Relationships of the Megamerinidae

(Diptera: Nerioidea)

With 5 figures

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Summary

The recent Megamerinidae are here restricted to the genera *Megamerina* RONDANI and *Texara* WALKER. A more inclusive concept of the Megamerinidae (sensu HENDEL) is characterised by a set of 7 apomorphic character states. This set is shown to have been separately derived almost in its entirety as a convergent cluster in 10 different schizophoran taxa, other than those included by HENDEL. The set therefore has little phylogenetic significance. Though the Megamerinidae are often placed in the superfamily Diopsoidea (subjective syn. Nothyboidea), morphological evidence is presented to indicate a closer relationship to the Nerioidea. The relationships of the fossil and Recent genera are considered.

Zusammenfassung

Den rezenten Megamerinidae werden lediglich die Gattungen *Megamerina* RONDANI und *Texara* WALKER zugeordnet. Nach einem weitergefaßten Konzept (sensu HENDEL) ist die Familie durch 7 Apomorphien charakterisiert. Es wird jedoch gezeigt, daß diese von geringer phylogenetischer Bedeutung sind, da sie sich fast allesamt und in derselben Kombination konvergent in 10 verschiedenen Taxa der Schizophora herausbildeten, die von HENDEL nicht den Megamerinidae zugeordnet wurden. Obwohl die Megamerinidae oft zu den Diopsoidea (subjektives Synonym: Nothyboidea) gestellt werden, weisen morphologische Merkmale auf eine nähere Verwandtschaft zu den Nerioidea hin. Die Verwandtschaftsbeziehungen fossiler und rezenter Gattungen werden untersucht.

Introduction

This group was set up as a subfamily, Megamerininae, of 'Acalyptrate Musciden' by HENDEL (1913) and BEZZI (1913). It is apparent that this parallel action arose from correspondence, as both authors included the genera *Texara* WALKER, 1854, *Syringogaster* CRESSON, 1912, *Syrittomyia* HENDEL (as nov. gen. in 1913), *Gobrya* WALKER, 1860, and the type genus *Megamerina* RONDANI, 1861 (syns. *Lissa* MEIGEN, 1826; *Lissodema* BLANCHARD, 1845, syn. nov.; both junior homonyms, see HENNIG 1941). The Megamerinidae were given family rank by HENDEL (1916, as Megameridae). HENNIG (1965) added the Tertiary fossil *Palaeotanypeza spinosa* MEUNIER.

Although HENNIG (1965) regarded the Megamerinidae s.l. as an indubitably monophyletic group, PRADO (1969) removed *Syringogaster* to the Syringogastridae. GRIFFITHS (1972) and J. MCALPINE (1989) discussed the relationships of the Megamerinidae and concurred with PRADO's action, but neither was familiar with the morphology of *Gobrya*. COLLESS and MCALPINE (1970) indicated that the location of *Gobrya* (syn. *Syrittomyia*) in the Megamerinidae was 'erroneous', and later (1991) doubtfully referred it to the Nothybidae. The placement of *Gobrya* is reconsidered by D. MCALPINE (in press B), but only the genera *Megamerina* and *Texara* are retained in the Megamerinidae. The Megamerinidae s. str. are a very small family of very low morphological diversity occurring only in the Palaearctic and Oriental Regions.

For purposes of discussion, the superfamily Diopsoidea provisionally includes the families Syringogastridae, Diopsidae, Nothybidae, Psilidae, and perhaps Somatiidae and Tanypezidae, as well as the genus *Gobrya* WALKER. The superfamily Nerioidea (syn. Micropezoidea) includes the Cypselosomatidae, Micropezidae, Neriidae, and Pseudopomyzidae, to which are added the Megamerinidae.

Problems in delimitation of Megamerinidae

The family Megamerinidae sensu HENDEL has a consistent set of characters (not all mentioned by HENDEL), obviously apomorphic in relation to the groundplan of Schizophora, as follows: (1) body form elongate; (2) bristles on anterior part of thorax (generally including humeral or postpronotal, anterior notopleural, presutural, anterior dorsocentral) absent; (3) wing narrowed basally; (4) metapleuron and metasternum together forming prominent base for attachment of hind coxae; (5) metathorax with deep postcoxal bridge; (6) hind femur enlarged and ventrally spinose; (7) abdomen narrowly attached to thorax, effectively hinge-like at junction. HENNIG (1958; 1965) also emphasised the loss of the ocellar bristle as an apomorphy of the Megamerinidae. In view of the occurence of this condition in a number of other Diopsoidea (sensu COLLESS and MCALPINE 1991; subjective synonym Nothyboidea) and Nerioidea, and the presence of the bristle in some *Syringogaster* species, I am not including it in this set.

