CONTRIBUTIONS IN SCIENCE

A FURTHER NEW GENUS OF PRIMITIVE PHORID FLY (DIPTERA: PHORIDAE) FROM BALTIC AMBER AND ITS PHYLOGENETIC IMPLICATIONS

BRIAN V. BROWN
The scientific publications of the Natural History Museum of Los Angeles County have been issued at irregular intervals in three major series; the issues in each series are numbered individually, and numbers run consecutively, regardless of the subject matter.

- Contributions in Science, a miscellaneous series of technical papers describing original research in the life and earth sciences.
- Science Bulletin, a miscellaneous series of monographs describing original research in the life and earth sciences. This series was discontinued in 1978 with the issue of Numbers 29 and 30; monographs are now published by the Museum in Contributions in Science.
- Science Series, long articles and collections of papers on natural history topics.

Copies of this publication are available through the Scholarly Publications Office at 213/763-3330 or by visiting our website at (http://www.nhm.org) for a PDF file version.
ABSTRACT. A new genus and species of primitive phorid fly preserved in Baltic amber, *Ulrichophora lobata*, is described. It is compared to the similar *Archiphora robusta* (Meunier) from Baltic amber and the extant *Archiphora patagonica* Schmitz, from which it differs most notably by the well-developed anal lobe and the setation of the scutum. This latter character and its possible phylogenetic utility are discussed in relation to other extinct and extant phorids. Further observations on the holotype of *A. robusta* indicate that it is probably not congeneric with the extant *A. patagonica* (Schmitz), and *A. robusta* is given the new generic name *Hennigophora* (new combination). A key to the Baltic amber sciadocerines is given. A definition is given of a new, currently rankless group, Euphorida, which includes all Phoridae except Sciadocerinae and Prioriphorinae.

INTRODUCTION

The primitive phorids classified in the subfamilies Sciadocerinae (formerly family Sciadoceridae; Disney, 2001) and Prioriphorinae are a fascinating assemblage of mostly extinct forms with a previously unsuspected diversity. New discoveries of these primitive phorids have been made recently (Mostovski, 1996, 1999; Arillo and Mostovski, 1999; Grimaldi and Cumming, 1999; Brown, 2002; Grimaldi et al., 2002) from various Mesozoic and Cenozoic amber deposits, and more are likely to be found (e.g., figures in Grimaldi and Engel, 2005). In their structure, these flies bridge some of the gaps between the two extinct species of sciadocerines—*Sciadocera rufomaculata* White, 1916, from Australia and New Zealand, and *Archiphora patagonica* Schmitz, 1929, from Chile—and the other extinct species of the large family Phoridae. Their large and increasingly better-known structural diversity both provides information on the evolution of these groups and confounds our understanding of their history.

With the acquisition for study of three newly collected specimens of sciadocerines from late Eocene Baltic amber (Larsson, 1978), I began to review the structure of the oldest-known Baltic sciadocerine, *Archiphora robusta* (Meunier, 1905). After close examination, I realized that there were some inaccuracies in Hennig’s (1964) redescription of this species, that some of the supposed similarities with *A. patagonica* were incorrect, and that the three new specimens represented a new taxon. The ramifications of these observations are explored in this paper.

METHODS AND MATERIALS

Amber specimens were examined and photographed while immersed in heavy mineral oil. Scanning electron micrographs (SEMs) of extant specimens were made with a Hitachi S-3000N SEM and standard coating procedures. Images of all specimens were deposited in Morphbank (www.morphbank.net). Structural terms used are those of J. McAlpine (1981).

SYSTEMATICS

Family Phoridae Curtis, 1833
Subfamily Sciadocerinae Schmitz, 1929

*Ulrichophora* new genus

DIAGNOSIS. Sciadocerinae. Scutum with many setulae and few dorsocentral setae only; lacking acrostichal setae (Fig. 1). Wing with well-developed anal lobe (Figs. 4, 5).

The other sciadocerine genera—*Archiphora* Schmitz, 1929, *Eosciadocera* Hong, 1981, and *Sciadocera* White, 1916—differ in having scuta with well-developed, complete rows of dorsocentral and acrostichal setae, and in lacking random setae on the scutum.

TYPE SPECIES. *Ulrichophora lobata* new species.

