

# The genus *Sciarotricha* gen. n. (Sciaridae) and the phylogeny of recent and fossil Sciaroidea (Diptera)

HEIKKI HIPPA and PEKKA VILKAMAA

Insect Syst. Evol. Hippa, H. and Vilkamaa, P.: The genus *Sciarotricha* gen.n. (Sciaridae) and the phylogeny of recent and fossil Sciaroidea (Diptera). *Insect Syst. Evol.* 36: 121-144. Copenhagen, June, 2005. ISSN 1399-560X.



The phylogeny of the main groups of the Sciaroidea, including the fossil Antefungivoridae†, Archizelmiridae†, Mesosciophilidae†, Pleciofungivoridae, Pleciomimidae†, Protopleciidae† and Bolitophilidae: Mangasinae†, and an extant new taxon, was studied by parsimony analysis. Two cladistic analyses of seventy-eight morphological characters from adults were made. One analysis, with forty-one extant taxa in the ingroup and the other, with the addition of twelve fossil taxa, both produced two most parsimonious cladograms. The phylogenetic hypotheses obtained differed from each other, and in part also to a great extent from previous ones although most of the traditionally recognized groups appeared monophyletic, including the speciose Cecidomyiidae and Sciaridae. The Cecidomyiidae (fossil analysis) or the Keroplatidae-Ditomyiidae (extant analysis) appeared as the sister-group of the rest of the Sciaroidea. Following on from these analyses, we propose emending the current Sciaridae to include the following subfamilies: Archizelmirinae† stat. n., Rangomaraminae stat. n., Sciarinae, Sciarosominae subfam. n. and Sciarotrichinae subfam. n. A new taxon from Namibia, *Sciarotricha biloba* gen. n., sp. n. is described, and, according to the phylogenetic analysis, is placed in the Sciaridae (Sciarotrichinae). The sister-group of the Sciaridae as newly defined is the Mycetophilidae group, in the extant analysis including the Mycetophilidae, Manotidae, Lygistorrhinidae, *Pterogymnus* and *Sciaropota*, and in the fossil analysis even including the Mesosciophilidae† and the *Ohakunea* group (*Ohakunea*+ *Colonomyia*).

Heikki Hippa, Swedish Museum of Natural History, PO Box 50007, S-104 05 Stockholm, Sweden (heikki.hippa@nrm.se)  
Pekka Vilkamaa, Finnish Museum of Natural History, Zoological Museum, PO Box 17, FI-00014 University of Helsinki, Finland (pekka.vilkamaa@helsinki.fi)

## Introduction

The Sciaroidea is a superfamily of the Diptera with a worldwide distribution, and includes about ten currently recognized extant families and six fossil families dating from the Lower Jurassic onwards (see Grimaldi & Blagoderov 2004). Some of the groups are extremely successful and speciose, such as the Sciaridae, Cecidomyiidae and Mycetophilidae, whilst others are species-poor but nevertheless phylogenetically intriguing (the *Heterotricha* group, Rangomaramidae, *Ohakunea*, *Colonomyia*). There is a consensus regarding the placement of the Sciaroidea in the Bibionomorpha but not as regards the groups that should be included: for example, the Cecidomyiidae are sometimes excluded (Söli *et al.* 2000).

In addition to the 'classic' works of Hennig (1968, 1973) and Tuomikoski (1961, 1966), different hypotheses about the phylogeny of various groups of the Bibionomorpha or Sciaroidea have been published in recent decades, some using traditional methods of character analysis (Wood & Borkent 1989, Matile 1990, Blaschke-Berthold 1994, Shcherbakov *et al.* 1995, Jaschhof & Didham 2002, Grimaldi *et al.* 2003, Jaschhof 2004), others using cladistic computer methods (Amorim 1992, Oosterbroek & Courtney 1995, Matile 1997, Söli 1997). Blagoderov & Grimaldi (2004) presented a quantitative cladistic analysis of some subgroups of the Sciaroidea, but additionally gave a detailed discussion of various important characters previously used to infer phylogenies within the Sciar-

oidea. So far as our own work is concerned, the paper by Matile (1997) is most relevant as it included most of the groups that we analyse here and in a similar numerical analysis. There is little consensus between the various hypotheses regarding sciaroid phylogeny, perhaps the most striking disagreement being the question of whether or not the Cecidomyiidae and Sciaridae are sister-groups (Vilkamaa & Hippa 1998).

The present study was prompted by recent advances in the field, including the publication of important papers by Chandler (2002) and Jaschhof (2004) on the enigmatic *Heterotricha* group of genera, by Jaschhof & Didham (2002) on the new family Rangomaramidae, by Grimaldi *et al.* (2003) on the Mesozoic Archizelmiridae, by Blagoderov & Grimaldi (2004) on the Sciaroidea in Cretaceous ambers, and, not least, by the discovery of an exceptional new taxon from Namibia, which is described below.

Our aim was to obtain a phylogenetic hypothesis of the relationships between all the main groups of the Sciaroidea, including well-documented fossils, by means of a cladistic analysis using morphological characters from the adults, as the immature stages of many crucial taxa are unknown. Our main focus was on the Sciaridae and their phylogenetic position, but we also wanted to determine the phylogenetically correct placement for the problematic, unplaced genera within the Sciaroidea, including our new genus.

## Material and methods

*The specimens.* - In the main, the material was studied with a compound microscope from slide-mounted specimens, although pinned and ethanol/glycerol-preserved material was used mainly when studying larger specimens and when different angles of view were necessary. *Heterotricha* in Baltic amber were studied with a stereomicroscope after cutting and polishing the blocks. Some of the material was available to us only from published descriptions in the literature.

The material of *Sciarotricha* was collected with dry-collecting light traps and was subsequently stored in ethanol. Part of the material was studied in ethanol, where it is still stored, and part was mounted from ethanol on to microscope slides in "euparal" after dehydrating it in absolute ethanol. For morphological analysis, including the drawings, some specimens were treated with potassium

hydroxide (KOH) before mounting in euparal. The structures of the male hypopygium were also studied from KOH-treated specimens under a stereomicroscope. The illustrations were made with the help of a drawing tube attached to a Leitz Diaplan compound microscope.

The following abbreviations are used for institutes where material of the new species is located:

BMNH	The Natural History Museum, London, UK
MZH	Zoological Museum, Finnish Museum of Natural History, Helsinki, Finland
NMNW	National Museum of Namibia, Windhoek, Namibia
NRM	Swedish Museum of Natural History, Stockholm, Sweden

*Phylogenetic methods.* - The data matrix (Table 2) was manipulated with the computer program WinClada, version 1.0 (Nixon, 1999). Phylogenetic relationships were studied by parsimony analysis using the computer program NONA, version 2.0 (Goloboff, 1993), used together with WinClada to search for the most parsimonious cladograms. The search parameters used with NONA were 'hold/100000, hold/100, mult\*100 and TBR+max\*'. Characters were treated as unordered and with equal weights. With the above commands and settings, the program makes a heuristic search and swaps branches with 'tree bisection-reconnection'. The unsupported nodes were collapsed to accept only unambiguous support in the strictest sense. The resulting cladograms and character optimizations were studied with WinClada. The ingroup (Table 1) of the first analysis included all the groups of recent Sciaroidea usually given a family or subfamily rank. Whenever possible, a species from the type-genus was chosen as a terminal, as well as species from all the available genera of obscure family placement (the *Heterotricha* group of Chandler 2002, *Ohakunea*, *Colonomyia*). *Paleoplatyura* was chosen as an additional Keroplatidae as it is considered to be very plesiomorphic (Chandler 2002). A few different structural types were chosen from the Sciaridae, 1) because the monophyly of the family is frequently questioned, 2) because some of them share apparent apomorphic character states with the new genus *Sciarotricha* as well as with some of the genera placed in the *Heterotricha* group, and 3) to help to resolve the postulated sister-group relation-

Table 1. Terminals of the phylogenetic analyses

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For the fossil families, the nomenclature and generic affinities follow Evenhuis (1994).

## Outgroup:

Bibionidae: *Plecia* sp. (Ecuador)

## Ingroup:

Antefungivoridae†: *Antefungivora prima* Rohdendorf (Mesozoic, Karatau); characters from Rohdendorf (1938).Archizelmiridae†: *Archizelmira americana* Grimaldi *et al.* (Late Cretaceous, New Jersey amber); characters from Grimaldi *et al.* (2003).Archizelmiridae†: *Archizelmira baissa* Grimaldi *et al.* (Early Cretaceous, Russia, Transbaikal); characters from Grimaldi *et al.* (2003).Archizelmiridae†: *Archizelmira kazachstanica* Rohdendorf (Upper Jurassic, Kazakhstan, Karatau); characters from Grimaldi *et al.* (2003).Archizelmiridae†: *Burmazelmira aristica* Grimaldi *et al.* (Mid-Cretaceous, Burmese amber); characters from Grimaldi *et al.* (2003).Archizelmiridae†: *Zelmiarcha lebanensis* Grimaldi *et al.* (Cretaceous, Lebanese amber); characters from Grimaldi *et al.* (2003).Bolitophilidae: *Bolitophila cinerea* Meigen (Finland).

Bolitophilidae, Mangasinae†: Mangasinae gen. sp.; Characters from Kovalev (1986) and Chandler (2002).

Cecidomyiidae, Catotrichinae: *Catotricha americana* (Felt) (North America).Cecidomyiidae, Catotrichinae: *Catotricha fraterna* Jaschhof (Australia).Cecidomyiidae, Lestremiinae: *Lestremia cinerea* Macquart (Sweden).Cecidomyiidae, Lestremiinae: *Micromya* sp. (Sweden).Cecidomyiidae, Porricondylinae: *Porricondyla* sp. (Finland).Cecidomyiidae, Cecidomyiinae: *Cecidomyia* sp. (Finland).Diadocidiidae: *Diadocidia ferruginea* Meigen (Finland).Ditomyiidae: *Ditomyia fasciata* (Meigen) (Finland).Keroplastidae: *Keroplatus sesioides* (Wahlberg) (Finland).Keroplastidae: *Macrocera* sp. (Finland).Keroplastidae: *Arachnocampa luminosa* (Skuse); characters from Matile (1990).Keroplastidae: *Paleoplatyura* sp. (Baltic amber; North America); characters from Meunier (1899), Johannsen (1910), Vockerth (1981) and Chandler (2002).Lygistorrhinidae: *Lygistorrhina sanctaecatharinae* Thompson (North America).Mangasiidae†: *Mangas exilis* Kovalev (Mesozoic, Russia, Transbaikal); characters from Kovalev (1986) and Chandler (2002).Manotidae: *Promanota malaisei* Tuomikoski (Burma).Mesosciophilidae†: *Mesosciophila venosa* Rohdendorf (Upper Jurassic, Kazakhstan); characters from Rohdendorf (1946), and, for assistance with interpretation of the characters, Blagoderov (1993) was used.Mycetophilidae: *Mycetophila fungorum* (De Geer) (Finland).Mycetophilidae: *Sciophila* sp. (Finland).Pleciotungivoridae†: *Pleciotungivora latipennis* Rohdendorf (Mesozoic, Karatau); characters from Rohdendorf (1938).Pleciomimidae†: *Pleciomima sepulta* Rohdendorf (Mesozoic, Karatau); characters from Rohdendorf (1938).

ship between the Sciaridae and the Cecidomyiidae (Wood & Borkent 1989, Oosterbroek & Courtney 1995) or between the Rangomaramidae + Cecidomyiidae and the Sciaridae (Jaschhof & Didham 2002).