On the face of it, this combination of apomorphies (hereafter termed the megamerinoid character set) looks like good evidence for monophyly, but consideration of the morphology of other taxa does not support the case. Each of the following 10 schizophoran taxa (a-j) has a large number of elements of the megamerinoid character set, but due consideration of the relationships of these taxa indicates an independent arisal of the set in each. Many other taxa have evolved smaller numbers of the megamerinoid elements, and the following list of taxa is probably incomplete. (a) The genus *Nestima* OSTEN SACKEN, 1881, (Micropezidae) has all elements, except that (6) is only slightly developed and the anterior notopleural bristle is present. (b) *Richardia tephritina* ENDERLEIN, 1912, (Richardiidae) has all elements except (2) and only slight development of (3). (c) The genus *Xenaspis* OSTEN SACKEN, 1881, (Platystomatidae) has all elements except (6), but a reduced anterior notopleural is present. (d) The subfamily Angitulinae (Platystomatidae) has all elements except (6). (e) The genus *Adrama* WALKER, 1859, (Tephritidae) has all elements, except that the wing is only slightly narrowed basally and the anterior notopleural is present. (f) The genus *Phytalmia* GERSTAECKER, 1860, (Tephritidae) has all elements except (6). (g) *Thecomyia limbata* (WIEDEMANN, 1830) (Sciomyzidae) has all elements except (3), but only slight development of (7). (h) *Hypselothyrea claudensis* BOCK, 1982 (Drosophilidae) has all elements except (6), but the notopleurals, though reduced, are both present. (i) An undetermined Malaysian taxon of Oscinellinae (Chloropidae)

has all elements except the presence of hind femoral spines and loss of the anterior notopleural - the metathoracic features are very pronounced. (j) *Cylindromyia fenestrata* PARAMONOV, 1956, (Tachinidae) has all elements except (2), but only slight development of (3) and (6). Outside the Schizophora, there is a marked approach to the megamerinoid character set in some *Zaclava* spp. (Bombyliidae, subfamily Systropinae, or Toxophorinae in classification of YEATES, 1994) and, to a smaller extent, in *Ceriana ablepta* RIEK, 1954, (Syrphidae).

These examples indicate that the elements of the megamerinoid character set have often evolved together as a convergent cluster in various schizophoran lineages. Thus, in cladistic analysis, it is not legitimate to score each element as a whole, independent apomorphy, and presence of the complete set cannot be taken as indicative of recent common origin among its possessors without good supporting evidence. The strong evidence for sister-group relationship between Syringogastridae (as a separate taxon from other megamerinid-like taxa) and Diopsidae (D. MCALPINE in press B) illustrates how misleading the megamerinoid character set can be. True megamerinids lack the distinctive synapomorphies which unite the families Syringogastridae and Diopsidae.

J. MCALPINE (1989) gives 3 synapomorphies for 'extant Megamerinidae and Syringogastridae' (the term 'extant', from the immediate context, intended to exclude the Tertiary genus *Palaeotanypeza* MEUNIER, 1917, from the discussion). These are: 1, ocellar plate enlarged; 2, hind femur, only, enlarged and bearing 2 rows of stout ventral setae; 3, spermathecae reduced to 2 (doubled in Syringogastridae). According to cladistic methodology, he would appear to be proposing these synapomorphies as prima facie evidence for monophyly of the group Megamerinidae + Syringogastridae as shown in his fig. 116.2. I disagree with this character evaluation for the following reasons. The ocellar plate (frontal or ocellar triangle), though large and well defined in *Syringogaster*, is quite undifferentiated in the extant megamerinid genera *Megamerina* and *Texara*, and there is no recorded evidence of such a differentiated plate in the fossil *Palaeotanypeza* (HENNIG 1965). The possession of enlarged, ventrally spinose hind femora is dealt with under my discussion of the megamerinoid character set above. The number of spermathecae in *Syringogaster* is disputed or, perhaps, variable (3 according to HENNIG, 1958, 2 according to PRADO 1969, 4 according to J. MCALPINE 1989). Even if 4 is the actual groundplan number for Syringogastridae, this number could be arrived at directly by acquisition of symmetry in the 1+2 spermathecal arrangement, and the assumption of doubling after reduction to 0+2 looks remarkably like tailoring the evidence to fit a desired conclusion. (PRADO's figures and description of syringogastrid spermathecae do not seem amenable to any hypothesis involving derivation from a 1+1 condition, and FEIJEN (1983: 57) describes how in the diopsid genus *Cladodiopsis* SÉGUY, 1949, a fourth spermatheca appears to be added to the 1+2 pattern.)