*Ulrichophora lobata* new species

Figures 1–5

DESCRIPTION. Body length 2.6–2.7 mm. Frons approximately one-third head width (Fig. 1); lacking medial furrow; with one pair inner vertical, one pair ocellar, one pair reclinate
fronto-orbital setae near dorsal one-third, one pair interfrontal setae near midlength. Complete row of postocular setae present. One extremely long, curved genal seta present on posterofrontal margin of head (Fig. 2). Flagellomere 1 of antenna elongate-oval (Figs. 1, 2), slightly pointed at apex, not greatly enlarged; arista slightly dorsal of apex. Palpus extremely small. Labellae of proboscis enlarged, expanded, bare (Fig. 2). Scutal disk dorsocentrally with small, even setulae; four posterior dorsocentral setae present, anteriormost of which is only slightly larger than scutal setulae, second seta slightly larger, setae 3–4 much larger (Fig. 1), row converging anteriorly; two intra-alar setae: one in anterior one-third (which might belong to another row, being relatively ventral in position), the second in posterior one-third; two posterior supra-alar setae present; one large basal postpronotal setae present; notopleuron with four long setae. Scutellum with two pairs of large setae. Aneupisternum without setae. Foretibia with one short anterodorsal seta near apex; tarsomerses as in Figure 3. Mid- and hind leg with anteroventral seta on apical one-third of femur; tibia with anterior seta near midlength. Tibiae without dorsal longitudinal setal palisades (found in many Phoridae); longitudinal setal palisades present on at least fore- and hind tarsomere 1 (visible in holotype). Empodium not visible, possibly absent. Wing as in Figures 4 and 5; similar to that of extant sciadocerines (Figs. 6, 7) except more elongate; costa extends nearly to wing tip; base of M_{1+2} present; CuA_{2} present; numerous (about 20) alular setae present; anal lobe large; entire surface of wing microtrichose. Venter of abdomen with well-developed setose sternites. Male terminalia small, details difficult to observe, best seen on left side of holotype.

**HOLOTYPE.** ♂, RUSSIA: Kaliningrad, Baltic amber (catalog number LACM ENT 159890) (Natural History Museum of Los Angeles County).

**PARATYPES.** ♂, GERMANY: Bitterfeld amber (private collection Paulson); one specimen (sex indeterminate; specimen is largely obscured), Baltic amber (Zoologisches Forschungsmuseum A. König, Bonn).
ETYMOLOGY. This name is in honor of Dr. Hans Ulrich (Bonn), who kindly lent me his specimen of *U. lobata*, and who has been highly supportive of my phorid studies.

CLASSIFICATION. Relationships among the primitive Phoridae are not well resolved. The subfamily Sciadocerinae is only weakly supported in most analyses (Brown, 1992; Grimaldi and Cumming, 1999; Mostovski, 1999) and outside of the two extant species might not be monophyletic. A full revision of these groups is outside the scope of this paper, but for now *U. lobata* can be classified in a questionably monophyletic Sciadocerinae.

IMPLICATIONS OF THE NEW GENUS

The description of the new genus of sciadocerine phorid has implications for four subjects dis-
cussed herein: the value of scutal setation in phylogenetic reconstruction of the lower Cyclorrhapha; status of the genus Archiphora; monophyly of the Sciadocerinae and Prioriphorinae; and monophyly of a group within the Phoridae, exclusive of Sciadocerinae and Prioriphorinae.

SETATION OF THE SCUTUM

The setation of the scutum of the new species is of interest in relation to that of other phorids and related families. Specifically, the presence of acrostichal and dorsocentral setal rows, and of scattered, random setulae, varies widely. The evolution of these setation patterns was treated in a paper by Simpson et al. (1999), but this treatment omitted detailed analysis of the lower cycorrhaphan families (="Aschiza"), including phorids.

The composition of the non-monophyletic lower Cyclorrhapha (whose status was reviewed by Yeates and Wiegmann, 1999) is controversial. Syrphidae and Pipunculidae appear to be more closely related to the Schizophora than to other lower Cyclorrhapha, have random long scutal setae, and are not treated in further detail here. Opetiidae are questionably related to the Platypezoidea (Collins and Wiegmann, 2002) and might be basal to the entire Cyclorrhapha; furthermore, composition of the Platypezoidea is contentious (Cumming et al., 1995; Collins and Wiegmann, 2002).

Hennig (1979) noted the tendency of Platypezidae, Sciadoceridae and Phoridae to develop a single median row of acrostichal setae, but cautioned that the direction of change from random setulae to single row of acrostichal setae (or vice versa) was not established, and might have occurred more than once.

States of scutal setation for the various families are reviewed below, with special emphasis on the acrostical and dorsocentral rows and on the presence of random setulae.

Asiloidea (outgroup taxon) – The Asiloidea, or a portion therein, is considered to be the sister group to the Eremoneura (Sinclair et al., 1994). There is a single median row of acrostichal setae in some genera in this group (for example, in at least some species of the dasypogonine asilid genera Blepharepium Rondani, 1848, and Callinicus Loew, 1872), some have differentiated dorsocentral setae, and some have scattered dorsal random setulae, with or without differentiated dorsocentral setae.