In the second analysis, the fossil families Antefungivoridae, Archizelmiridae, Mesosciophilidae, Pleciotungivoridae, Pleciomimidae, Propleciidae and Bolitophilidae: Mangasinae were included in addition to the recent taxa. The Eoditomyiidae (Ansorge 1996) was not included because we suspect that it may belong to an older clade than our outgroup+ingroup.

The genus *Plecia* (Bibionidae), which is com-

monly regarded as lying outside the Sciaroidea and in the Bibionomorpha (e.g. Amorim 1992), was chosen as an outgroup.

The characters were taken only from adults because the immature stages are poorly known in many of the crucial groups studied. The male genitalia of Sciaroidea are extremely variable, and due to difficulties in interpreting homologous structures (see Jaschhof & Didham 2002, Jaschhof 2004) they are mostly omitted from the analysis.

*Characters used in the phylogenetic analysis.* -

With many of the fossils, essentially only the wing vein characters are known and available for cod-



2. Antennal flagellum evenly broad or almost so (0) (Vockeroth 1981: Figs 3 – 7, 9, 10); flagellum strongly tapering, the last flagellomeres several times thinner than the basal ones (1) (Grimaldi *et al.* 2003: Figs 8:1, 3, 9: 1, 10:2, 3).
3. The node of the basal antennal flagellomere long, at least 5 times as long as broad (0) (Vockeroth 1981: Fig. 2); short, at most 4 times as long as broad (1) (Fig. 3A, Vockeroth 1981: Figs 1, 3– 10).  
The difference between these states is usually clear. *Rangomarama* may be a borderline case. We have coded it as 1. Coding as “0” or “?” does not affect the trees. *Catotricha* is coded as “?” because of the difficulty in defining the node in a manner homologous with the other taxa with an elongate flagellomere.
4. Antennal flagellomeres single-noded (0) (Fig. 3A, 4B; Vockeroth 1981: Figs 3 – 7, 9, 10); double-noded (1) (Jaschhof 1998: Figs 13 e, 23 c; Gagné 1981: Figs 60 – 64).  
In many Cecidomyiidae, Cecidomyiinae, the flagellomeres have a double node, the two parts being separated by a constriction. In Cecidomyiidae, Catotrichinae, there is also a double node but the more apical one seems to be more of a setose swelling on the neck of the flagellomere. In many other Cecidomyiidae there is a more a less distinct non-setose swelling (see Jaschhof 1998) on the apical part of the neck of the flagellomere. We have coded all these cases as double-noded.
5. Antennal flagellomeres with monoporous sensillae (0) (Fig. 4A, B; Gagné 1981: Figs 39, 41, 42, 43, 44); with polyporous sensillae or circumfilia (1) (Gagné 1981: Figs 40, 46, 56, 60).  
These setae can be scattered, or they tend to appear in whorls in the Cecidomyiidae and some Bibionidae. No distinction between these cases has been made. We do not share the opinion of Jaschhof (2000) that the longer seta-like vestiture of the Cecidomyiidae, including his hooded sensillae, are not setae or trichoid sensillae. We have interpreted the structures called “scales” as Grimaldi *et al.* (2003) have done, Fig. 8:3, as strong setae.
6. Maxillary palp with 5 palpomeres (0); (Fig. 4C; Söli 1997: Fig. 8A, F); with 4 palpomeres (1) (Jaschhof 1998: Fig. 1); with 3 palpomeres or less (2) (Söli 1997: Fig. 8D, E).

- The complete or maximum number of palpomeres in the Sciaroidea is 5 (cf. Jaschhof 2000). The reduced number is the result of the obliteration of the basal segment by union with the original palpomere 2, or by total obliteration. Even this basal segment may be obscured because of its union with the original palpomere 3, which is apparently always present. The reduced number may even be the result of obliteration/union of the apical segment/s.
7. Palpomere 4 attached at the apex of palpomere 3 (0) (Fig. 4C); attached on the ventral side of palpomere 3 and far from its apex (1) (Vockeroth 1981: Fig. 8).
  8. Head normal (0) (Fig 3; Vockeroth 1981: Figs 6, 7); long and deflexed (1) (Shaw 1948: Figs 16 – 21, Vockeroth 1981: Fig. 9).
  9. Scutum with a non-setose stripe at least between lateral and dorsocentral-acrostichal setae (0) (Fig. 5A; Söli 1997: Fig. 13; Hutson *et al.* 1980: Figs 18-19); scutum completely setose (1) (Hutson *et al.* 1980: Figs 20-23).
  10. Mesepimeron posteroventrally extending to posterior margin of katepisternum and ventral end of pleurotergite (0) (Fig. 5A, B, C); abbreviated and not reaching the ventral margin of pleura (1) (Shaw 1948: Fig. 9).
  11. The anterior/anteroventral margin of mesepimeron ends ventrally opposite the middle coxa (0) (Fig. 5A); ends at the anterodorsal corner of episternum 3 (1) (Fig. 5B, C).  
This is a character which separates the Sciaridae in the traditional sense from other Sciaroidea, as already pointed out by Shaw (1948) and Matile (1990).
  12. Laterotergite flat (0) (Fig. 5A); bulging (1) (Söli 1997: Figs 14A, C, D).
  13. Anteroventral margin of laterotergite straight to slightly curved (0) (Shaw 1948: Figs I:2 – 7); roundly curved on entire anteroventral half (Fig. 5A, B, C; Shaw 1948: Fig I:1).
  14. Suture between laterotergite and mediotergite distinct (0); absent (1).  
The absence of a clear suture between laterotergite and mediotergite was used as one of the characters of the Rangomaramidae by Jaschhof & Didham (2002).
  15. Laterotergite non-setose (0) (Fig. 5B, C); setose (1) (Fig. 5A).
  16. Pleural pit well-developed (0) (Fig. 5A, C); weakly developed or absent (1) (Fig. 5B).

The origin or invagination point of the pleural apodeme at the junction of the anepisternum, anepimeron and katepisternum may be open or closed. When open it is called the pleural pit. All intermediate stages occur within the Sciaroidea or Bibionomorpha. For present purposes, we classify the pleural pit as well-developed when it is large, exposed in lateral view, and when the anterior margin of the anepisternum is interrupted by the pit. In these cases the pleural apodeme is also a long, curved, funnel-like structure.

17. Episternum 3 non-setose (0) (Fig. 5A, B, C); setose (1).

18. Phragma developed, intruding into the base of the abdomen (0) (Figs 5A, B, C; Chandler 2002: Figs 93 – 100); phragma undeveloped, not intruding into the abdomen (1) (Chandler 2002: Fig. 101).

In most Sciaroidea the posteroventral part of the metanotum appears as a bulge of variable size and intrudes more or less deeply into the base of the abdomen (cf Chandler 2002). It is very prominent in the Cecidomyiidae and Sciaridae. In the present analysis, only *Mycetophila*, *Sciophila*, *Lygistorrhina*, *Pterogymnus*, *Sciaropota* and *Promanota* have the phragma undeveloped.

19. Pterostigma absent (0) (Fig. 5D); present (1) (Vockeroth 1981: Fig. 13).

20. Wing shape elongate (0) (Fig. 5D); round (1) (Grimaldi *et al.* (2003): Figs 1:1, 2, 4: 1, 2).

The usual wing shape in the Sciaroidea is elongate, much longer than wide, but roundish forms occur here and there. In the present analysis the roundish form occurs only in the two species of *Archizelmira* (see Grimaldi *et al.* 2003).

21. Anal lobe of wing 90 degrees or more (0) (Fig. 5D); anal lobe of wing less than 90 degrees, i.e. its margin towards wing base recurrent (1) (Hardy 1981: Figs 6, 7, 9, 10, 11; Grimaldi *et al.* 2003: Figs 7:4, 8:4, 9:2, 10:1).

The very strong anal lobe (1) occurs in the present analysis only in some Archizelmiridae and in the Bibionidae. It is also prominent in some Keroplatidae (Vockeroth 1981: Fig.16) but not in the same way as in the Bibionidae and Archizelmiridae.

22. Wing membrane setose (0) (Vockeroth 1981: Figs 11 – 14, 45.); non-setose (Fig. 5D).

The wing membrane is coded as setose even if

the setose area is very restricted, as in *Mycetophila fungorum* which we have studied.

23. The section of costa beyond the tip of R5 long, several times as long as its width (0) (Vockeroth 1981: Figs 13, 14, 15); short, at most three times as long as wide (1) (Fig. 3 D; Vockeroth 1981: Fig 11); absent or almost so (2) (Vockeroth 1981: Fig. 12).

24. Costal break absent (0) (Fig 5D; Gagné 1981: Fig. 23); present (1) (Gagné 1981: Figs 12, 14 – 22).

In the Cecidomyiidae the costa continues as a faint vein-like thickening from the thick anterior portion ending at the tip of R5 or between R5 and M and around the posterior wing margin. The thickened posterior margin can even be seen in some other Sciaroidea. In most Cecidomyiidae there is a clear break between the thick anterior and thin posterior parts. In the Catotrichinae the break appears only as a break in the marginal setosity of the wing, and it is coded as for other Cecidomyiidae. We have not observed a costal break or a break in the setosity in any other sciaroid.

25. Subcosta ending in the costa (0) (Vockeroth 1981; Figs 13, 16, 17, 18, 19, 20); ending free (1) (Fig. 5D, Vockeroth 1981; Figs 11, 12, 15, 21, 22).

