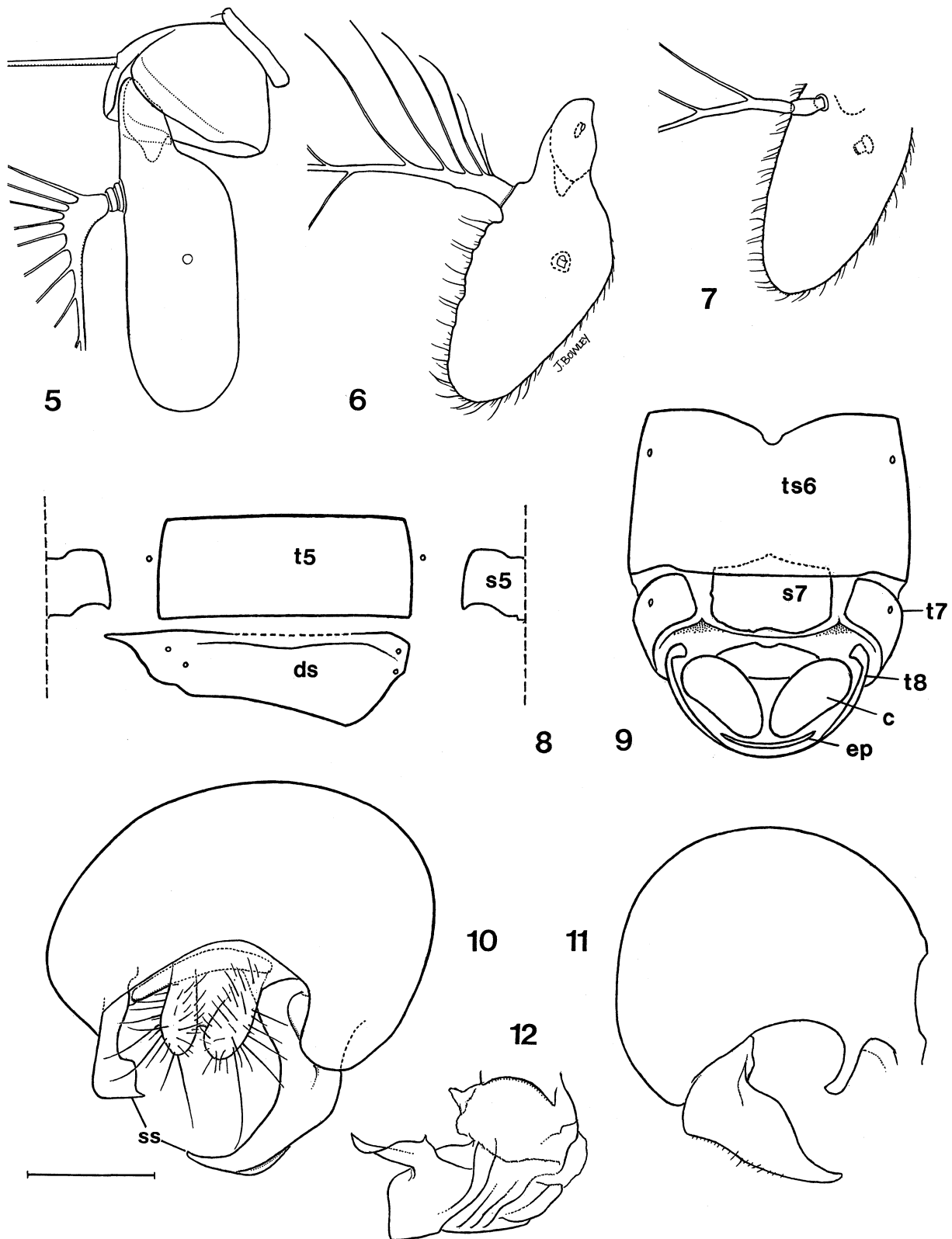
Table 2. Classification of taxa of Diptera-Eremoneura mentioned in text.