For these reasons and from additional data discussed below and by D. MCALPINE (in press B), my further consideration of Megamerinidae refers only to the genera *Megamerina* and *Texara*.

The nerioid affinities of the Megamerinidae

While most authors have classified the Megamerinidae in the Diopsoidea (Nothyboidea), D. MCALPINE (1966) referred the Megamerinidae to the superfamily Micropezoidea (the name then in use for Nerioidea) and this position was still accepted by COLLESS and MCALPINE (1991), though no analysis of the evidence had been published. This evidence is reviewed here.

The facial structure of the Megamerinidae is very reminiscent of that of many nerioid flies. It has the sharply defined subtriangular membranous area below, which extends as an almost linear median seam to between the antennal sockets. The sclerotised part of the face consists of a pair of lateral plates separated by this median zone, each bearing no visible suture other than the long lateral arm of the ptilinal fissure. In many nerioids, including *Pseudopomyza* STROBL, 1893, (particularly subgenus *Dete* MCALPINE, 1994) *Polypathomyia* KRIVOSHEINA, 1979, (Pseudopomyzidae), and *Calycopteryx* EATON, 1875, (Micropezidae), there is a visible parafacial suture parallel with the lateral arm of the ptilinal fissure on the lateral plate. There is no such suture visible in the Megamerinidae, so that the suspicion arises that the lateral plate consists wholly of the parafacial, the true face (mesofacial) being quite desclerotized, and the medial margin of the plate coinciding with the parafacial suture. However, in several nerioid genera, e.g. *Pseudopomyzella* HENNIG, 1969, *Latheticomyia* WHEELER, 1956, (Pseudopomyzidae), *Compsobata* CZERNY, 1930, (Micropezidae, Calobatinae), and *Cothornobata* CZERNY, 1932, (Micropezidae, Eurybatinae) the parafacial suture is shortened or not discernible on the lateral plate, and the facial structure appears similar to that of the megamerinids. The other taxa referred to Diopsoidea (Nothyboidea) do not have a nerioid type of facial structure, with the exception of the Tanypezidae (including *Strongylophthalmyia* HELLER, 1902), the position of which in this superfamily is also suspect (D. MCALPINE, in press B).

In the Megamerinidae the ptilinal fissure has a characteristic H-like form, with its upper lip forming a narrow frontal lobe. This is a very unusual structure in the Schizophora, but is equally developed in some *Crepidochetus* spp. (Micropezidae, Eurybatinae) and *Compsobata* spp. (Micropezidae, Calobatinae), and developed to some extent in a number of other micropezids, though I have not seen it in any other acalyptrate family. In some Neriidae, e.g. *Rhoptrum* ENDERLEIN, 1922, there is also such a median lobe, with soft lateral margins which, with slight infolding, could produce the M-shaped condition approaching that of Megamerinidae. Also, in *Rhoptrum* there is a broad sclerotised plate at the summit of the parafacial, but this is not horizontal and does not overlap the supra-antennal sclerite as in Megamerinidae.
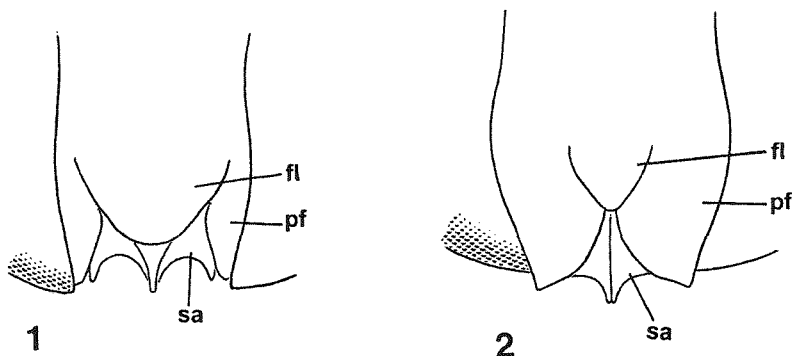
Figs 1, 2: Ptilinal region of head, dorsal view, of 1, *Compsobata univitta* (WALKER); 2, *Texara* sp. fl, median frontal lobe; pf, parafacial plate; sa, supra-antennal plate.