Empidoidea (outgroup taxon) – In the various groups of Empidoidea and Dolichopodidae there are different types of scutal setation present: random setulae without large dorsocentral and acrostichal setae (as in some fossils illustrated by Grimaldi and Cumming, 1999), one acrostichal row, and two acrostichal rows (Sinclair and Cumming, 2006).

Schizophora (outgroup taxon) – Various states are found in this group, although a thorough review is beyond the scope of this paper. Some have random setulae and large marginal setae (as in extant phorids); some have a single median row of acrostichal setae, as in some acalyptrates: Leiomyza Macquart, 1835 (Asteiidae), Stenomicroscoptera Coquillett, 1900 (Periscelididae), some Aulacigaster Macquart, 1835 (Aulacigasteridae), Nemo D. McAlpine, 1983 (Neminiidae), Neomeoneutes Hennig, 1972 (Carnidae); many have two acrostichal rows (for example in most calyptrates).

Chimeromyia Grimaldi and Cumming, 1999 – The three species of these strange flies were placed in the Eremoneura (Empidoidea + Cyclorrhapha), although with family unknown, by Grimaldi and Cumming (1999). There is a single median row of acrostical setae, plus the usual lateral rows of dorsocentral setae; random setulae are apparently absent.

Opetiidae – According to Chandler (2001: fig. 3) Opetia nigra Meigen, 1830, has random small setulae, no acrostical setae, and larger dorsocentral setae similar to those of U. lobata, except that the dorsocentral row is more complete anteriorly. There are about six differentiated dorsocentral setae, of which the posterior two are clearly larger.

Platypezidae – The setae of the dorsum of many extant platypezids are organized into rows, sometimes with a single medial acrostical row, a dorsocentral row, and fewer intra-alar and supra-alar setae (Fig. 8). The medial setae (acrostical and most dorsocentral), however, are clearly smaller than the larger peripheral setae, and the acrostical row is often absent (Fig. 9). Random setulae are absent.

An exception to the general conditions found in platypezids is one possible fossil platypezid, Electrosania cretica (described by Grimaldi and Cumming, 1999), in which there are random setulae, and in which dorsocentral and acrostical rows are lacking. The placement of this species in Platypezidae is controversial, however, as it has some unusually primitive characters.

Lonchopteridae – Extant species of this family, all of which are in the genus Lonchoptera Meigen, 1803, lack random setulae, lack acrostical setae, and have relatively few, large dorsocentral setae (Fig. 10). Cretaceous fossil genera described by Grimaldi and Cumming (1999) apparently also have dorsocentral setae, but the full setation of the scutum cannot be seen.

Ironomyiidae – There are three extant species of Ironomyia: I. nigromaculata White, 1916 and two undescribed species (D. McAlpine, in press). In a recent review of the group, D. McAlpine (in press) noted that these species displayed many to no long, pilose dorsal setulae, and large marginal setae only. In the Cretaceous fossil Cretonomyia pristina J. McAlpine, 1973, there are small
random setulae, and few small marginal setae (J. McAlpine, 1973). Other fossils occur (Mostovski, 1995; Grimaldi and Cumming, 1999), but D. McAlpine (in press) had doubts that they were related to *Ironomyia* and *Cretonomyia*; furthermore, he questioned whether this family was related to the others considered here. Molecular analysis should help answer this question, and it is unfortunate that the study of Collins and Wiegmann (2002) did not include a specimen of this family.

Cretaceous phorid fossils – There are many taxa described in the non-monophyletic morass of fossils classified in the Sciadoceridae (now Sciadocerinae) and Prioriphorinae; the latter is a holding place erected by Mostovski (1996) for those taxa that more closely resemble phorids. Fossil phorids have not always been documented in sufficient detail for this character.

*Agaphora rara* Mostovski, 1999 – According to Mostovski (1999), there is a single median acrostichal setal row and dorsocentral rows, but the setae are relatively small except for that on the posteriormost dorsocentral aspect, which is twice the length of the others. No mention is made of random setulae. The scutal setation of the other

species in this genus, *A. iunior* Mostovski, is not mentioned.

*Archiphora pria* Grimaldi and Cumming, 1999 – The scutum of this species is obscured and cannot be reliably characterized.

*Archisciada lebanensis* Grimaldi and Cumming, 1999 – There are random setulae on the scutum of this species.

*Euiphora grimaldii* Arillo and Mostovski, 1999 – In their drawing (Arillo and Mostovski, 1999:fig. 2) and description of this species, the scutal setation is interpreted as setae in irregular rows, including a pair of acrostichal rows. The photograph of this species (Arillo and Mostovski, 1999:fig. 1), however, shows what I consider random setulae on the scutum, with larger marginal setae.

*Gemmaphora numerosa* Mostovski, 1999 – According to Mostovski (1999), there is a median row of acrostichal setae (irregular anteriorly), 12 dorsocentral setae, and random setulae. Presumably, the random setulae are anterolateral, as in *Archiphora patagonica* (Fig. 11).