SERIES (GRADE) ASCHIZA	Superfamily Chloropoidea
Superfamily Platypezoidea (Phoroidea)*	Chloropidae
?Opetiidae	<i>Aragara</i> Walker
?Lonchopteridae	Superfamily Tephritoidea
Platypezidae	Platystomatidae
Ironomyiidae	Angitulinae
Sciadoceridae	<i>Giraffomyia</i> Sharp
Phoridae	Richardiidae
Superfamily Syrphoidea	Superfamily Asteioidea
Syrphidae	Periscelididae
	Periscelidinae
	<i>Scutops</i> Coquillett
	<i>Periscelis</i> Loew
SERIES SCHIZOPHORA	Stenomicroinae
Superfamily Diopsoidea (Nothyboidea)*	<i>Stenomicroa</i> Coquillett
Ungrouped	Unplaced
Psilidae	<i>Cyamops</i> Melander
<i>Loxocera</i> Meigen	Neurochaetidae
<i>Psila</i> Meigen	<i>Anthoclusia</i> Hennig
Nothybidae	<i>Neurocytta</i> D. McAlpine
<i>Nothybus</i> Rondani	<i>Neurotexis</i> D. McAlpine
Gobryidae	<i>Neurochaeta</i> D. McAlpine
<i>Gobrya</i> Walker (<i>Syritomyia</i> Hendel)*	Teratomyzidae
Diopsoinea	Superfamily Ephydroidea