I have taken the Pseudopomyzidae (D. MCALPINE 1996) as a generally very plesiomorphic group of the Nerioidea. Pseudopomyzids often have a simple, horizontal ptilinal fissure with the usual descending lateral arms, but in some forms, including *Polypathomyia stackelbergi*

KRIVOSHEINA, 1979, and *Pseudopomyza* (*Rhinopomyzella*) spp. the upper lip of the fissure is produced as a short median lobe. It thus shows a tendency towards the M-shaped form, though without definite lateral angles.

These examples illustrate how a ptilinal fissure like that of Megamerinidae may have been derived from a morphology occurring widely among the Nerioidea but not developed in other acalyptrate superfamilies. Probably then, these basic elements leading to the H-like fissure constitute a synapomorphy, but the fullest development of the feature has been attained separately in several nerioid taxa.

The antennal socket of the Megamerinidae has a narrowly raised, well sclerotised rim except on the ventral side. This is typical of many nerioid taxa, in common with some other acalyptrate flies, but contrasts with the condition in Syringogastridae, *Gobrya*, and, to a degree, with Nothybidae. In the megamerinids this condition is associated with the division of the adjacent exposed lunule into 2 distinct, horizontal supra-antennal plates by a narrow, deeply incised median groove. Such a divided lunule occurs in most micropezids and neriids, but in many of these the floor of the median groove is somewhat widened or raised into a rounded ridge. In the Diopsoidea the lunule is generally only quite narrowly exposed, and does not have a visible median groove.

The antenna of the Megamerinidae has the same basic structure as that of primitive nerioid taxa, e.g. *Heloclusia* MALLOCH, 1933 (Pseudopomyzidae) and *Calycopteryx* (Micropezidae). While this does not involve any distinctive synapomorphy, it is very different from the antennal structure of most Diopsoidea (other than Tanypezidae and Diopsidae) as described by me (D. MCALPINE, in press B).

The prosternum in the Megamerinidae consists of an elongate, posteriorly narrowed basisternum, separate from the more anterior presternum and without precoxal bridges. Such a prosternum (form A of SPEIGHT, 1969) is the usual type for the Nerioidea, though occurring widely also among other acalyptrates. Prosternal morphology provides part of the general evidence of agreement between Megamerinidae and Nerioidea, without providing an acceptable synapomorphy.

The abdominal segments behind segment 7 in female megamerinids are largely desclerotised and very extensile. The cerci are short, free and appressed. These features are present in the Nerioidea, but are less typical of the Diopsoidea, though present in part in the Psilidae and Tanypezidae.