26. Subcosta setose (0) (Vockeroth 1981: Fig. 16); non-setose (1) (Fig. 5D).

27. Vein sc-r present (0) (Tuomikoski 1966: Fig. 5; Vockeroth 1981: Figs 13, 48); absent (1) (Fig. 5D).

We consider *Promanota*, in which sc appears to end in R, to have sc-r.

28. Geniculus radialis absent (0) (Hardy 1981: Figs 6 – 11); present (1) (Fig. 5D, E).

The base of R at the humeral cross vein is either straight or there is a step-like shift, the geniculus radialis, towards the costa at the humeral cross vein.

29. Vein R1 extending well into the apical half of the wing (0) (Vockeroth 1981: 11, 12, 13); extending to the middle of the wing (1) (Fig. 5D); extending only over the basal half of the wing (2) (Gagné 1981: Fig. 12).

30. R1 long (0) (Fig. 5A; Vockeroth 1981: Fig. 59); short (1) (Gagné 1981: Fig. 12).

The length of R is very variable. It is only coded here as “short” in those cases where it is very short, transverse or transversely diagonal,

and not longer than Rs.

31. Vein R4 present (0) (Vockeroth 1981: Figs 11 m- 13, 16 – 20, 23 – 26); absent (1) (Fig. 5A; Vockeroth 1981: Figs 14, 15, 22).
32. R4 ending in costa (0) (Vockeroth 1981: Figs 11, 12, 16, 17, 19); in R1 (1) (Vockeroth 1981: Figs 13, 18, 23, 24).
33. R5 or R4+5 curved (0) (Fig. 5A); straight (1) (Vockeroth 1981: Fig. 47).  
R5 is usually curved, following the curvature of the costa, but in a few cases it is straight or almost so.
34. Vein Rs diagonal (0) (Vockeroth 1981: Figs 11 – 13, 15 – 20); transverse (1) (Vockeroth 1981: Figs 14, 38.); recurrent (2) (Grimaldi *et al.* 2003: Figs 4:1, 2, 3).  
The distinction between these states is usually clear. *Rangomarama matilei* is coded as diagonal but is a borderline case. The other species of *Rangomarama* have a distinctly transverse Rs. The distinction between states 1 and 2 may be obscure in some cases in the Sciaridae. A clearly recurrent Rs (“slanted” in Grimaldi *et al.* 2003) seems to be present only in the Archizelmiridae which are thus the only cases that we have coded as state 2.
35. Vein Rs normal (0) (Fig. 5A; Vockeroth 1981: Figs 11 – 20); unusually long, 3 to 4 times as long as the width of costal cell (1) (Jaschhof & Didham 2002: Figs 5 – 7).  
State 1 is coded only for *Rangomarama*. In *Diadocidia* and some Keroplatidae, Rs is also long but it is very diagonal. The character state would perhaps be better described as an unusually long distance between R1 and R4+5.
36. Position of vein Rs at the middle of the wing (0) (Vockeroth 1981: Figs 11 – 13); in the basal half of the wing (1) (Fig. 5A).  
These states are not always completely clear. The borderline cases are resolved by subjective estimates rather than by exact measurements.
37. Base of vein Rs (junction with R) normal, sclerotized (0) (Vockeroth 1981: Fig. 11); unsclerotized (1) (Vockeroth 1981: Figs 14, 16).  
The unsclerotized break at the base of Rs is characteristic of the Ditomyiidae and Diadocidiidae, and also of many Keroplatidae.
38. Vein r-m transverse (0) (Vockeroth 1981: Figs 12-14, 19); longitudinal (1) (Fig. 5A).  
We have coded r-m as transverse in cases when it is strictly transverse and when it is obliquely transverse. It is coded as longitudinal when r-m seems to be a continuation of R4+5 without any angle. It is coded as r-m absent when R and M are united or connected with a scarcely discernible r-m. Cases in which the vein is absent are coded as inapplicable (‘-’).
39. Vein r-m normal, long (0) (Fig. 5D; Vockeroth 1981: Figs 12, 13, 14, 19); very short or absent (1) (Vockeroth 1981: Figs 11, 15 – 18, 20).  
An absent r-m means that a part of R and M are in direct contact at some point or are confluent over a shorter or longer distance. In the latter case there is a vein frm (character 40).
40. Vein frm absent (0) (Fig. 5A); present (1) (Vockeroth 1981: Figs 15 – 18, 20).  
When vein r-m is absent, there may be an unusual vein portion, frm, between stM and Rs. When R and M are touching only at one point, we have coded it as state 0.
41. Vein stM short (0) (Fig. 5A; Vockeroth 1981: Figs 31, 71; Chandler 2002: Figs 4, 11, 15); long (1) (Chandler 2002: Figs 52, 53, 63).  
Vein stM has been coded as short when it is distinctly shorter than the medial fork, and as long when it is of approximately the same length or distinctly longer. For a few borderline cases in the *Heterotricha* group, we follow Jaschhof’s (2004) interpretation. Those cases in the Cecidomyiidae in which M is unforked are coded as 1 because we regard it as obvious that they are derived by an extreme lengthening of stM (cf. Jaschhof 1998: Fig. 43g) or by the obliteration of a short M1 (cf. Panelius 1965: Fig. 7a).
42. Vein portion M+ absent (0) (Fig. 5D; Vockeroth 1981: Figs 12, 38); present (1) (Vockeroth 1981: Figs 13, 19).  
M+ appears on M between veins r-m and bm-cu when these are not contiguous.
43. Basal part of vein M present (0) (Vockeroth 1981: Fig. 19); present as a non-sclerotized fold (1) (Chandler 2002: Figs 37 – 38); absent (2) (Fig. 5D; Vockeroth 1981: Fig. 11)  
In most Sciaroidea the basal part of M is absent (Chandler 2002). In the Bibionidae it is a normally sclerotized vein. In some Sciaroidea it is clearly discernible as a weakly or partly weakly sclerotized vein which is more than simply a longitudinal fold on the

- wing membrane. All these cases are coded as 0. The folds shown by Chandler (2002) in many species of the *Heterotricha* group, probably visible only in dry unmounted specimens, are coded as 1.
44. Vein m-cu connected to CuA1 (0) (Vockeroth 1981: Fig. 12); to stCu (1) (Fig. 5D; Vockeroth 1981: Fig. 71).
  45. Vein m-cu transverse (0); oblique (1); parallel with R (2); converging with R towards wing base (3).
  46. CuA1 and CuA2 divergent (0); parallel on basal two thirds (1).
  47. stCu short, much shorter than CuA2 (0) (Fig. 5D); long, longer than CuA2 (Vockeroth 1981: Fig. 38)
  48. CuA2 evenly curved (0) (Fig. 5D); sinuous (1) (Grimaldi *et al.* 2003: Figs 9:2, 10:1) This character was used by Grimaldi *et al.* (2003) as a synapomorphy of *Archimelzira* and *Burmazelmira*.
  49. Vein A1 extending to wing margin (0) (Vockeroth 1981: Figs 11, 12); abbreviated (1) (Fig. 5D; Vockeroth 1981: Figs 15, 38).
  50. Basal part of vein 1A normal, thin and poorly sclerotized (0) (Fig. 5D); thickened and sclerotized (1) (Jaschhof & Didham 2002: Figs 5 – 7).
  51. Vein M dorsally setose (0); non-setose (1).
  52. Vein CuA1 dorsally setose (0); non-setose (1).
  53. Vein CuA2 dorsally setose (0); non-setose (1). A thickened and abruptly truncated basal portion of A1 is a characteristic of *Rangomarama*. There are faint indications of a similar development in *Sciarosoma* and *Sciaropota*.
  54. Veins R4+5 and M1 parallel or divergent (0) (Fig. 5D; Vockeroth 1981: Fig. 15); convergent towards wing margin (1) (Gagné 1981: Figs 18, 20).
  55. Basal cell parallel-sided or widening towards apex (0); widening towards base (1).
  56. Tibial spur/s present (0); absent (1).
  57. Tibial organ absent (0); present (1) (Fig. 4D; Söli 1997: Fig. 20 A - E).
  58. Tibiae medially with normal microtrichia (0); without normal microtrichia (1). The Cecidomyiidae differ from other Sciaroidea by having short, normal microtrichia along the whole tibia and lacking the enlarged trichia (non-socketed setae) in addition to setae (socketed setae). In other Sciaroidea, normal microtrichia are found only at the base of the tibia, and rarely also in other places among enlarged trichia.
  59. The longer tibial vestiture with socketed setae only (0); with socketed setae and enlarged microtrichia which are as large as the setae (1) (Fig. 4E, D). No distinction has generally been made in the literature between different types of tibial vestiture except for the stronger spines and the weaker hairs or setae. The element usually called "seta" consists of two different kinds, those with sockets (trichoid sensillae) and those without sockets. The latter are probably enlarged microtrichia.
  60. Tibial and tarsal setae normal (0) (Fig. 4D, E); scale-like (1) (Jaschhof 1998: Fig. 8D). The scale-like vestiture occurs only in Cecidomyiidae. The scales can occur on all body parts. When necessary, we have chosen the fore tibia as a reference point, or in extreme cases the fore basitarsomere.
  61. Tibial vestiture normal (0) (Söli *et al.* 2000: Fig. 27); in rows (1) (Söli *et al.* 2000: Figs 26, 29-30). The arrangement of the tibial vestiture is a commonly-used character in sciaroid systematics. In most cases the character states are quite clear, but there are also cases which are difficult to judge. We have regarded a taxon as belonging to state 1 if there is a clear indication that the vestiture is arranged in rows at least on the apical part of the fore tibia.
  62. Coxae short (0) (Jaschhof 1998: Fig. 3); long (1) (Fig. 4A). We have not used any special measurements to estimate the states of this character. There is a clear difference between the Bibionidae and Cecidomyiidae, which have the coxae scarcely longer than broad, and the other Sciaroidea, which have them much longer than broad, especially the fore coxa.
  63. Basitarsomeres normal, longer than tarsomere 2 (0) (Gagné 1981: Fig. 80); basitarsomeres short, shorter than tarsomere 2 (1) (Gagné 1981: Fig. 81). State 1 is found only in the Cecidomyiidae and is traditionally used to separate the Cecidomyiinae and Porricondyliinae from the other groups.
  64. Abdominal tergites with plaques (0) (Jaschhof 2000: Fig. 17); without plaques (1). The plaques appear as roundish or oval,



sharply delimited, more or less distinctly depressed areas without the normal surface structure of the tergites. They can be concolorous with the adjacent area of the tergite, but usually they are paler, but sometimes even darker. They are usually easily seen, but in some cases are very difficult to discern, e.g. *Sciaropota*.