Syringogastridae	Drosophilidae
<i>Syringogaster</i> Cresson	<i>Drosophila</i> Fallén
Diopsidae	Curtonotidae
Centrioncinae	<i>Axinota</i> Wulp
<i>Centrioncus</i> Speiser (<i>Teloglabus</i> Feijen)*	<i>Cyrtona</i> Séguy
Diopsinae (Sphyracephalinae)*	<i>Curtonotum</i> Macquart
<i>Prosphyracephala</i> Hennig	Diastatidae
<i>Sphyracephala</i> Say	Ephydridae
<i>Pseudodiopsis</i> Hendel	<i>Ochthera</i> Latreille
<i>Diopsina</i> Curran	<i>Stratiothyrea</i> de Meijere
<i>Diasemopsis</i> Rondani	Cryptochetidae
<i>Cyrtodiopsis</i> Frey	Superfamily Muscoidea (Calyptratae)*
<i>Teleopsis</i> Rondani	Glossinidae
<i>Diopsis</i> Linné	Superfamily Uncertain
Superfamily Sciomyzoidea	Tanypezidae (Strongylophthalmyiidae)*
Coelopidae	<i>Tanypeza</i> Fallén
<i>Coelopa</i> Meigen	<i>Neotanypeza</i> Hendel
Superfamily Heleomyzoidea	<i>Strongylophthalmyia</i> Heller
Heleomyzidae (Heteromyzidae)*	Somatiidae