The megamerinid aedeagal structure (showing detailed similarity between *Megamerina* and *Texara*, according to HENNIG 1941 and my own studies) is reminiscent of that of more primitive nerioids in a number of points (compare figs 3, 4). The hypandrium of megamerinids is comparatively large and elongate, and, while that of the cypselosomatid *Clisa* MCALPINE, 1993, and the neriids is reduced, that of certain micropezids is less so. The basiphallus of megamerinids does not project more or less freely from the hypandrium as in typical nerioids, but is attached to the latter on more than its basal half by a membrane. There appears to be no true aedeagal apodeme comparable with that of many typical nerioids, but this is perhaps incorporated in the posterior rod-like sclerite of the basiphallus which is attached to the anterior end of the hypandrium. The pair of complex processes connected to both the hypandrium and basiphallus, perhaps to be identified as gonites, may be taken as indicating how these structures become transferred from the hypandrium (probable plesiomorphic condition) to the basiphallus (to which they are attached in Pseudopomyzidae, Cypselosomatidae, and Neriidae).
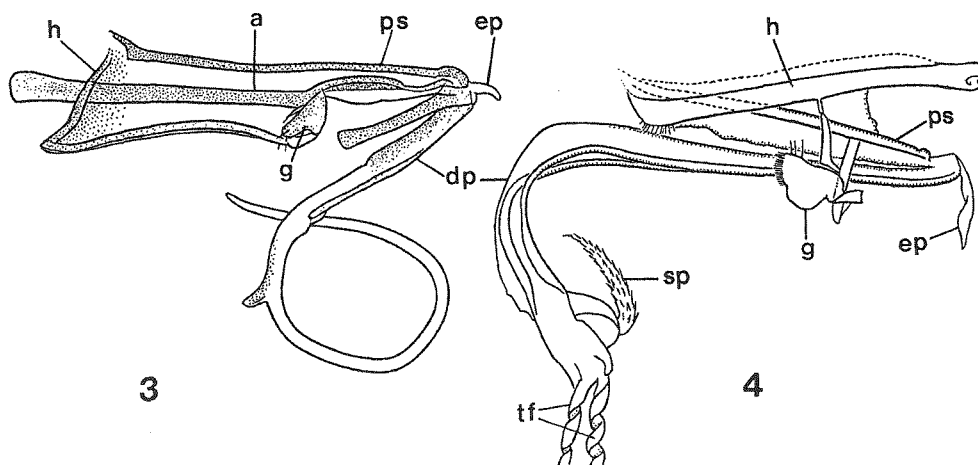
Figs 3, 4: Hypandrium and aedeagus from left of (3) *Clisa australis* (MCALPINE), (4) *Texara* sp. (?*dioctrioides* WALKER, only bases of helicoid terminal filaments shown). a, aedeagal apodeme. dp, distiphallus. ep, epiphallus. g, gonite. h, hypandrium. l, link sclerite. ps, posterior sclerite of basiphallus. r, rod connecting gonite to basiphallus. sp, scabrous process of distiphallus. tf, terminal filament of distiphallus.

The leaf-like epiphallus arising from the posterior side of the junction of basiphallus and distiphallus in megamerinids is perhaps homologous with a similar structure in the Cypselosomatidae (but the adjacent anterior process in cypselosomatids is perhaps a special development in that family). The aedeagal structure of at least some micropezids also shows detailed homology with that of megamerinids. In certain *Metopochetus* spp. (D. MCALPINE in press A) all the parts except those of the distal part of the distiphallus are readily identified with those of megamerinids, including the link sclerite, connecting the gonite (located on the basiphallus in both taxa) to the hypandrium, and the rod-like sclerite of basiphallus. As in many nerioids, the distiphallus of the megamerinids is an elongate, basally rigid structure, with more flexible distal part, but its complex apex, with a scabrous process, must be considered a special development of this family. My study of the terminal parts of the distiphallus in Micropezidae (MCALPINE in press A) demonstrates remarkable structural diversity in this part.

I find in the 2 available species of *Texara* (from W. Malaysia and Taiwan) a pair of long terminal helicoid filaments on the distiphallus (Fig. 2) and this condition is in agreement with material described by GRIFFITHS (1972, fig. 98) under the name *Megamerina dolium* (FABRICIUS, 1805). However such filaments are typically absent in *M. dolium* (see HENNIG 1941: fig. 2, SÉGUY 1934: fig. 270, the latter under the name *Megamerina loxocerina* (FALLÉN, 1820), a widely accepted synonym of *M. dolium*.) This discrepancy suggests that GRIFFITHS' material is not conspecific with that of SÉGUY and HENNIG, a possibility that seems to have further support from apparent differences in the gonite. On the other hand, after the removal of *M. savolaineni* FREY, 1956, to *Texara*, only one species has been considered to belong in *Megamerina* (NARTSHUK 1984). STEYSKAL (1977) mentions 2 species of *Megamerina*, but his second species is *M. rufipes* (GIMMERTHAL, 1834) (pers. comm.), treated as a synonym of *M. dolium* by NARTSHUK.