*Makiska dvija* Mostovski, 1999 – According to Mostovski (1999), there is a single median row of acrostichal setae and a well-developed dorsocentral row. No mention is made of random setulae.

*Prioriphora canadambrana* McAlpine and Martin, 1966 – The original description of this species depicts the scutum as having a platyzeid-like setation, with a single median acrostichal row, and complete dorsocentral rows. Smaller setae are depicted on the anterolateral corners only.

*Prioriphora casei* Grimaldi and Cumming, 1999 – This species has random setulae on the scutum, similar to those of most extant phorids.

*Prioriphora cheburashka* Mostovski, 1999 – According to Mostovski (1999), this species has nine to 10 acrostichals in a single median row, nine to 10 dorsocentral setae, and random setulae on the scutum.

*Prioriphora intermedia* Brown and Pike, 1990 – This species has a single median acrostichal row, and well-developed dorsocentral setae. No mention is made of random setulae (Brown and Pike, 1990).

*Prioriphora luzzi* Grimaldi and Cumming, 1999 – According to the description of this species, there is a single median acrostichal row, as well as a pair of paramedial acrostichal rows anteriorly, and scattered acrostichals. I have not seen a specimen of this species, and the thorax is not figured, so the extent of the dorsocentral setae (which are briefly mentioned) is unknown.

*Prioriphora polyankae* Mostovski, 1996 – This species has a single median acrostichal row of nine setae, plus a row of nine dorsocentral setae (with the posterior dorsocentral setae larger). Mostovski’s original description (Mostovski, 1996) indicated that there were two acrostichal rows, but he later corrected this error (Mostovski, 1999). There are no random setulae indicated.

*Prioriphora sp.* – The descriptions of *P. longicostalis* and *P. setifemoralis* by Brown and Pike (1990) noted that the scutal setation cannot be seen in these specimens.

*Sciadophora bostoni* McAlpine and Martin, 1966 – This species has long scutal setae, organized in a single medial acrostichal row and two complete dorsocentral rows. No random setulae are present.

This fossil was incorrectly listed as being deposited in the Canadian National Collection in the original description (McAlpine and Martin, 1966). In fact, it was retained by the collector, who subsequently sold it to the author. It is now deposited in the Los Angeles County Museum (LACM). In order to stabilize the fossil, it has been mounted in a block of clear epoxy.

*Varya lalita* Mostovski, 1999 – The original description (Mostovski, 1999) mentions well-developed dorsocentral setae, but no others.

Myanmar amber phorid – *Eosciadocera belodis* Hong, 1981 and *E. setosa* Brown, 2002 – These two species have a single median acrostichal row, well-developed dorsocentral and intra-alar rows, and are without random setulae.

Ryszard Szadziewski has an additional specimen of *E. setosa* in which he can see a well-developed empodium (R. Szadziewski, personal communication). The lack of an empodium is a character used by McAlpine (1989) to justify the family Sciadoceridae, but he noted that it is also absent in Lonchopteridae. Grimaldi and Cumming (1999) used this character to define the Sciadoceridae, exclusive of their fossil *Archisciada lebanensis*. Based on their analysis, *Eosciadocera* should also be excluded and placed near the base of their Sciadoceridae.

*Archiphora robusta* (Meunier) – I re-examined the holotype of this species (see further discussion, below). The scutum has three acrostical setae in a single median row, and six dorsocentral setae. There are a few (fewer than 10) smaller setae in the anterolateral corner, similar to those in *A. patagonica*, *P. canadambrana*, and *S. rufomaculata*.

Extant Sciadocerinae – These flies have well-developed dorsal rows of setae, almost entirely without setulae. In *Sciadocera* there is a single median acrostical row, two dorsocentral rows, and two intra-alar setae (Fig. 12). In *Archiphora* the acrostichal row is represented by two (Fig. 11) to four setae only; otherwise it is similar to *Sciadocera*.

Extant phorids (except sciadocerines) – Most have small even setulae on the dorsum of the scutum, with larger setae mostly marginal in
position (Fig. 13). Each setula is clearly socketed (Fig. 14). Some phorids have a few extra dorso-central setae (e.g., Fig. 15), up to four in total (Schmitz, 1938). Disney (2001) noted some phorids lack the small setulae of the thorax, but this is likely a secondary loss at least in some social insect-associated species (Platydipteron Borgmeier and Prado, 1975, Laishania Kung and Brown, 2005). In Platydipteron balli Brown, 1994 (Fig. 16), for example, there are scattered large setae without the small setulae. Schmitz (1938) wrote that the scutal setae sometimes become bristlelike between the posterior dorso-central setae, and more rarely along the median line, which he referred to as a single row of acrostichal setae. Unfortunately, he did not name any taxa with this character, so I could not examine it, but it must be extremely rare. Some species of the genus Hypocera Lioy, 1864, have a pair of marginal (posterior) setae medial to the usual dorsocentral setae that I (Brown and Buck, 1998; Brown, 1999) named acrostichal setae. These are present only as a pair of posterior setae on the scutum, however, and do not form rows; probably they are an autapomorphic development within these species.