65. Abdominal tergites with two or more pairs of plaques (0) (Jaschhof 2000: Fig. 17); with one pair of plaques (1).
66. Posterior margin of male tergite 9 simple (0) (Chandler 2002: Fig. 18); with prominent ornamented lobes (1) (Chandler 2002: Figs 33, 50).
67. The strong setae/megasetae on male tergite 9 simple (0); double or cleft (1) (Jaschhof & Didham 2002: Fig. 30).  
The cleft enlarged setae on male tergite 9 were noted by Jaschhof & Didham (2002) in one species of *Rangomarama*. We found that there are similar setae in *Chiletricha* and *Rhynchoheterotricha*. They do not occur in *Ohakunea* in which there are enlarged setae in the same position.
68. Tegmen absent (0); present (1) (Steffan 1981: Figs 20 – 23; Gagné 1981: Figs 82 – 87; Jaschhof & Didham 2002: Fig. 71).  
By “tegmen” we mean a plate formed by medially fused parameres. A tegmen occurs in all the Cecidomyiidae and Sciaridae and in two species of the Rangomaramidae. This structure has not been studied in a large number of the groups included in the present analysis.
69. Aedeagal teeth absent (0) (Fig. 6A, C); present (1) (Vilkamaa 2000: Fig. 9B).

In most genera of the Sciaridae, the apical part of the aedeagus bears small pointed tooth-like structures. These are clearly modified microtrichia and a complete morphological series from normal microtrichia to teeth can be seen in the family. The presence of these teeth was listed as a synapomorphy of Sciaridae by Blaschke-Berthold (1994) The microtrichia on the aedeagus can be found in many groups of the Sciaroidea, but they are often difficult to observe. They are present in at least most Cecidomyiidae, and in some cases modifications to the teeth can be seen (Jaschhof 1998: Fig. 43d and Fig. 74) though not in the ingroup taxa in the present analysis. In *Rangomarama* there are microtrichia in the

same way as in many Sciaridae and at least as in *Sciarosoma*.

70. Female sternum 8 normal (0) (Fig. 7B); posteriorly high and concave (1) (Chandler 2002: Figs 25, 26, 35).
71. Female sternum 8 with normal setae (0) (Fig. 7B); with a dense fringe of posteriorly directed setae (1) (Chandler 2002: Figs 25, 26, 36).
72. Female sternum 9 normal (0) (Figs 7A, B); unusually large and sclerotized (1) (Chandler 2002: Figs 10, 25, 36).
73. Female tergite 10 with normal hairs (0) (Fig. 7B); with densely placed, long, golden hairs (1) (Chandler 2002: Figs 8, 10).
74. Female cercus two-segmented (0) (Fig. 7A, B); one-segmented or the apical segment greatly reduced in size (1) (Gagné 1981: Fig. 121).
75. Female cercal segment 1 normal (0) (Fig. 7B); produced apicodorsally (1) (Chandler 2002: Figs 25, 26).  
The basal segment of the cercus is unmodified in all the taxa we studied, except in *Chiletricha* and *Rhynchoheterotricha*. In the former, the segment is bluntly produced apicodorsally, whilst in the latter there is a sclerotized curved horn-like projection.
76. Female cercal segment 2 simple (0) (Fig. 7A, B); modified (1) (Chandler 2002: Figs 8, 10).  
The cercal segment 2 is very uniformly elongate-oval in the Sciaroidea. In *Colonomyia* it is very narrow and finger-like apicolaterally on segment 1. In *Heterotricha* and *Rhynchoheterotricha* the apical part is curved laterad in the former, dorsolaterad in the latter.
77. Female spermathecae sclerotized (0) (Fig. 7A, B); unsclerotized (1).

## Results and discussion

The analysis with only the extant taxa in the ingroup produced two most parsimonious cladograms, the strict consensus of which (241 steps, CI 36, RI 73) was fully resolved except for a trichotomy in one of the two main clades. However, there was much homoplasy in the data. The clade including the Keroplatidae and Ditomyiidae (node A, supported by five character state changes) appeared as the sister-group of all other ingroup taxa (Fig. 1). Our data supported a hypothesis of a close relationship between Keroplatidae and Ditomyiidae (B, three character state changes) but could not resolve the exact relationships among

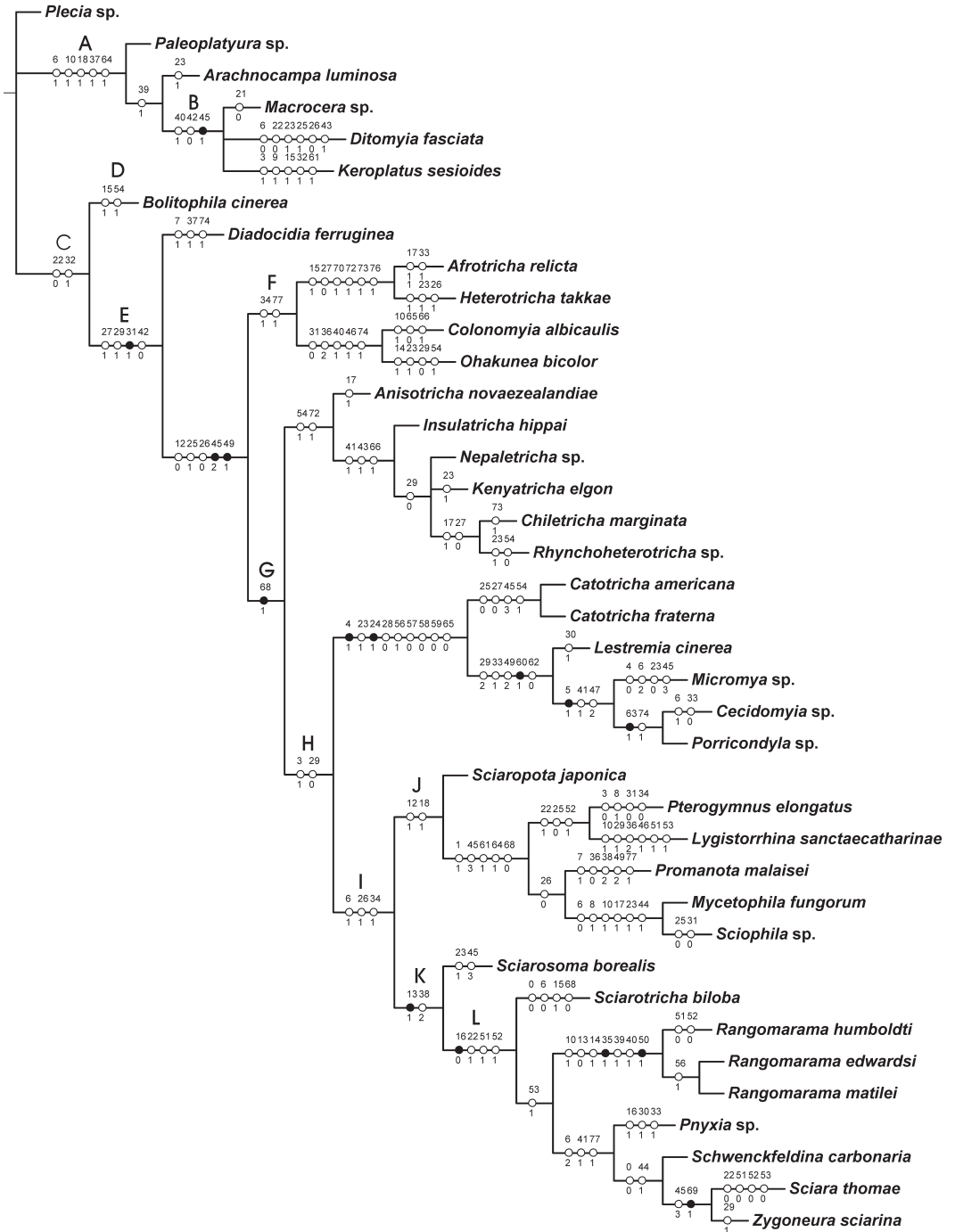


Fig. 1. Phylogeny of the extant Sciaroidea. The strict consensus of two most parsimonious cladograms (241 steps, CI 36, RI 73) obtained with the program NONA. Letters above hatch marks refer to clades discussed in the text, numbers above hatch marks (open = homoplasious, black = unique) refer to characters, numbers under hatch marks refer to state changes to the state indicated. Only unambiguous changes are shown.

these. This result contrasted with the cladistic result of Matile (1997), based on 30 morphological characters, which suggested a sister-group relationship between the Keroplatidae and Diadocidiidae, whereas the Ditomyiidae had a more apical position in the phylogenetic system.

The other main clade, (node C), including the rest of the ingroup terminals, showed *Bolitophila* and *Diadocidia* successively in the most basal positions (nodes D and E). The *Heterotricha* group of genera appeared polyphyletic, to an even greater extent than suggested by Chandler (2002), but none of its elements appeared as the sister-group of the Sciaridae, as suggested by Chandler (2002). *Heterotricha* itself and *Anisotricha* formed the sister-group of *Colonymyia* + *Ohakunea* (node F). The two latter genera, which have been without a clear family assignment, were sister-groups as had been conjectured by Jaschhof & Hippa (2002), Chandler (2002) and Hippa & Jaschhof (2004).

Six of the genera in the *Heterotricha* group, including the new *Insulatracha* Jaschhof (2004), formed a monophyletic group which appeared as the sister-group of the Cecidomyiidae + (Mycetophilidae group of (sub)families + Sciaridae) in our new concept (node G). The Mycetophilidae clade (node J), with the groups most traditionally included (e.g. Vockeroth 1981), also included *Pterogymnus* as suggested by Chandler (2002), and *Sciaropota*, and appeared as the sister clade of the sciarid clade (node I). Jaschhof (2004) discussed the difficulty of using the highly contradictory evidence of the genitalic characters for inferring the phylogeny among the genera of the *Heterotricha* group. Our parsimonious solution, based only on the extant taxa, differed from both his and Chandler's (2002) conclusions but agreed with both in the obvious non-monophyly of the group.