Heleomyzini	<i>Somatia</i> Schiner
<i>Heteromyza</i> Fallén	
Rhinatorini	
<i>Rhinotora</i> Schiner	
Superfamily Nerioidae	
Pseudopomyzidae	
<i>Heloclusia</i> Malloch	
<i>Latheticomyia</i> Wheeler	
Micropezidae	
Megamerinidae	

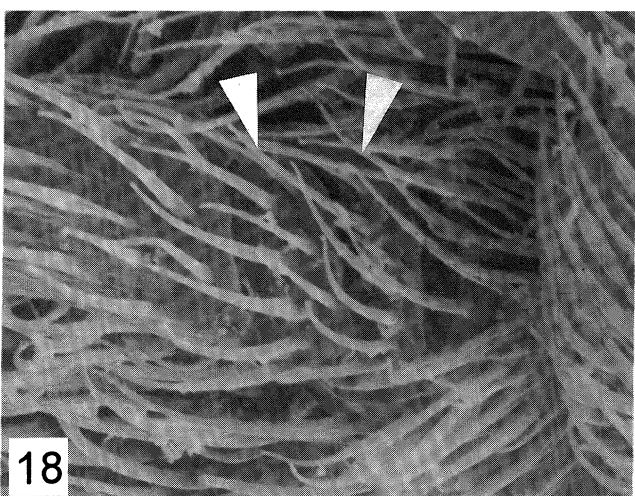
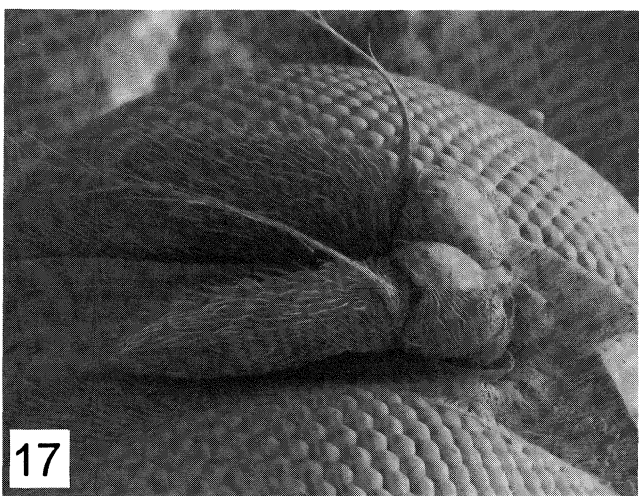
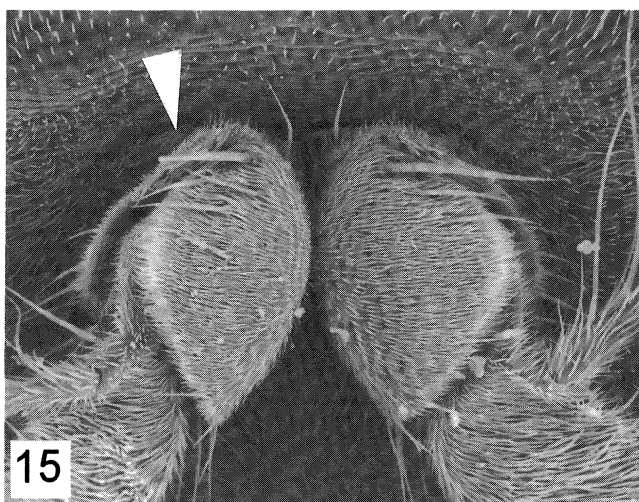
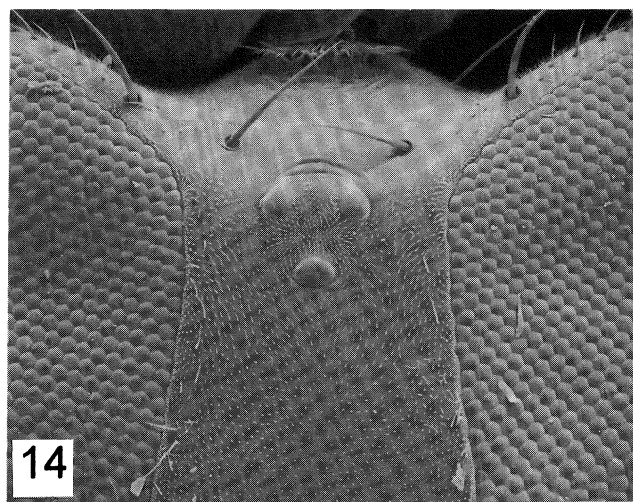
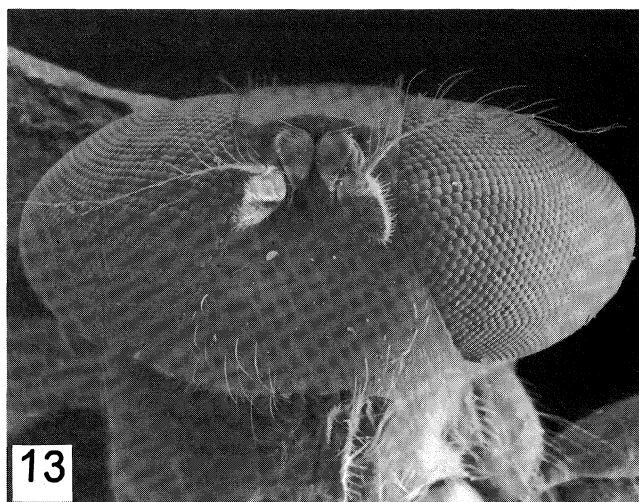
* Names in brackets are treated as synonyms.



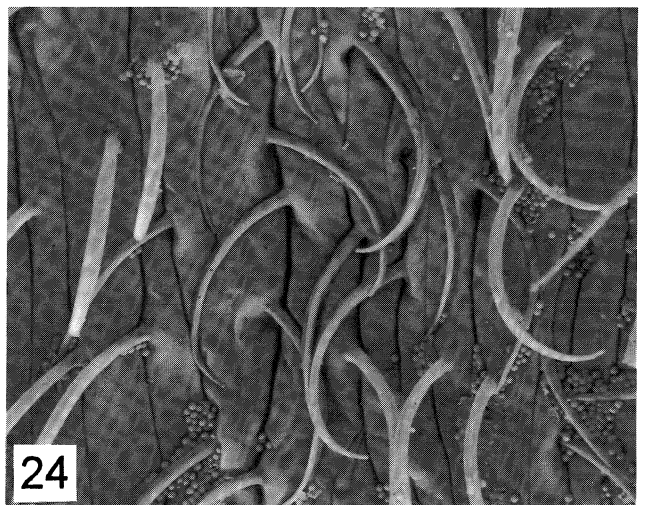
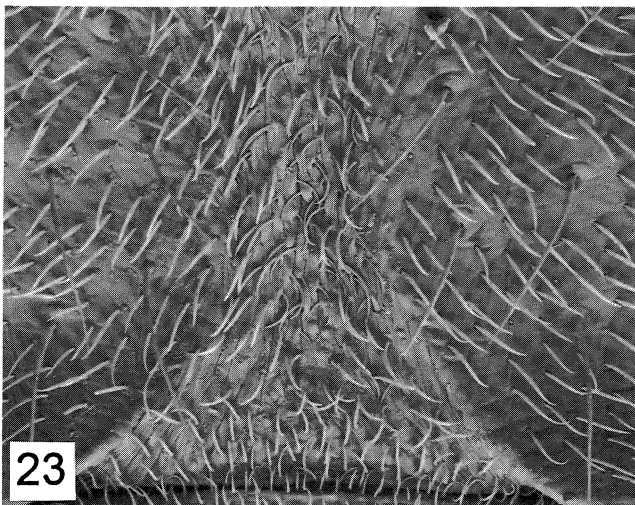
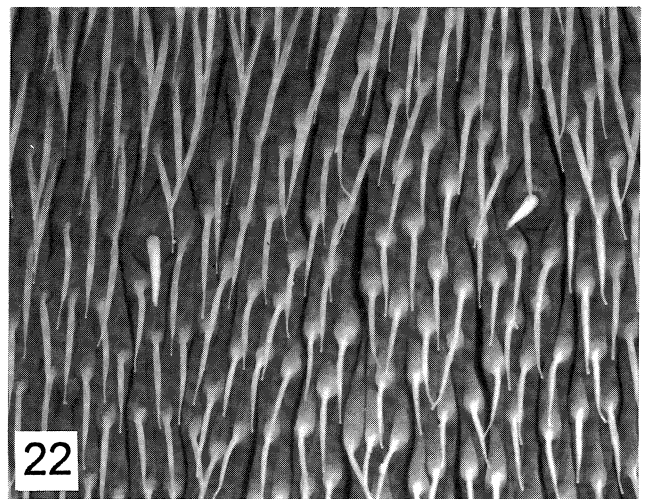
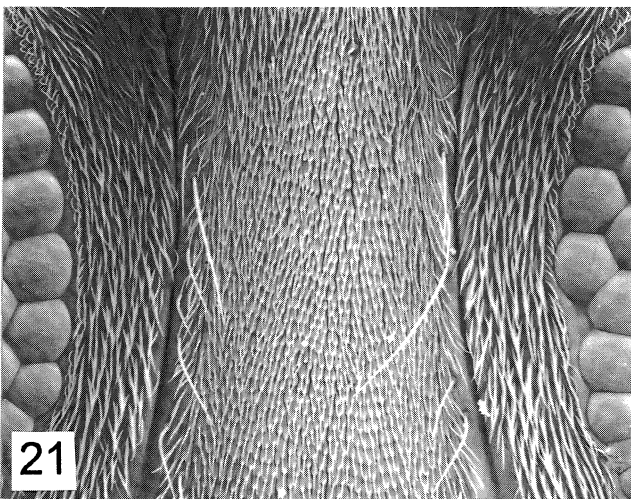
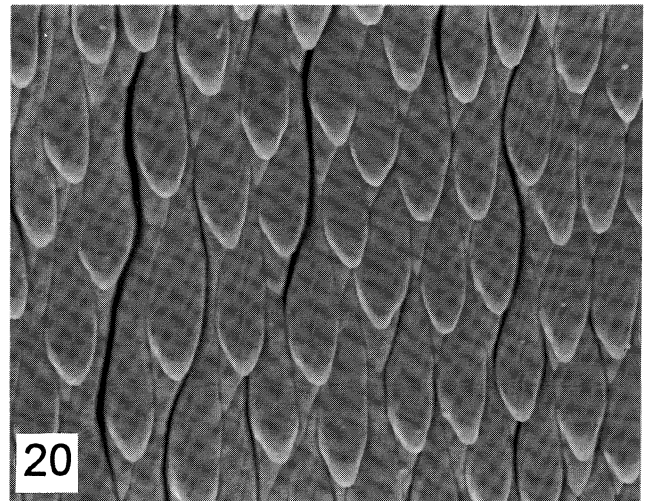
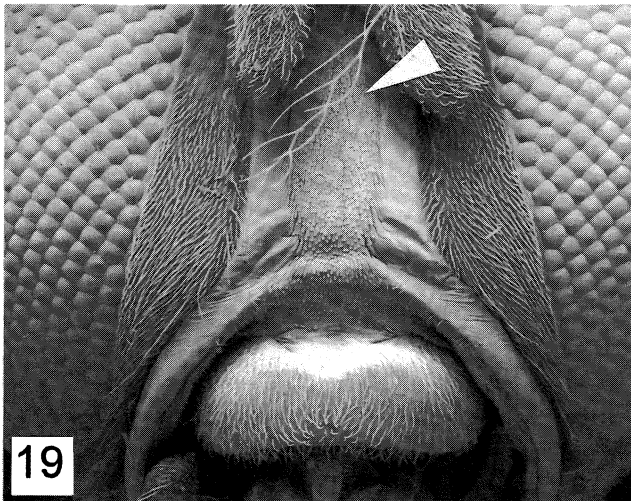
Figs 1–4. 1, *Gobrya cyanea* (Enderlein), adult male. 2, *G. cyanea*, prosternum. 3, *Nothybus decorus* de Meijere, adult female. 4, *N. decorus*, prosternum.