In the phorid subfamily Termitoxeniinae some minute species are without setulae on the scutum and instead have scattered (or poorly organized) larger setae and no setulae (Fig. 17); however, some larger termitoxeniine species have the usual random setulae and larger marginal setae. There are some molecular data linking termitoxeniines with the genera Dohrniphora Dahl, Diploneura Lioy, and Thaumatoxena Breddin and Börner (Cook et al., 2004), but in our preliminary molecular data (Brown and Smith, in preparation) using many more genes and taxa, the same species come out in a much different part of the tree. For now I simply note the possibly primitive state found in this group.

**SUMMARY OF SCUTAL SETAE IN CYCLORRHAPHA**

Based on this review of the scutal setae of lower Cyclorrhapha, it is possible to generalize (as did Hennig, 1979, and Sinclair and Cumming, 2006) that a single acrostichal row, or the tendency to develop such a row, is primitively present in Platypezoidea (based on its presence in Sciadocerinae, some Prioriphorinae, and some Platypeziidae) although it is absent in some taxa (Opetiidae, Lonchopteridae, Ironomyiidae, most Phoridae).

The presence of a single row of acrostichal setae is in contrast to the paired acrostichal setae found in many Schizophora, although a single row is found in some schizophoran taxa. Thus, the conclusion of Simpson et al. (1999:p. 1354) that the pattern for Cyclorrhapha was set in the common ancestor of the group is not entirely correct, as there was apparently one group tending towards a single acrostichal row (Platypezoidea) and another towards two rows (Schizophora).

Based on developmental evidence, it is probable that the presence of two acrostichal setal rows is a more primitive character state than having just one row (P. Simpson, Cambridge University, personal communication). The thorax is derived from two physically separated imaginal discs, and the two halves of the adult notum fuse along the dorsal midline just before pupation when precursors for the bristles are already formed. Thus, there cannot be a single median row at the time of formation of bristle precursors. Simpson (personal communication) assumes, but has not directly visualized, that a single row must arise from movement of the precursors from a row on either side that align to form a single one. Analogous limited movement of precursors of microchaetes (=setulae of this paper, and which form rows in some Drosophilidae) has been shown to take place in Drosophila (Renaud and Simpson, in press).

Hennig (1979) stated that the direction of evolution of scutal setation in the Phoridae seemed to indicate that random setulae and no acrostichal row seems to have evolved from ancestors lacking random setulae and with a single median acrostichal row. The descriptions of Euliphora, Gemmaphora, Ulrichophora, and the Burmese phorid, however, shows that the situation is even more complicated, with some sciadocerine-like flies having the same characters as the more derived extant phorids.

Of the families of Platypezoidea, nearly all have some taxa with random setulae and some taxa with a single median row of acrostichal setae; the exceptions are Lonchopteridae, which lack random setulae and acrostichal setae (contrary to Simpson et al. [1999] who stated all “Aschiza” have species with random setulae), and Ironomyiidae, which lack dorsocentral and acrostichal setae; possibly Platypeziidae should be added to this list, depending on the classification of Electrosania. Where the presence or absence of random setulae or acrostichal setae is derived or primitive is not yet known, but the presence of random setulae and acrostichal setal rows seems to be mutually exclusive. Further research is needed, incorporating these and other characters into phylogenetic analyses.

**IMPLICATIONS FOR GENUS ARCHIPHORA SCHMITZ**

Hennig (1964) placed Meunier's Napomyza robusta in the genus Archiphora based on two characters: the reduced anal lobe (which he referred to as axillary lobe or “axillarlappen”), and the reduced cell cup (=anal cell).

The anal lobe is indeed reduced in both Archiphora patagonica and A. robusta. By itself,
however, it is a relatively weak synapomorphy of the genus; such reduction occurs in many taxa and is widespread in Phoridae. The wing of the two species is similar in shape (short, rounded), another possible character linking them, although one that might be functionally linked to the reduced anal lobe.

The reduction of cell cup is not a valid synapomorphy of Archiphora. A comparison of a wing photograph of a male *A. patagonica* (Fig. 6) with that of a male *Sciadocera rufomaculata* (Fig. 7) shows that this cell is equivalent in the two extant species. In my re-examination of the specimen of *A. robusta* I was able to obtain a different view from Hennig’s (1964:fig. 5) drawing, and found that cell cup is much larger (see Fig. 18) than portrayed in Hennig’s figure. This character is thus shown to be completely spurious.