Our hypothesis on the position of the Cecidomyiidae (node H) is not in accordance with the views of Matile (1990, 1997), Blaschke-Berthold (1994), and Blagoderov & Grimaldi (2004) who placed the Cecidomyiidae as the sister-group of all the other Sciaroidea studied by them (but see the fossil analysis below). Our result also strongly contradicts the hypotheses of Wood & Borkent (1989) and Oosterbroek & Courtney (1995) who regarded the Cecidomyiidae and Sciaridae as sister-groups (a relationship that is also still shown in the 'Tree of Life' on the Internet). In these latter phylogenies, the evidence for the Cecidomyiidae + Sciaridae relationship was based mainly on a few

larval or cytological characters, which are only known in a few scattered exemplar taxa of the present ingroup. The only macromorphological character of the adults used by these authors is the 'costalization of the wing veins' and the holoptic compound eyes but so far as our material is concerned, this cannot be regarded as a synapomorphy of the Cecidomyiidae + Sciaridae. Hennig (1973) had serious doubts about the cytological evidence for the Cecidomyiidae + Sciaridae sister-group relationship. Jaschhof & Didham (2002) regarded the Cecidomyiidae + Rangomaramidae to be the sister-group of the Sciaridae. The association of the Rangomaramidae and Cecidomyiidae by Jaschhof & Didham (2002) was based on one synapomorphy, the lack of tibial spurs, but this is not actually correct because the plesiomorphic state, the presence of spurs, is present in at least one species of *Rangomarama*.

The sciarid clade (node K) included four main groups/clades: the *Sciarosoma* group/clade, the *Sciarotricha* group/clade, the *Rangomarama* group/clade and the *Sciara* group/clade. The position of *Sciarosoma* as the sister-group of all the rest of the sciarid clade was relatively weakly supported by two characters, one of which, the roundly curved anteroventral margin of laterotergite (13: 1), is unique. The support for *Sciarotricha* as the sister-group of the *Rangomarama* + *Sciara* group was stronger, based on four character changes, of which the occurrence of the developed pleural pit (character 16: 1) is unique (node L).

The *Rangomarama* group was ranked as the family Rangomaramidae and postulated to be the sister-group of the Cecidomyiidae by Jaschhof & Didham (2002) (see comment under Cecidomyiidae above). According to the present phylogeny, *Rangomarama* is the sister-group of the Sciaridae in the strict sense. Although this relationship was not strongly supported by character evidence, it was the only parsimonious solution obtained from the present data.

The second analysis, with the fossil Sciaroidea included in the ingroup, also produced two most parsimonious cladograms, the strict consensus of which (268 steps, CI 32, RI 69) was fully resolved except for two trichotomies (Fig. 2). The solution was partly identical, but partly greatly different, from the one with only the extant taxa. In the fossil cladogram, the Cecidomyiidae appeared in a different clade at the base of the cladogram, separated from all the other groups (node a). In the

other major clade, most fossil taxa were in the same apical clades together with *Bolitophila*, *Dia-docidia*, *Ditomyia* and the Keroplatidae (node b). The fossil Mangasidae, originally described as a subfamily of the Bolitophilidae, is polyphyletic: the type genus belongs to the 'keroplatid clade' (node c), but Mangasinae gen. sp. of Kovalev (1986) is the sister-group of *Bolitophila* (node d). Chandler (2002) noted that *Mangas* does not belong to the Bolitophilidae. The core of the *Heterotricha* group appeared monophyletic, provided that *Sciaropota* and *Sciarosoma* are excluded. *Ohakunea* + *Colonomyia* appeared closer to *Sciaropota* + Mycetophilidae (node e). The recently described Mesozoic genus *Thereotricha* (Blagoderov & Grimaldi 2004), assigned to Sciaroidea incertae sedis, probably belongs to the *Sciaropota* + Mycetophilidae clade because of the wholly setose scutum. We did not include *Thereotricha* in our matrix because we could not interpret many of the wing characters. The sciarid clade as a whole (node f), with the inclusion of *Sciarosoma* and the new *Sciarotricha*, was identical with the extant analysis except that the *Archizelmira* group now appeared as the sister-group of the *Sciara* group. An identical result was obtained when only the Archizelmiridae from among the fossil taxa was included in the analysis.

According to the present parsimonious result, *Rangomarama* is the sister-group of the Sciaridae in the strict sense + the *Archizelmira* group (node g), based on the non-setose wing vein CuA2 (53:1). However, this character state has a reversal into the setose type in *Sciara*.

The *Sciara* group or Sciaridae in the traditional meaning is monophyletic (node i). The Mesozoic archizelmirids are monophyletic (node j), as suggested by Grimaldi *et al.* (2003), and they are the sister-group of the *Sciara* group (node h). However, the characters of the *Archizelmira* group are poorly known and we would not be surprised if this sister-group relationship just with the *Sciara* group would later be shown to be incorrect. Grimaldi *et al.* (2003) considered many characters common to the Sciaridae and Archizelmiridae as convergences, e.g. the wing venation, including the basal displacement of the cubital veins, and the well-developed pulvilli. We analysed the wing venation characters in detail, whereas the characters of the tarsal claws and pulvillar structures would need a SEM examination of all the groups in question and were excluded. Contrary to our

results, Grimaldi *et al.* (2003) also considered the Archizelmiridae, together with *Heterotricha* and *Ohakunea*, for example, to be the basal groups of the Sciaroidea. However, they did not present a numerical matrix or a rigorous parsimony analysis to support their views on the position of the different sciaroid groups. Blagoderov & Grimaldi (2004) derived the wing venation of the Archizelmiridae from that of the Ditomyiidae.

The results of the extant and fossil analyses taxa were in part rather different. The high level of homoplasy in the data must at least partly explain the great effect of taxon sampling on the cladogram topology. It is hard to say which of the two results is a 'better' phylogeny. The fossil analysis is better in having more recognized taxa of the study group included, a drawback is that many of the characters were not available for study in the fossils. Interestingly, the sciarid clade (node f in Fig. 2) remained stable, the *Archizelmira* clade always being the sister clade of the *Sciara* clade, whereas other parts of the cladogram changed when inclusion or exclusion of one or more of the other sciaroid fossils were tried in analyses. However, if fossils are included in the analysis, it seems difficult to judge why representatives of all the main groups available for study should not be included.

### Ranking of the clades and redefinition of the Sciaridae

The currently accepted family classification of the Sciaroidea seems for the most part to be cladistically well founded, so far as can be determined from the study of only a few representative taxa. It may be a matter of opinion as to whether it is necessary to separate the Ditomyiidae from the Keroplatidae at the family level. The hierarchical level of the internal classification of the mycetophilid clade remains open because only a limited variety of the extant and fossil taxa were included in the analysis. It seems that the Mesozoic Mesosciophilidae is an integral part of Mycetophilidae s. l., not a sister-group of any larger clade. Our results support Chandler's (2002) suggestion that it is an available family or subfamily assignment for the recent similar *Pterogymnus*. If the Mesosciophilidae is accepted as a family, then the family level status for the Lygistorrhinidae is also correct, although we suggest that there is a closer relationship between the Mycetophilidae and Lygistorrhinidae, as Blagoderov & Grimaldi (2004)

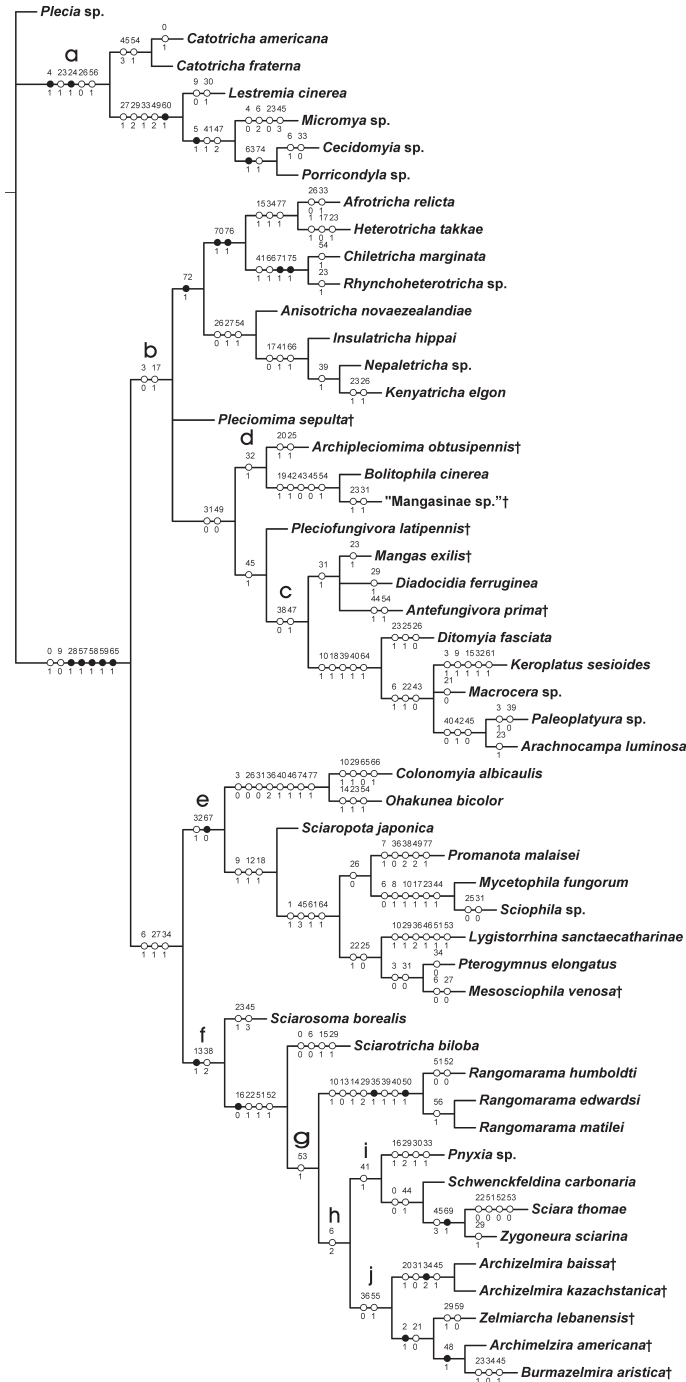


Fig. 2. Phylogeny of extant and fossil Sciaroidea. The strict consensus of two most parsimonious cladograms (268 steps, CI 32, RI 73) obtained with the program NONA. Letters above hatch marks refer to clades discussed in the text, numbers above hatch marks (open = homoplasious, black = unique) refer to characters, numbers under hatch marks refer to state changes to the state indicated. Only unambiguous changes are shown.

Table 3. The new concept of Sciaridae. Of Sciarinae, only the genera used in the analyses are listed.