Pending a thorough study of this problem, I cannot determine whether the presence of helicoid filaments on the distiphallus is a groundplan condition of the Megamerinidae or not, but I suspect that they may be present only in *Texara* spp.

A megamerinid condition that is unlike that of any typical nerioid is the reduction of abdominal tergite 6 in the male. This is readily explained as a megamerinid autapomorphy, but I am not aware of any similar case of reduction within the considerable morphological diversity of nerioid taxa. The great reduction of the aedeagal apodeme is also a megamerinid apomorphy that is atypical of the Nerioidea, though paralleled in some micropezids (some species of *Metopochetus* ENDERLEIN, 1922, see D. MCALPINE in press A).

The structure of abdominal segment 7 in female megamerinids has given some difficulty for the hypothesis that the Megamerinidae belong in the Nerioidea. In the latter superfamily, tergite 7 and sternite 7 are largely fused to form an enlarged ovipositor sheath or oviscape, markedly reduced only in certain eurybatine micropezids, and spiracle 7 is placed in a short lateral incision at the anterior end of this tergosternite. In *Megamerina* (HENNIG 1958: fig. 82) segment 7 is elongate with a separate sclerotised tergite and sternite and intervening pleural membrane containing the spiracle. This looks like a more plesiomorphic condition than that of the groundplan of Nerioidea. My examination of the female postabdomen of 2 *Texara* species reveals approximate agreement with the condition in *Megamerina*, but also raises doubts as to whether this is a true plesiomorphy. Though the pleural membrane of segment 7 is soft and liable to collapse inwards, it and the tergite and sternite have the same satiny texture (indicative of complex surface ultrastructure), in contrast to the preabdominal sclerites, which are glossy to partly pruinescent. Also, the line of demarcation between pleural membrane and sclerites of segment 7 is not equally sharp over the whole length of the segment, and the area around spiracle 7 is not markedly less sclerotised than the lateral part of the tergite.

From these details it appears that the external structure of segment 7 in female megamerinids is less plesiomorphic (more differentiated from the preceding segments) than has been supposed, and it is by no means clear that it cannot have been derived from that of a nerioid-like ancestor. I conclude that the relationships of the Megamerinidae lie with the superfamily Nerioidea as indicated particularly by facial and aedeagal structure and also by several less decisive similarities. The question remains whether the Megamerinidae are a sister group to the rest of the superfamily, as suggested by the possibly plesiomorphic structure of abdominal segment 7 in the female, or whether they are more closely related to a particular nerioid taxon, perhaps the Micropezidae, as suggested by some features (possible synapomorphies) of aedeagal structure described above. I am unable to answer this question from the morphological data available to me at present.

Some groundplan autapomorphies of the Megamerinidae

These are deduced as characters apomorphic (AA) in respect of those in a hypothetical somewhat heleomyzid-like nerioid ancestor as discussed by D. MCALPINE (1996).

(a) Ptilinal fissure inversely U-shaped (P)/ ptilinal fissure H-shaped (AA).

(b) Face of similar width in both sexes (P)/ face of male narrowed (AA).

(c) Ocellar bristle present (P)/ ocellar bristle absent (AA).

(d) Postvertical bristle present (P)/ postvertical bristle absent (AA).

(e) Postclypeus (prelabrum) U-shaped, of moderate depth (P)/ postclypeus reduced and flattened (almost 2-dimensional) (AA).

(f) Megamerinoid character set (see above) undeveloped (P)/ entire megamerinoid character set present (AA).

(g) Postnotopleural ridge rounded off, little developed (P)/ postnotopleural ridge forming horizontal, sharp-edged lamella (AA).

(h) Hairs (setulae) on fore tibia similar to those on other tibiae (P)/ fore tibia more densely and coarsely haired than other tibiae (AA).

(i) Costa with break at subcostal position (P)/ costa unbroken (AA).

(j) Vein 7 (A$_2$) represented by an unpigmented crease beyond alular incision (P)/ vein 7 indistinguishable beyond alular incision (AA).

(k) Tergite 6 of male well developed (P)/ tergite 6 of male much reduced (AA).

(l) Left spiracle 6 of male resembling other abdominal spiracles (P)/ left spiracle 6 reduced (AA).

(m) Aedeagal apodeme well developed (P)/ aedeagal apodeme much reduced (AA).