Hennig (1964) declared the specimen of *Archiphora robusta* to be a female. In my opinion this is incorrect; the terminalia are indeed small, but they are also small in males of *A. patagonica* and *Sciadocera rufomaculata*. Furthermore, in ventral view details are visible that show the specimen is a male, particularly the presence of large, median cercal lobes and epandrium- and surstylus-like sclerites (Fig. 19).

The determination that the specimen of *A. robusta* is a male greatly undermines the case for *Archiphora patagonica* and *A. robusta* being congeneric. A synapomorphic character state of the two extant sciadocerines, *A. patagonica* and *S. rufomaculata*, is that flagellomere 1 of males is greatly enlarged (although this character also occurs widely in the Phoridae), with a coincident reduction in the length of the frons and the loss of the interfrontal seta. In the single specimen of *A. robusta*, flagellomere 1 is small, the frons is long, and the interfrontal seta is present (Hennig, 1964:fig. 10).

In both extant species, *A. patagonica* and *S. rufomaculata*, the common base of wing veins M₁ and M₂ is reduced (Figs. 6, 7); in *S. rufomaculata* it is virtually absent. This is another potential synapomorphic character of the two species. In contrast, the medial base in *A. robusta* is apparently well developed. Therefore, recognition of *A. robusta* as part of genus *Archiphora* would render the genus paraphyletic (Fig. 24).

With limited evidence to link *A. patagonica* and *A. robusta*, and noting the possible synapomorphic characters of *A. patagonica* and *S. rufomaculata*, I propose a new genus name *Hennigophora* to include the type species *H. robusta* (Meunier) (new combination). Diagnosis of this taxon is as follows: male with flagellomere 1 relatively small; frons large, with frontal setae as in *Archiphora patagonica* (Fig. 21); scutum with

---

well-developed rows of setae consisting of one median acrostichal row and one dorsocentral row on each side; base of M₁ + M₂ well developed; anal lobe small; empodium absent; male terminalia with separate surstylus on left side.

In order to clarify the recognition of the Baltic sciadocerines, I present the following key to species:

KEY TO BALTIC AMBER FOSSIL SCIADOCERINAE

1. Scutum with small random setulae and only a few large dorsocentral setae (Fig. 1) ........................................ Ulrichophora lobata n. sp.
- Scutum lacking random setulae, but with rows of large dorsocentral and acrostichal setae (as in Figs. 11, 12) .................................................. 2

2. Frons narrow, about one-quarter head width; scutellum with 10–12 setae .................................................. Eosciadocera setosa Brown
- Frons broader, about one-half head width; scutellum with 4 setae .................................................. Hennigophora robusta (Meunier)

A further species of Archiphora, A. pria, was described from Cretaceous New Jersey amber (Grimaldi and Cumming, 1999). This species has a well-developed base of vein M, unlike A. patagonica and Sciadocera rufomaculata; has numerous frontal setae; has a scutum possibly with random setulae and apparently has no medial macrosetae (although the scutum is obscured). It probably should be placed in another genus.

MONOPHYLY OF SCIADOCERINAE AND PRIORIPHORINAE

Sciadocerinae – I supported the monophyly of this group (Brown, 1992) in my revision of phorid classification with some hesitation. Of the four characters I proposed, two were internal characters that are not visible in fossils. One of the other two characters, the enlarged male flagellomeres, apparently applies only to the extant species of the subfamily, as discussed above. The only remaining character is the asymmetrical male terminalia, a condition that is also widespread in many Phoridae and that is difficult to observe in amber fossils. This last character was also the one used to define Sciadoceridae by Grimaldi and Cumming (1999) in their phylogeny.

Disney (1991) proposed that the presence of enlarged anterior femoral setae on the mid- and hind legs as a synapomorphy of Sciadocerinae (as Sciadoceridae), and they are indeed present in Sciadocera, Archiphora, Eosciadocera, Hennigophora, and Ulrichophora. They also occur in Lonchoptera, however, and in some Prioriphorinae: on the midfemur of most Prioriphora (except P. intermedia Brown and Pike, 1990) and also the hind femur of P. setifemoralis Brown and Pike, 1990. The midfemoral seta is present in Archisciada, but the seta is absent from the hind femur. Unfortunately, the terminalia of Prioriphora fossils are not easily visible, and it is impossible to tell whether they are asymmetrical or not. It is possible that the presence of an anterior seta on the midfemur could be used to group Prioriphora with Sciadocerinae, but this would contradict some other hypothesized apomorphies. Further research is required, and it would be especially important to examine further specimens.

Basing the monophyly of the subfamily Sciadocerinae on the asymmetrical terminalia, an often convergent and difficult-to-observe character, is tenuous and unsatisfactory. It is possible that this “subfamily” is part of a paraphyletic stem group, in which the fork of the radial veins is still extremely long and the base of M₁ + M₂ is still present (although reduced in Archiphora patagonica and absent in Sciadocera rufomaculata).