Subfamily	Genus
Archizelmirinae† stat. n.	<i>Archizelmira</i> Rodendorf, 1962 <i>Archimelzira</i> Grimaldi, De Souza Amorim & Blagoderov, 2003 <i>Burmazelmira</i> Grimaldi, De Souza Amorim & Blagoderov, 2003 <i>Zelmiarcha</i> Grimaldi, De Souza Amorim & Blagoderov, 2003
Rangomaraminae stat. n.	<i>Rangomarama</i> Jaschhof & Didham, 2002
Sciarinae	<i>Pnyxia</i> Johannsen, 1912 <i>Schwenckfeldina</i> Frey, 1942 <i>Sciara</i> Meigen, 1803 <i>Zygoneura</i> Meigen, 1830
Sciarosominae subfam. n.	<i>Sciarosoma</i> Chandler, 2002
Sciarotrichinae subfam. n.	<i>Sciarotricha</i> gen. n

have done. We do not at present have any strong view on the status of the *Heterotricha* group, other than on *Sciarosoma*. It is, however, clear that the genera in question cannot be included in any existing family and that two or three new families or subfamilies are needed for a formal classification. Even the position and classification of the *Ohakunea* group (*Ohakunea* + *Colonomyia*) remains open. We are continuing with further studies on the phylogeny and status of the *Heterotricha* and *Ohakunea* groups.

So far as the classification of the sciarid clade is concerned, there are several possibilities: 1) The existing families Archizelmiridae, Sciaridae and Rangomaramidae could be accepted as family rank taxa and two new families could be founded for *Sciarotricha* and *Sciarosoma*, 2) The whole clade could be regarded as the family Sciaridae, with or without subfamilies, 3) The Sciaridae could be delimited anywhere between these extremes and the more basal clades could be regarded as families. To maintain some kind of intelligibility and practical usefulness in the family level division of the Sciaroidea, we prefer to consider the whole clade of similar taxa as the family Sciaridae with five subfamilies. Our proposal for the classification of Sciaridae, including a short diagnosis of the family and subfamilies, is as follows (for summary, see Table 3).

### Family Sciaridae Billberg, 1820

Type-genus *Sciara* Meigen, 1803

For a historical review and synonymy, see Steffan (1966) and Menzel & Mohrig (2000).

*Diagnostic characters.* - Holoptic or dichoptic, ocelli in an equilateral triangle, palp with 5 to 1 palpomeres, scutum with lateral, dorsocentral and acrostichal setae separated by bare spaces, pleural pit undeveloped to well-developed, epimeron ventrally extending to ventral margin of pleura or shortened, in the former case its anterior margin ending from opposite middle coxa to anterodorsal corner of episternum 3, pleurotergite flat, setose or non-setose, thoracic abdominal junction broad, phragma well-developed, intruding into basal part of abdomen, coxae much longer than broad, costal break absent, Sc ending free, sc-r present or absent, R2 present or absent, Rs from transverse to oblique, r-m oblique or in line with R4+5, long to short or even absent so that frm (fusion of radius and media) may be present, basal part of M absent so that there is no longitudinal fold on the membrane of basal cell, bm-cu ending either on CuA1 or on stCuA, A1 not extending to wing margin, tibial vestiture not in rows, comprising socketed setae and enlarged microtrichia of the size of the former, tibial spurs present or absent, abdominal terga with one pair of plaques, hypopygium variable, gonostyli simple or deeply incised so that there is a dorsal and a ventral branch, parameres separate or medially fused to form a tegmen, aedeagus with or without microtrichia which, when present, may be modified into triangular teeth, female genitalia 'normal', cercus two-segmented, sclerotized spermathecae present or absent.

The extant Sciaridae are distinguished from other Sciaroidea as follows: 1) From the Mycetophilidae, including *Sciaropota*, *Pterogymnus* and probably even the fossil Mesosciophilidae, Lygistorrhinidae, Manotidae, Mycetophilinae and

Sciophilinae, by having notal setae in lateral, dorso-central and acrostichal rows with bare spaces between, not evenly setose, by having a flat, not bulging, pleurotergite, by a broad thoracic-abdominal junction, from all but *Sciaropota* also by the lack of tergal plaques and an equilateral, not transversely broad ocellar triangle; furthermore, the tibial vestiture is not in rows as in most Mycetophilidae. 2) From *Ohakunea* and *Colonomyia* by the lack of R2, by having rs near the middle of wing, not placed extremely basally, by the lack of the vein portion from, by divergent Cu1 and Cu2, not parallel in basal half, and by having the female cercus with a well developed, normal segment 2 instead of having it rudimentary or absent. 3) From the taxa of the *Heterotricha* group by having r-m in line, not at an angle, with R5 and by having bm-cu converging with R towards the base of wing, not parallel, and by one or more of the following characters which are or may be variable within the *Heterotricha* group: sc-r absent, basal cell narrow, without a fold-like trace of the basal part of M, transverse or at most slightly oblique Rs (Rangomaraminae) and normal sciaroid female genitalia, without unusual modifications in the chaetotaxy of sternite 8 and tergite 10 and the cerci. 4) From the Keroplatidae, Diadocidiidae, Ditomyiidae and Bolitophilidae by the lack of any trace of the basal part of M or a broad basal cell, by the longitudinal, not transverse or almost transverse, bm-cu, by the abbreviated A which does not reach wing margin or almost so, and by the presence of tergal plaques and by the flat, not bulging, pleurotergite 5) From the Cecidomyiidae by the presence of enlarged seta-like microtrichia on tibiae, by the lack of a costal break, by the presence of a geniculus radialis, by the long coxae, by having only one pair of tergal plaques, and also, in most cases (except most Rangomaraminae), by the presence of tibial spurs.

The incompletely known fossil Sciaridae (Archizelmirinae) differ from other Sciaroidea, recent and fossil, by having Rs almost at the middle of the wing, not in the basal half, and by having the basal cell of the wing broadest subbasally, not at the middle or in the apical half.

#### **Sciaridae (Sciarosominae) subfam. n.**

Type genus *Sciarosoma* Chandler, 2002.

*Genera included.* - *Sciarosoma* Chandler, 2002 (Palearctic).

*Diagnostic characters.* - Dichoptic, palp with 5 palpomeres, pleural pit undeveloped, anterior margin of mesothoracic anepimeron ending at middle coxa, widened ventrally, pleurotergite non-setose, R2 absent, Rs in basal half of wing, stCu absent, stM shorter than M2, tibial spurs well-developed, gonostylus bilobed, tegmen absent, female characters unknown.

Distinguished from the Sciaridae (Sciarinae) by having the anterior margin of the anepimeron terminating ventrally at the middle coxa, not more posteriorly at episternum 3, by lacking the pleural pit and tegmen, and by having stM shorter than M fork; from the Sciaridae (Sciarotrichinae) and most of the Sciaridae (Sciarinae) by the dichoptic eyes; and from the Sciaridae (Rangomaraminae) by having the anepimeron extending to ventral margin of pleura and by a normal, not unusually long, Rs. Distinguished from the fossil Sciaridae (Archizelmirinae) by the normal basal cell that does not widen towards base, and by having Rs in basal half of wing, not at the middle or in apical half.

#### **Sciaridae (Sciarotrichinae) subfam. n.**

Type-genus *Sciarotricha* gen. n.

*Genera included.* - *Sciarotricha* gen. n. (southern Africa).

*Diagnostic characters.* - Holoptic, palp with 5 palpomeres, pleural pit well developed, anteroventral margin of anepimeron ending at middle coxa, ventral part of anepimeron widened apically, pleurotergite setose, R2 absent, Rs in basal half of wing, stCu absent or present, stM shorter than M2, tibial spurs well developed, gonostylus bilobed, tegmen absent, female with sclerotized spermathecae.

Distinguished from the other subfamilies by the combination of holoptic eyes and ventrally expanded epimeron, the anteroventral margin of which ends opposite middle coxa. The bilobed gonostylus distinguishes the type-species from other Sciaridae except for *Sciarosoma*. See also under *Sciarotricha* below.

#### **Sciaridae (Rangomaraminae), Jaschhof & Didham, 2002, stat. n.**

Type-genus *Rangomarama* Jaschhof & Didham, 2002

*Genera included.* - *Rangomarama* Jaschhof & Didham (New Zealand).

*Diagnostic characters.* - Dichoptic, palp with less than 5 palpomeres, pleural pit developed, anepimeron shortened, not reaching the ventral margin of pleura, pleurotergite non-setose, R2 absent, Rs in basal half of wing, unusually long, stCu absent, r-m short and oblique or absent, shorter than M2, tibial spurs rudimentary or absent, gonostylus one-lobed, tegmen present, female with sclerotized spermathecae absent.

Distinguished from other recent Sciaridae by the unusually long Rs, by the mesothoracic epimeron abbreviated, not reaching the ventral margin of thorax, and by having the posterior margin of pleurotergite obliterated.

### Sciaridae (Archizelmirinae) Rohdendorf, 1962, stat. n.

Type-genus *Archizelmira* Rohdendorf, 1962

*Genera included.* - *Archizelmira* Rohdendorf (Mesozoic), *Archimelzira* Grimaldi *et al.* (Mesozoic) *Zelmiarcha* Grimaldi *et al.* (Mesozoic), *Burmazelmira* Grimaldi *et al.* (Mesozoic).

*Diagnostic characters.* - Dichoptic, palp with less than 5 palpomeres, pleural characters unknown, R2 present or absent, Rs at the middle of wing, r-m longitudinal, stCu absent, stM shorter than M2, gonostylus one-lobed, tegmen apparently present, female characters unknown.

Distinguished from the other subfamilies by the unusually apical position of Rs and by the cell limited by R1, Rs, r-m, m-cu, CuA1 and Cua2 (basal cell) being broadest in its basal half.

### Sciaridae (Sciarinae) Billberg, 1820.

Type-genus *Sciara* Meigen, 1803

For a historical review and synonymy, see Steffan (1966).

*Genera included.* - About 80 genera (cf Menzel & Mohrig 2000). Distribution worldwide.

*Diagnostic characters.* - Holoptic or dichoptic, palp with less than 5 palpomeres, pleural pit developed or underdeveloped, anteroventral margin of anepimeron complete, oblique, ending at anterodorsal corner of episternum 3, pleurotergite non-setose, R2 absent, Rs in basal half of wing, r-m

longitudinal, stCu present or absent, stM longer than M2, tibial spurs well developed, gonostylus one-lobed, tegmen present, female with sclerotized spermathecae absent.

Always distinguished from the other subfamilies by the character of the mesothoracic epimeron with its anterior margin ending at anterodorsal margin of episternum 3.

### The genus *Sciarotricha* gen. n.

Type-species *Sciarotricha biloba* sp. n.

*Description.* - Medium-sized Sciaroidea, wing length 1.5-2.0 mm.