(n) Distiphallus without differentiated scabrous process (P)/ distiphallus with scabrous process (AA).

The above characters are all present in the limited amount of available material of both megamerinid genera. Many of them are convergent with character states in certain other nerioid or diopsoid taxa, notably characters (a), (c), (d), (f), (i), (j), but, as a set, they are distinctive for the Megamerinidae. The 7 elements of the megamerinoid character set (f), discussed above, are evaluated as a single character for cladistic purposes. The following are particularly distinctive apomorphies for the Megamerinidae, indicative of the monophyly of the family: (h), (k), (l), (m), (n).

The development of the postnotopleural ridge into a sharp-edged horizontal lamella (g) is apparent in *Megamerina* and *Texara* spp. A similar development is present in the Coelopidae (D. MCALPINE, 1991: fig. 7), and it is probably a groundplan autapomorphy for *Coelopa* MEIGEN, 1830. This is clearly a convergent condition for the 2 families.

The identity of the postabdominal spiracles in male megamerinids is difficult to determine, so that only the clearly autapomorphic condition (l) is affirmed in the above list. GRIFFITHS (1972) records the absence of left spiracles 6 and 7 for material dubiously determined as *Megamerina dolium* (see above) and interprets the large remaining postabdominal spiracles as right spiracles 6 and 7. In the male of *Texara* sp. (W. Malaysia) (Fig. 5) I find the left spiracle 6 to be present in front of the left-side fragment of tergite 6 (this tergite being more reduced than in *M. dolium*), but it is smaller than the other 2 postabdominal spiracles, though apparently open and connected to a trachea. In *Texara* sp. (Taiwan) I find left spiracle 6 to be more reduced than in the above species and I cannot detect an external opening. The pattern of the postabdominal spiracles in this species therefore agrees with that described by GRIFFITHS.

An alternative interpretation of the identity of the large spiracle on the left side of the megamerinid protandrium might be left spiracle 7, but its position is very different from that of left spiracle 7 in other families of Nerioidea (e.g. *Pseudopomyza* MCALPINE 1994, fig. 2, *Heloclusia*, GRIFFITHS 1972, fig. 71, and *Metopochetus*, MCALPINE in press A). I therefore incline to GRIFFITHS' view that it is probably right spiracle 7, which has been displaced to the left side in the circumversion process (as in some heleomyzids, see MCALPINE 1985 figs 66, 67).
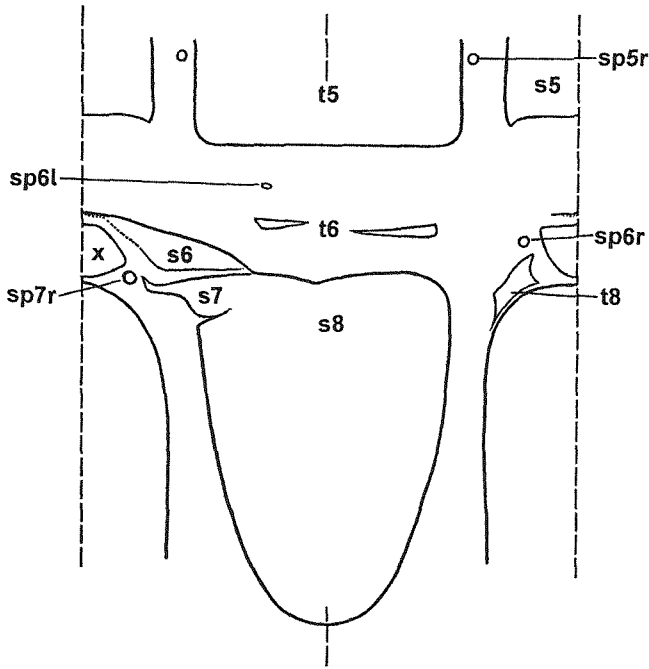
Fig. 5: *Texara* sp. (? *dioctrioides*). Protandrogram - sclerites and spiracles of segments 5-8 of male shown diagrammatically as split along median ventral line, hypandrium excised. s5-s8, sternites 5 to 8. sp6l., left spiracle 6. sp5r-sp7r, right spiracles 5 to 7. t6, tergite 6, fragmented. t8 ? tergite 8. x, unidentified sclerite.