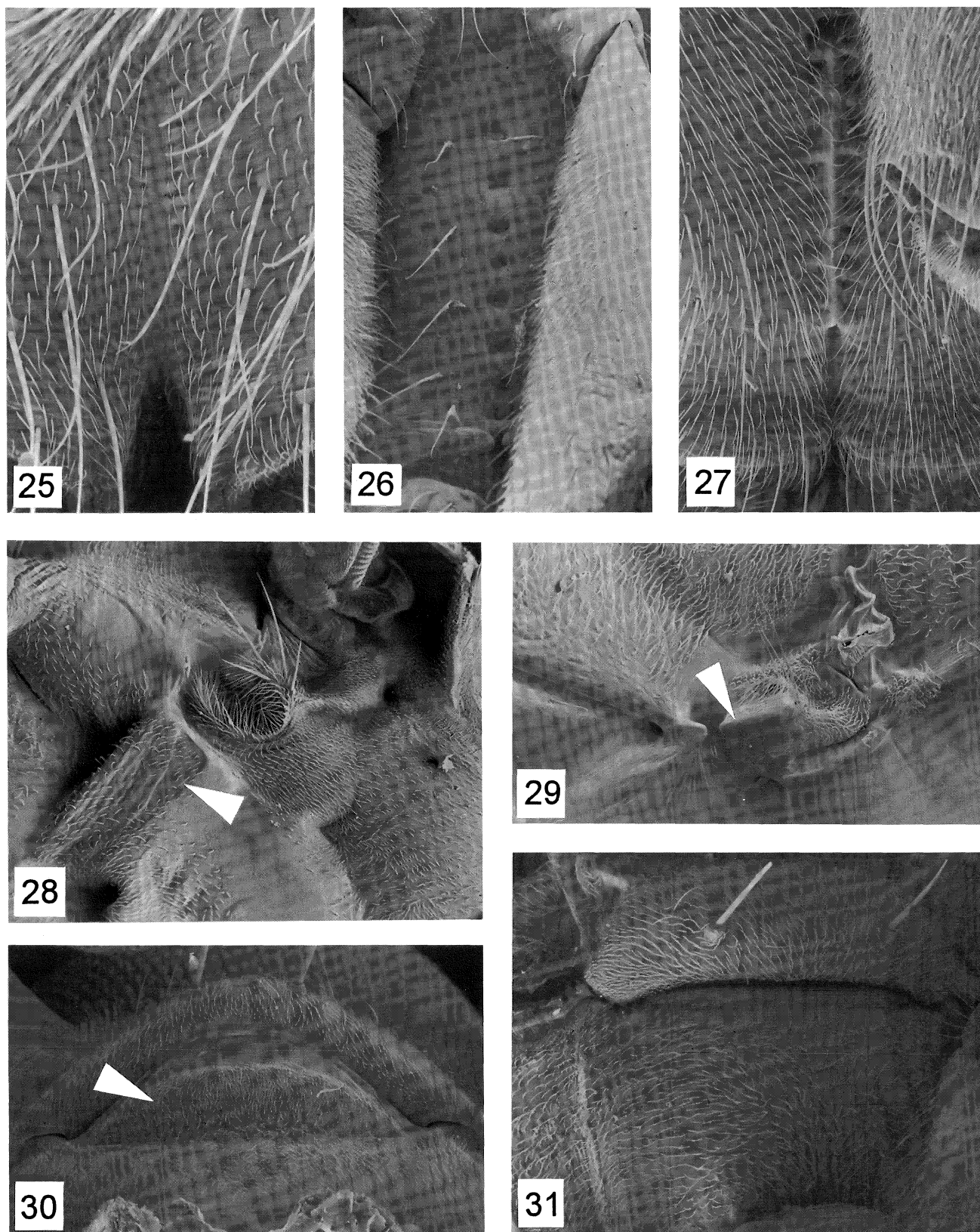
Figs 5–12. 5, *Nothybus decorus*, left antenna, vestiture and arista (segment 6) simplified. 6, *Gobrya cyanea*, antennal segments 3–6 (note absence of segments 4, 5). 7, *Somatia aestiva* (Fabricius), antennal segments 3–6. 8, *G. cyanea*, protandrogram (sclerites of segments 5–8 of male abdomen shown as if split along median ventral line and spread flat). 9, *G. cyanea*, female postabdomen, ventral view. 10, 11, *G. cyanea*, epandrium and associated structures, posterior and right lateral views. 12, *G. cyanea*, aedeagus, right lateral view. c, cercus. ds, compound dorsal sclerite probably including tergite 6 and sternites 6 to 8. ep, epiproct. s5–s7, sternites 5–7. ss, surstyli. t5–t8, tergites 5 to 8. ts6, tergosternite 6.