Alternate views are those of Mostovski (1999) and Disney (e.g., 2001). Mostovski (1999)
attempted to justify the Sciadocerinae by the presence of a poorly developed anal lobe, but also noted that both states were present in this group. This character is further undermined with the inclusion of *U. lobata*, with its large anal lobe, in the Sciadocerinae. Disney (1985 and elsewhere) maintains that the long, thin veins of most phorids are different from those in the sciadocerines, based on some mutants with unusual cross-veins that point to differing vein homologies. My disagreement with Disney’s hypothesis was outlined previously (Brown, 1992).

Prioriphorinae – Mostovski (1999) proposed that the Prioriphorinae were monophyletic, based on the absence of an empodium, a character that also occurs in some Sciadocerinae. One described species, *Euliphora grimaldii*, was classified as a prioriphorine by its authors (Arillo and Mostovski, 1999) in spite of its having an empodium. Given that some prioriphorines seem to be more similar to extant phorids (minus sciadocerines) than others, there is evidence that it is instead a grade group. It was considered a grade, or paraphyletic group, by McAlpine and Martin (1966), Brown (1992), and Grimaldi and Cumming (1999:fig. 65). See also the discussion of *Gemmaphora numerosa*, below.

Figures 20–23  Platypoidea, heads
Disney (2001) questioned my 1992 definition of the Phoridae as being those taxa with a distinctive wing venation. He stated that there are subsequently described fossil taxa that span the range of this character, and his own definition using longitudinal setal palisades on hind tarsomere 1 (and thus including former Sciadoceridae) is preferable to define a family. I do not object to including the former Sciadoceridae in the Phoridae because, as I noted previously (1992), the evidence to support sciadocerid monophyly is weak. The same can be said for subfamily Prioriphorinae Mostovski, which is likely not monophyletic. However, a name and diagnosis is needed to refer to a group including the non-sciadocerine, non-prioriphorine phorids. One possibility is to call this group subfamily Phorinae and demote the current phorid subfamilies (Phorine, Metopininae, and others) to tribes. The subfamily level has been used consistently through recent phorid history, however, for groups such as Metopininae, and until more definitive results on the internal phylogeny of Phoridae are available, I prefer to leave this ranking unchanged. Another option is to refer to this group as the Phoridae, s. str., as Sinclair and Cumming refer to their two groups Dolichopodidae s. lat. and Dolichopodidae s. str. I prefer not to refer to two groups by the same name, however, and feel that a new term, even if it is used almost exclusively by phorid workers, is necessary. I here propose a new, currently rankless, group, the Euphorida, that includes all phorids except Sciadocerinae and Prioriphorinae. This group, which is basically equal to the extant phorid subfamilies Hypocerinae, Aenigmatiinae (including Thaumatoxeninae), Phorinae, Conicerinae, Termitoxeninae, and Metopininae (as recognized by Brown, 1992) or extant Phoridae of Mostovski (1999), is defined as follows:

1) Dense setulae present on dorsum of scutum, and large setae mostly restricted to periphery of scutum. This character was proposed by Schmitz (1929) for the entire Phoridae at that time. There are a few apparently derived taxa that have lost the dense setulae (as discussed above), but such rare exceptions, in my opinion, do not disqualify this character as a strong diagnostic character of Euphorida. There are a few phorids that have, in addition to the posterior dorsocentral seta, one or two pairs of more anterior dorsocentral seta (e.g. some Spiniphora Malloch).

2) Radial veins with fork of $R_{2+3}$ and $R_{4+5}$ in apical third of Rs, rather than in basal one-third. Although there are some extant phorids with long radial forks, such as Megaselia prolifera Kung and Brown, this appears to be a secondarily derived condition. Most have a short fork.
3) Frons with one pair ocellar (or postocellar), one pair of inner vertical, two pairs of interfrontal, two pairs of fronto-orbital, and one or two (occasionally more) pairs of supra-antennal setae. Some derived phorids have lost some or all of these setae, but they are present in most.

The setation of the frons is pivotal to characterizing the Euphorida. Of the outgroups, most have the condition shown in female Archiphora patagonica (Fig. 21); males of A. patagonica and Sciadocera rufomaculata have the frons and frontal setation reduced, in conjunction with the enlarged flagellomere 1), in which there is one pair of ocellar setae, one pair of inner vertical setae, one pair of fronto-orbital setae, and one pair of interfrontal setae; this pattern is similar to that of Archiphora, but there are three additional pairs of small, medial setae of unknown homology. Some taxa lack one pair of setae found in A. patagonica, either the interfrontal or fronto-orbital: Agathomyia vernalia (Platypezidae; Fig. 22), Lonchoptera (Fig. 23), Sciadocera, and Prioriphora polyankae. The heads of most of Mostovski’s (1999) species are not drawn, so I am not certain about their setation, but there are more setae present in a few of his taxa, such as Agaphora spp. and Gemmaphora numerosa, as well as in Eosciadocera spp.