Fossil record

The only putative megamerinid fossil is *Palaeotanypeza spinosa* MEUNIER, 1917, from Baltic amber (probably upper Eocene). This species was redescribed from a neotype by HENNIG (1965), but this is not at present available to me, and my knowledge of the species is derived only from HENNIG's description and, to some extent, the illustrations of MEUNIER. In 1965 HENNIG had no suspicion that *Syringogaster* and *Gobrya* were not part of a monophyletic family Megamerinidae, and this fact must be remembered in evaluating his discussion of the fossil's affinities.

Of the above-listed megamerinid autapomorphies, only (c), (d), (i), and a few elements of (f) are known to be present in *Palaeotanypeza*. This is largely due to the condition of the neotype and perhaps partly due to failure of HENNIG to note some character states. Characters (c) and (d) are very commonly derived and have slight diagnostic or cladistic value, and (i) may not necessarily be an apomorphy for taxa without nerioid origins. Character (f), in so far as it can be ascertained, has not reliable diagnostic value. Probably because of the opacity of the amber, HENNIG's illustrations of the thorax do not demonstrate whether there is a long, extensively bridged prosternal region with short coxae, as in Nothybidae, or a relatively short prosternal

region with long coxae as in Syringogastridae. However his figs 38 and 39 seem to indicate one or other extreme condition. Typical megamerinids have a short prosternal region, with moderately large fore coxae inserted near the anterior end of the thorax. J. MCALPINE (1989) mentions the presence of a (metathoracic) postcoxal bridge in *Palaeotanypeza*, but this condition cannot be inferred from HENNIG's illustration and description, and J. MCALPINE apparently did not see the fossil. The habitus of *Palaeotanypeza*, as figured by HENNIG (1965: fig. 38) is rather like that of Syringogastridae, which also agrees with Megamerinidae in characters (c), (d), (f), and (i), through convergence. Hence there is room for doubt that *Palaeotanypeza* is a true megamerinid. On the other hand, the details of wing morphology and the extensive covering of setulae on the mesopleuron (anepisternite) in *Palaeotanypeza* are much more in agreement with Megamerinidae than with Syringogastridae, though they are not necessarily synapomorphies. The antenna of *Palaeotanypeza* as figured by MEUNIER (1917: pl. 16, fig. 76) resembles that of Megamerinidae much more than that of Syringogastridae, but also has some resemblace to that of *Centrioncus* SPEISER, 1910, a primitive diopsid retaining some syringogastrid-like character states. There is also a slight doubt if HENNIG's and MEUNIER's material of *P. spinosa* is conspecific or congeneric.

I retain *Palaeotanypeza* provisionally in the Megamerinidae, at least until the many doubtful points in its morphology are elucidated. I consider that its morphology and relationships are too little known to justify the phylogenetic theorising that has been based on it.

Recent genera

The Megamerinidae include 2 genera, about 7 valid described species, and several undescribed species (STEYSKAL, 1977 and in litt., after removal of *Gobrya* and *Syringogaster* spp.). Not enough is known about comparative morphology of these taxa to construct a phylogeny. The genus *Megamerina* has apparently a single species and is characterised by absence of the fronto-orbital bristle, an apparent apomorphy. My limited material of *Texara* is from 2 populations, Formosa (Taiwan) (probably *T. rufipes* (WALKER, 1849) from comparison with holotype), and West Malaysia (perhaps *T. dioctrioides* WALKER, 1860). These share 2 possible synapomorphies not present in *Megamerina*. (1) The fore femur has no posteroventral spines or differentiated setae. The presence of stout spines on the fore femur of *Megamerina*, which are much less developed in the female than in the male, may represent a plesiomorphic condition, as posteroventral bristles are present in the ground plan of Nerioidea. Alternatively the fore femoral spines may have arisen in conjunction with those of the hind femur, when their evolutionary status would be less clear. (2) Both available *Texara* species have segment 2 of the hind tarsus much shorter than segment 3. This contrasts with the condition in *Megamerina* and most other schizophorans. While this is apparently an apomorphy, I do not know if it occurs in the groundplan of *Texara*. Whether the presence of a pair of long spiral filaments on the distiphallus (discussed above) distinguishes *Texara* consistently from *Megamerina* should be elucidated by further study.

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