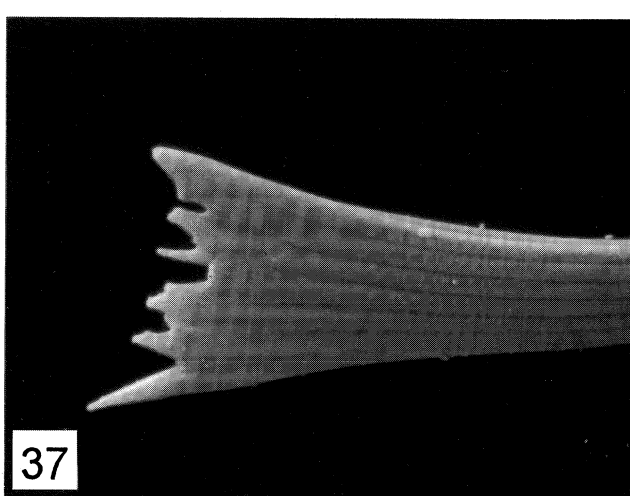
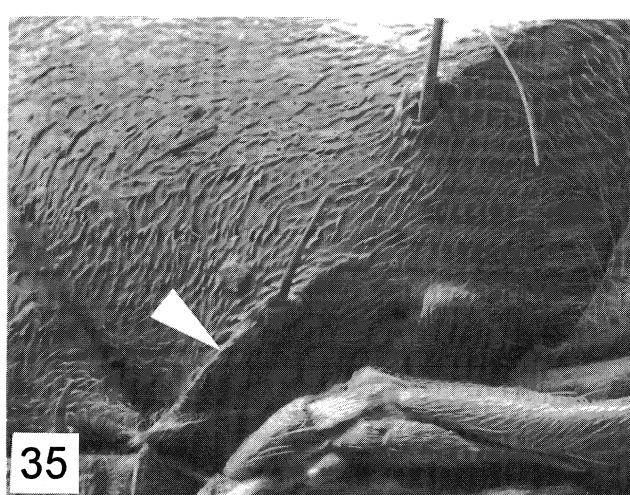
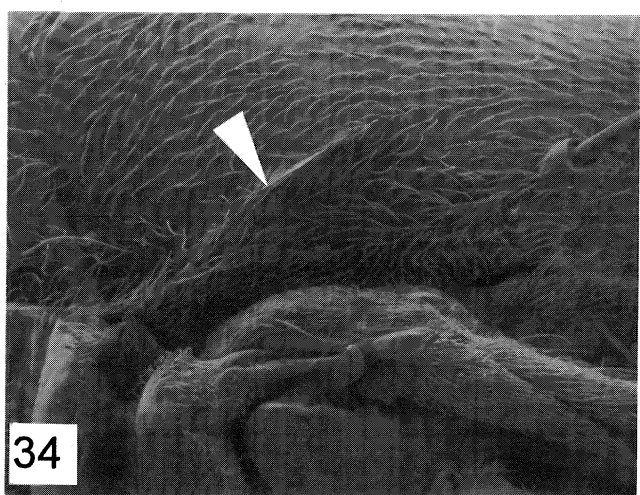
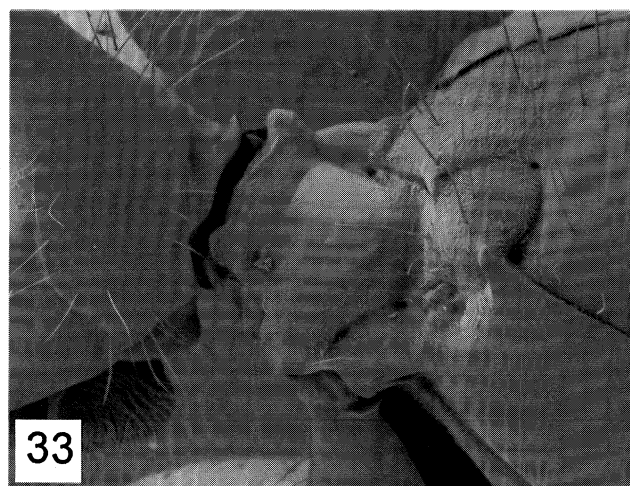
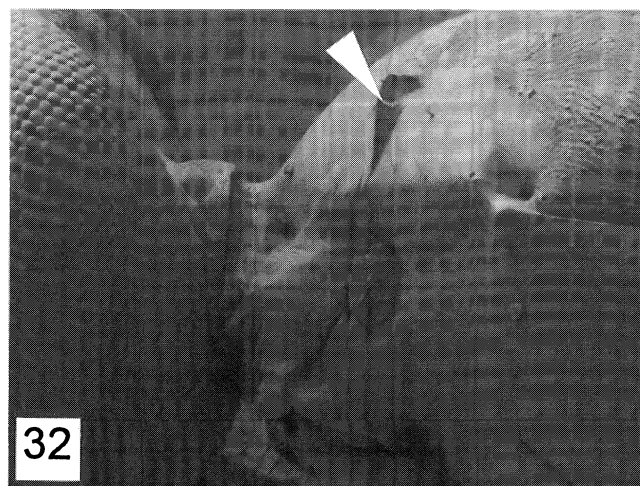
Figs 13–18. 13, *Gobrya cyanea*, head, facial view $\times 50$. 14, *G. cyanea*, vertical region of head $\times 105$. 15, *G. cyanea*, region of antennal bases $\times 249$, ptilinal fissure indicated. 16, *G. cyanea*, base of arista $\times 800$, showing direct insertion of segment 6 into socket of segment 3. 17, *Syringogaster* sp. (Costa Rica), facial region of head and antennae $\times 144$. 18, the same base of left arista $\times 1990$, segments 4, 5 indicated.