Head (Fig. 3). Eye bridge present, broad, 8 facets wide. Eyes large, in posterior view of head occupying a broad lateral area so that the occiput is narrow, without interfacetal microtrichia, with interfacetal setae which extend well beyond the curvature of facets. Ocelli three, in an equilateral triangle which is close to median eye margins. Anterior vertex short, non-setose. Prefrons setose, the setae subequal in size. Clypeus not distinctly separated from prefrons and labrum, non-setose. Antennal scape and pedicel (Fig. 3A) subglobose with a few dorsal and ventral setae, flagellum with 14 flagellomeres, subequal in size, the flagellomeral body about one-and-a-half times as long as wide, the neck short, about one fifth of the width of the body, the vestiture of the flagellomeral body (Fig. 3A, 4B) with seta-like sensillae arising from weak plate-like depressions, peg-like sensillae and hyaline sensillae and a few socketed setae on all flagellomeres, the ultimate flagellomere (Fig. 4A) apically with three socketed setae and two short hyaline pegs, microtrichia present only basally on flagellomere 1. Maxillary palp (Fig. 4C) with five segments, or with four segments plus palpifer; galea broad, short, pointed, without vestiture; palpomeres 3 and 4 several times longer than broad, palpomere 5 very elongate, more than 10 times as long as broad; palpifer non-setose, palpomere 2 with 2-3 setae, palpomeres 3-5 with numerous setae, palpomere 3 with numerous dorsal and lateral scattered hyaline sensillae.

Thorax (Fig. 5). Dark brown, setae dark. Scutum broadly setose laterally, with shorter and longer setae, dorsocentral setae in two rows, with longer and shorter setae, acrostichal setae in one row which extends over the whole length of scutum. Scutellum with numerous setae of unequal length. Anterior pronotum with a few setae, poste-



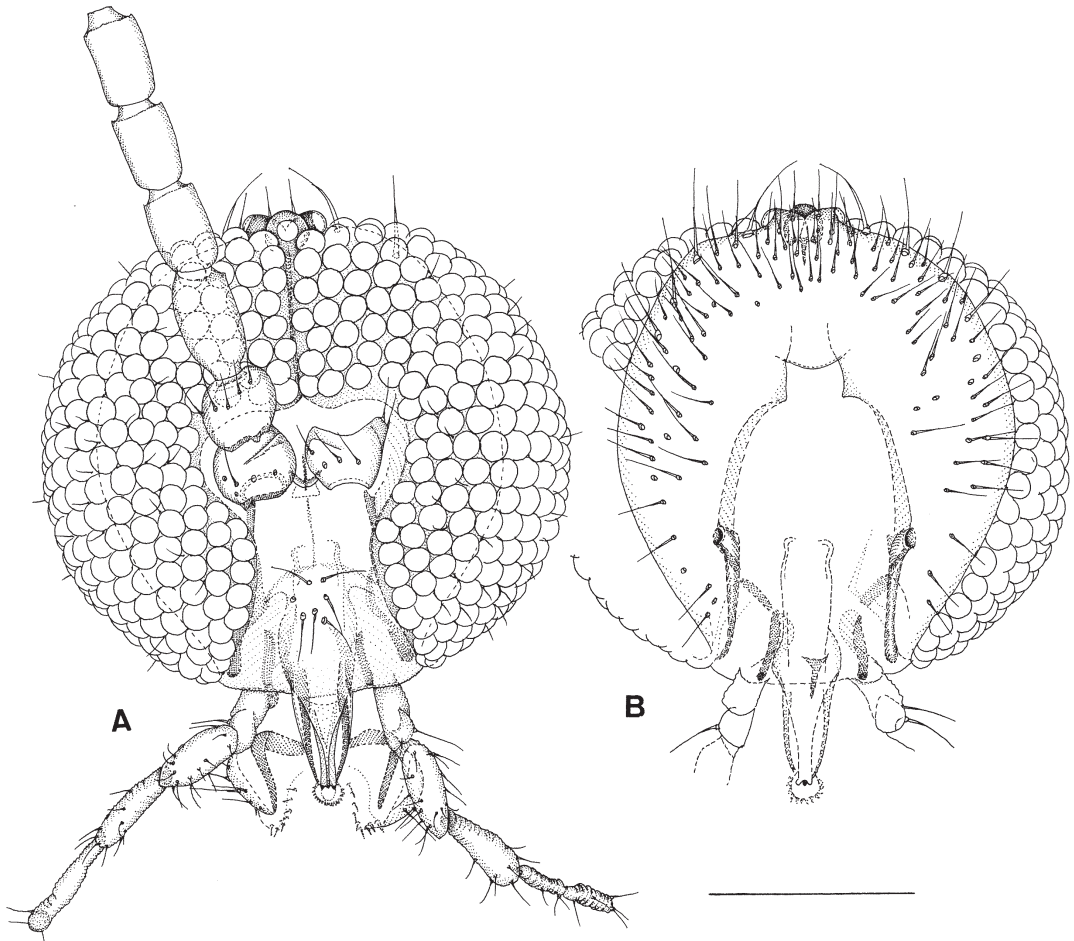


Fig. 3. *Sciarotricha biloba* sp. n. (paratype): male head (A), anterior view, and ditto (B), posterior view. Scale 0.20 mm.

rior pronotum non-setose, episternum 1 setose. Anepisternum with a deep v-shaped cleft dorsally, non-setose. Anepimeron with the anterior margin interrupted by the pleural pit, the posteroventral process reaching metepisternum and posteroventral margin of katepisternum, expanding towards apex, non-setose. Katepisternum deep, angulated dorsally at pleural pit, non-setose. Laterotergite with anterior margin rounded ventrally, setose. Metepisternum non-setose. Metanotum non-setose, phragma intruding into the base of abdomen. Wing (Fig. 5D). Hyaline, tinged with brown. Bm-cu joining with CuA1 or stCuA. R, R1, R 3+4 and basal part of Cu2 dorsally setose, other veins dorsally non-setose, all ventrally non-

setose; wing membrane non-setose, the setae on posterior wing margin only on dorsal side. Haltere short, the knob with dorsal and ventral stripe of setae. Legs (Fig. 4D, E). Unicolorous, slightly paler brown than thorax; slender. Coxae long, several times longer than broad, hind coxa slightly shorter than the others. Tibiae with both socketed setae and non-socketed setae (enlarged microtrichia), both subequal in size, tibial vestiture with weak indications of rows, middle and hind tibia with enlarged setae on all sides and both on dorsal and ventral sides apically, on fore tibia only apically, fore tibia prolaterally with a subapical patch of setae (tibial organ) in which the setae are in oblique rows. Tibial spurs 1+2+2, all subequal in

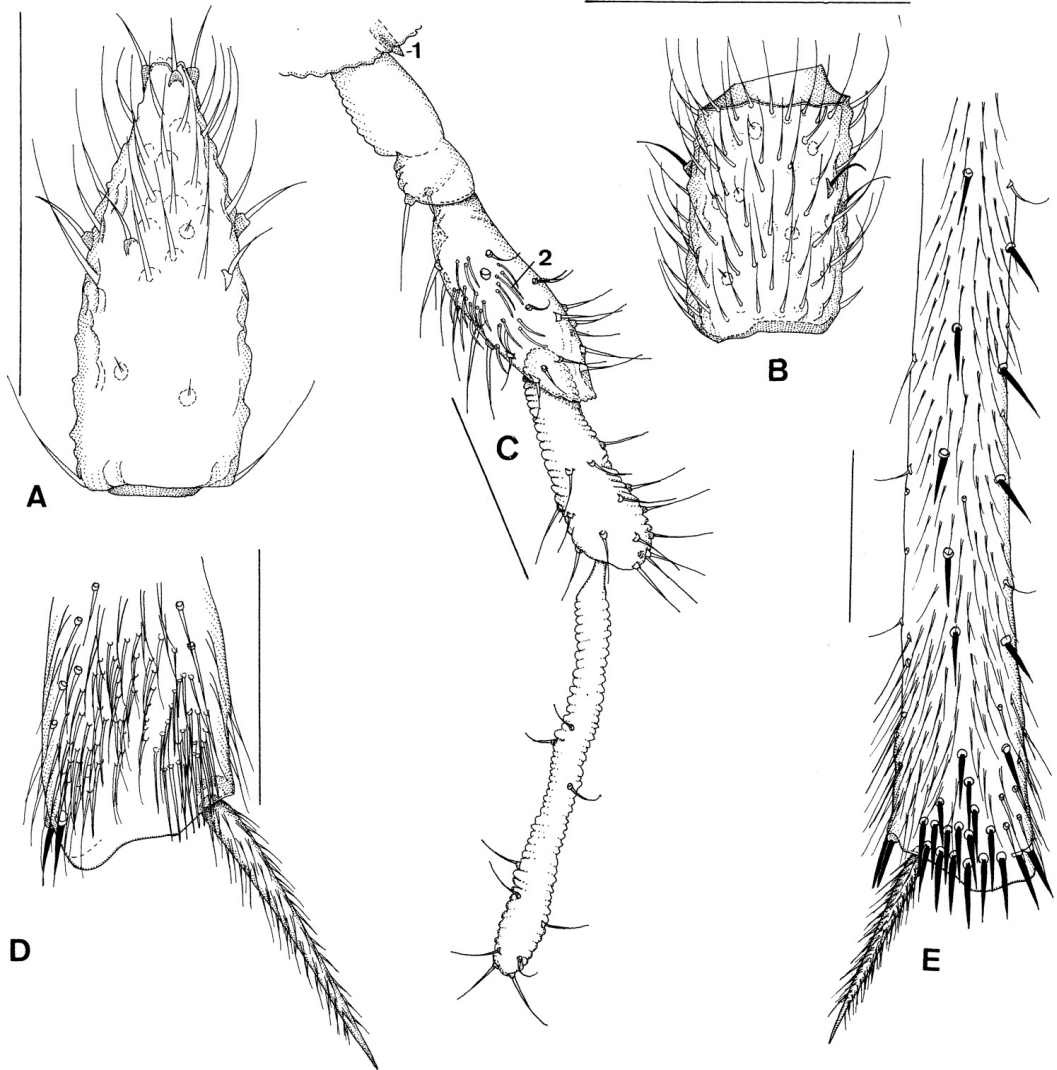


Fig. 4. *Sciarotricha biloba* sp. n. (holotype): antennal flagellomere 4 (A) and antennal flagellomere 14 (B), ventral view, maxillary palp (C), dorsal view, apical part of fore tibia with tibial organ (D), prolateral view, and apical half of hind tibia (E), retrolateral view. Scale 0.10 mm. – 1 = lacinia, 2 = hyaline sensillae.

size, longer than apical width of tibia. Tarsomeres short, basitarsomere less than half the length of tibia, the two basal tarsomeres with enlarged setae ventrally/lateroventrally, tarsomeres 3 and 4 only apically; tarsal claws simple, pulvilli and empodium branched.