The frontal setation of G. numerosa is especially interesting. According to the illustration of Mostovski (1999:fig. 10) there is a pair of inner and outer vertical setae, one pair of interfrontal setae, one pair of fronto-orbital setae, three small setae of unknown homology, and one pair of supra-antennal setae. This is the only known species outside of Euphorida with supra-antennal setae; however, no sciadocerine, prioriphorine, or other outgroup taxon has the stereotypical setation of the Euphorida, as described above.

4) Base of wing veins M1 and M2 absent.

This wing vein base is convergently absent in Sciadocera rufomaculata.

5) Cells cup and dm absent.

6) Venter of male abdomen with sclerites absent.

Ventral abdominal sclerites are present in Sciadocera, Archiphora patagonica, Hennigophora, Ulrichophora, and possibly Prioriphora canadambra. Unfortunately, it is not reported in other fossils.

7) Abdomen without thin sclerite between tergite 6 and terminalia (present in Sciadocera and Archiphora).

Unfortunately, this sclerite is not easily observed in most fossils.

8) Empodium present.

The empodium is absent in Sciadocera, Archiphora, Hennigophora, Ulrichophora, and most prioriphorines, but it is present in Archisciada, Eosciadocera, and Euliphora.

9) Femora without large setae.

There are a few relatively derived Euphorida that have large femoral setae (for example Melalonchma Brues and Melittophora Brues), but nearly all lack them.

The results of the character discussions in this paper are hand-plotted on the tree in Figure 24, which is also based on Brown (1992:fig. 5C) and Grimaldi and Cumming (1999:fig. 65). The hypothesized synapomorphic characters of each node are listed below:

Node 1 (defining Phoridae) – Hind basitarsus with longitudinal setal palisades (Disney, 2001). Although this character has not been widely reported in fossils, it is present at least in Hennigophora, Ulrichophora, and Sciadophora. Several further characters for this node were given by Brown (1992:pp. 13–15, characters 1b, 3–7, 8a, 9–14; also see fig. 5C); of these, character 11 (great reduction or loss of base of M1 + M2) is now considered valid at nodes 4 and 5 in Figure 24 (although there has apparently been some reversal, such as in Prioriphora luzzi; see Grimaldi and Cumming, 1999:fig. 57). Many of these characters are not visible in fossils.

Node 2 (defining Sciadocerinae) – Male terminalia asymmetrical. This character has only been confirmed in Archiphora, Sciadocera, and Archisciada. It has not been reported in any prioriphorine.

Node 3 – Empodia absent. Also absent in most Prioriphorinae.

Node 4 (defining extant Sciadocerinae) – Male flagellomere 1 enlarged and frons reduced; base of wing veins M1 + M2 reduced or absent.

Node 5 (defining Prioriphorinae + Euphorida) – Radial veins thickened; anal lobe reduced; CuA2 lost; cup lost; base of M1 + M3 shifted anteriorly.

Node 6 – Supra-antennal setae present.

Node 7 (defining Euphorida) – Fork of radial veins short; modern phorid frontal setation (as defined above). Scutum with random setulae, without acrostichal setae. Femora without large setae.

The proper placement of some characters, such as ventral sclerites in males, awaits further study of fossils. Many further nodes should be established, especially in the prioriphorines, and some characters will probably have to be moved to other nodes as more information becomes available.

ACKNOWLEDGMENTS

Illustrations were expertly prepared by Brian Koehler (Figs. 1, 5, 19, 20) and Jesse Cantley (Figs. 20–23); digital images were prepared by Brian Koehler and SEMs by Giar-Ann Kung. I thank Hans-Werner Hoffeins for kindly embedding the holotype specimen of Sciadophora bostoni in epoxy, Mike Reich for loan of the specimen of Archiphora robusta, Hans and Christel
Hoffeins for arranging the loan of the Paulson specimen of *U. lobata*, and Hans Ulrich for loan of his specimen of the same species. Additionally, Meg Cumming kindly sent me specimens of *Termitophilomyia zimbraunsi*. I am grateful to Matthias Buck for information on scutal setation in aclypterytes, Jeff Cumming for the same in empidoids, and Pat Simpson for important information on the development of acrostical setae. I thank Michael Oschin for generously supporting my work on amber fossils; this research was also supported by NSF grant DEB 0516420 to B. Brown and P. Smith, and grant DBI-0216506, which funded the purchase of the SEM.

**LITERATURE CITED**


Received 21 June 2006; accepted 8 January 2007.