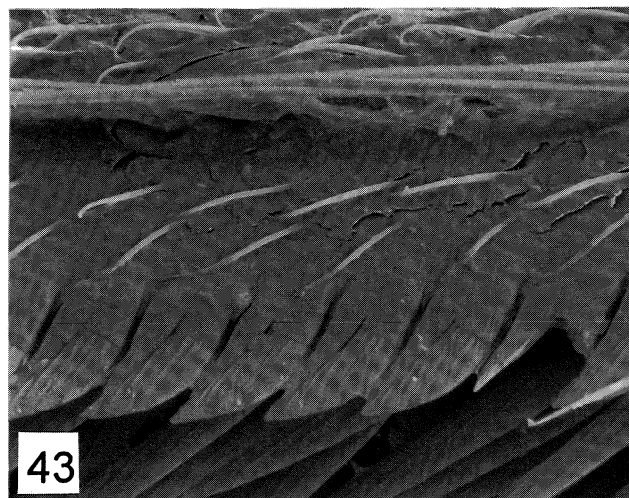
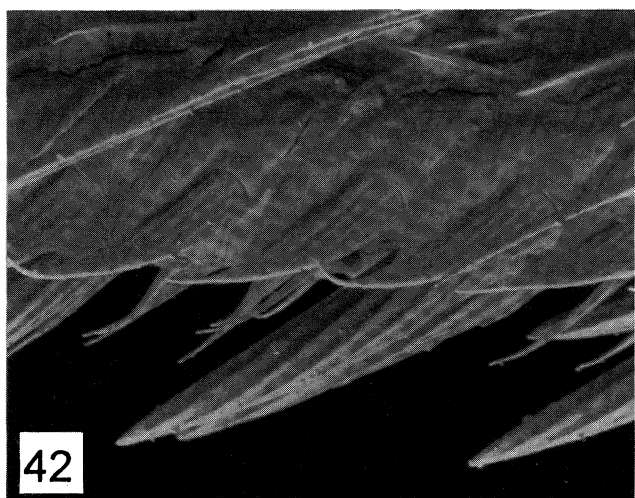
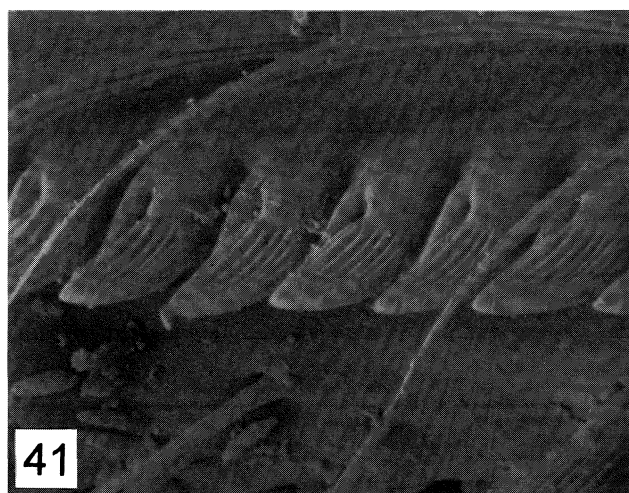
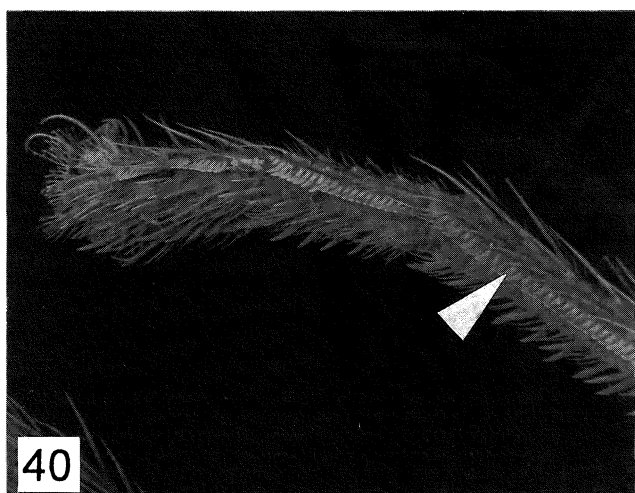
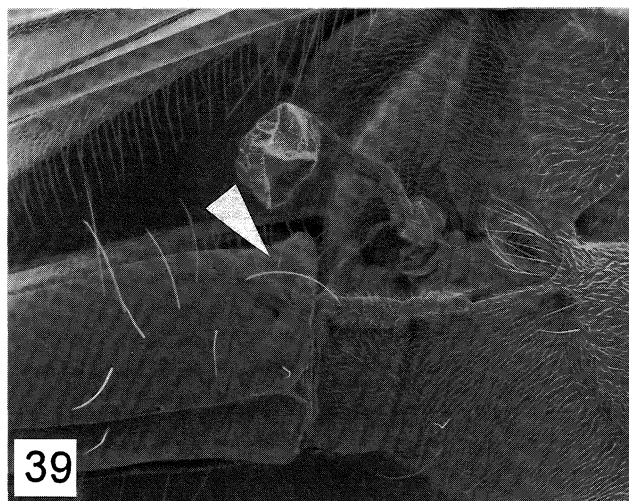
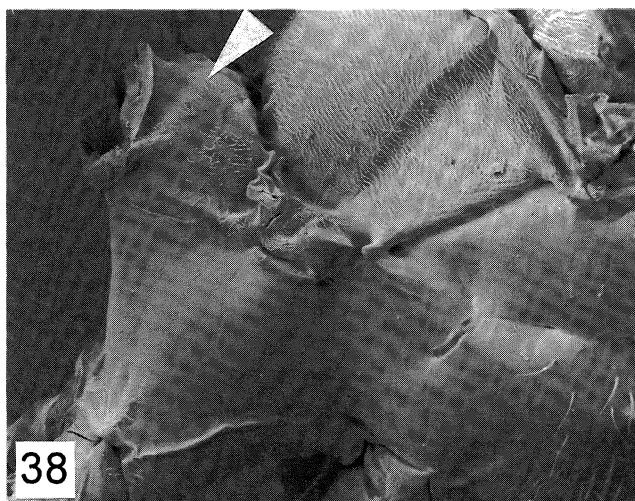
Figs 19–24. 19, *Syringogaster* sp. (Costa Rica), lower facial region $\times 138$, scaly central section indicated. 20, *Syringogaster papaveri* Prado, scaly crazed cuticle of face $\times 2350$. 21, *Centrioncus decoronotus* Feijen, mid facial region $\times 231$. 22, *C. decoronotus*, detail of central section of face $\times 1075$, showing microtrichose crazed cuticle and a pair of macrotrichia. 23, *Sphyracephala beccarii* Rondani, lower part of face and parafacials $\times 436$. 24, *S. beccarii*, microtrichose crazed cuticle of face $\times 2140$.



Figs 25–31. 25, *Gobrya cyanea*, median ventral region of sternopleura $\times 358$, showing rugosity (? incipient sternopleural pits). 26, *Syringogaster* sp. (Costa Rica), median ventral region of sternopleura $\times 185$, showing single median series of pits. 27, *Sphyracephala beccarii*, median ventral region of sternopleura $\times 235$, showing double series of pits. 28, *G. cyanea*, part of left side of thorax $\times 165$, showing metathoracic spiracle, katapimeral membrane indicated. 29, *Syringogaster papaveroi*, same part of thorax $\times 162$, haltere removed, cuticular spine indicated. 30, *G. cyanea*, scutellum and postscutellar structures $\times 149$, subscutellum indicated. 31, *Syringogaster* sp. (Costa Rica), same parts $\times 127$, subscutellum obsolete.



Figs 32–37. 32, *Syringogaster* sp. (Costa Rica), anterior part of thorax and occiput $\times 100$, humeral lamella indicated (absent in *S. papaveroi*). 33, *Cyrtodiopsis* sp. (W. Malaysia), same parts $\times 62$. 34, *Syringogaster* sp. (Costa Rica), left supra-alar region of thorax $\times 234$, supra-alar carina indicated, postalar bristle at right. 35, *Centrioncus decoronatus*, same parts $\times 138$, supra-alar carina (with supra-alar bristle) indicated, postalar bristle at upper right. 36, *Cyrtodiopsis* sp., same parts $\times 117$, supra-alar carina indicated, bristles not differentiated from modified hair-like macrotrichia. 37, *Cyrtodiopsis* sp., apex of modified macrotrichium of mesoscutum $\times 2810$.



Figs 38–43. 38, *Syringogaster papaveroi*, metathoracic region, right lateral view $\times 75$, abdomen and haltere removed, secondarily enlarged metanotum indicated. 39, *Cyrtodiopsis* sp., metathoracic region and base of abdomen $\times 79$, abdominal tergite 1 (indicated) concealing metanotum. 40, *Syringogaster* sp. (Costa Rica), mid tarsus, anterior view $\times 221$, sawline indicated. 41, the same, detail of sawline on mid basitarsus $\times 2250$. 42, *Centroncus decoronotus*, part of posterior sawline of mid basitarsus $\times 1740$. 43, *Cyrtodiopsis* sp., the same $\times 1485$.