Abdomen (Figs 6, 7). Brown. Tergites 2 – 7 each with one pair of plaques. Male sternite 7 and 8 with basolateral, dorsally directed, sclerotized

apodemes. Male sternite 9 united with hypopygium. Male hypopygium (Fig. 6). Tergite 9 small, with apicomedial process. Gonocoxites basomedially broadly fused, with a dorsal and a ventral apicomedial process, gonocoxal apodemes short, ending far posterior from the anterior margin of hypopygium, the apodemes of both sides medially united. Gonostylus bilobed. Parameres long, broad, separate. Aedeagus fused with the united

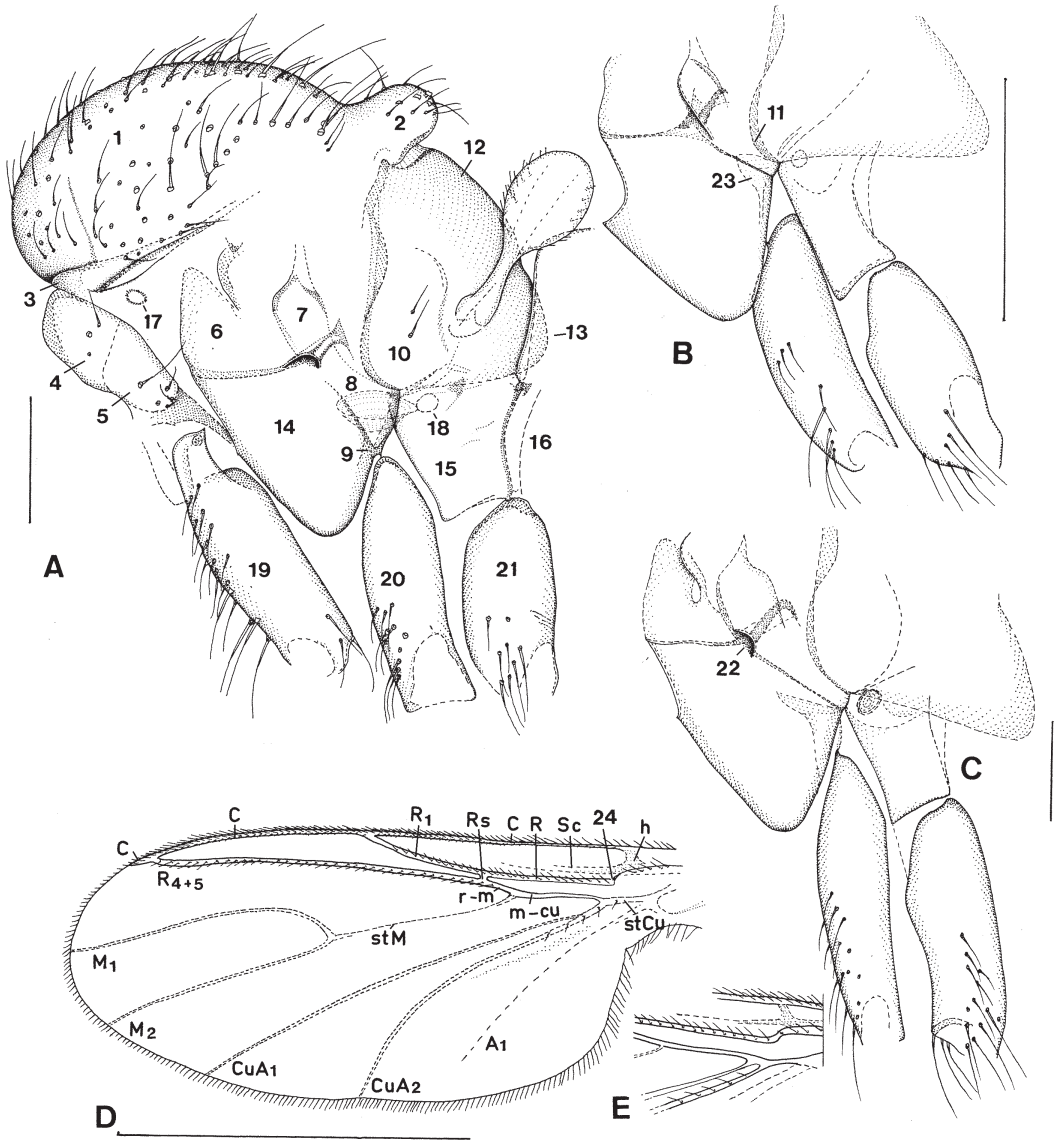


Fig. 5. Male thorax (A), ventral part of male thorax (B and C), lateral view, and male wing (D) and part of the basal part of wing (E), dorsal view. - A, D and E: *Sciarotricha biloba* sp. n. (paratypes). - B: *Pnyxia* sp. (Novosibirsk). - C: *Leptosciarella* sp. (Sweden). Scale 0.20 mm, for wing 0.10 mm - 1 = scutum, 2 = scutellum, 3 = posterior pronotum, 4 = anterior pronotum, 5 = episternum 1, 6 = anepisternum, 7 = anepimeron, 8 = posteroventral part of anepimeron, 9 = anteroventral corner of anepimeron, 10 = laterotergite, 11 = anteroventral margin of laterotergite, 12 = mediotergite, 13 = phragma, 14 = katepisternum, 15 = episternum 3, 16 = metanotum, 17 = anterior spiracle, 18 = posterior spiracle, 19 = fore coxa, 20 = middle coxa, 21 = hind coxa, 22 = pleural pit, 23 = furcasternum 2, 24 = geniculus radialis.

basal part of gonocoxite, its apical margin sclerotized horse-shoe-like, with normal microtrichia, genital rod short, dorsal of the aedeagal plate.

Tergite 10 sclerotized, with a few setae. Cercus large, intruding deeply ventral of sternite 10. Female terminalia (Fig. 7). Setosity normal.

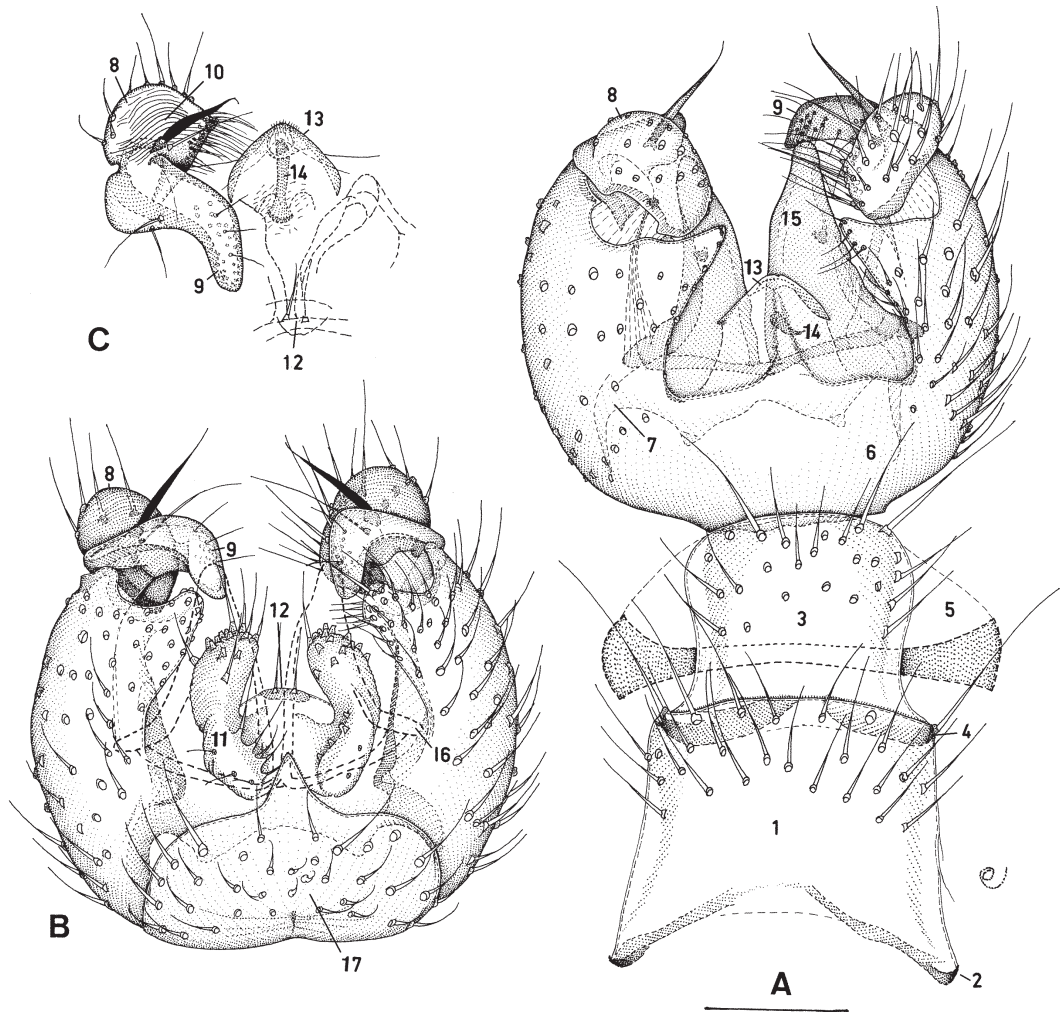


Fig. 6. *Sciarotricha biloba* sp. n. (holotype): male hypopygium, sternite and tergite 8 and sternite 7 (A), ventral view, male hypopygium (B), dorsal view, gonostylus, aedeagus and associated structures (C), dorsal view. – A and B holotype, C paratype. Scale 0.10 mm. – 1 = sternite 7, 2 = basolateral apophysis of sternite 8, 3 = sternite 8, 4 = basolateral apophysis of sternite 8, 5 = tergite 8, 6 = gonocoxite, 7 = gonocoxal apodemes, 8 = ventral lobe of gonostylus, 9 = dorsal lobe of gonostylus, 10 = curved ridges, 11 = cercus, 12 = sternite 10, 13 = aedeagus, 14 = genital rod, 15 = paramere, 16 = parameral apodemes, 17 = tergite 9, 18 = ventral apicomeres lobe of gonocoxite, 19 = dorsal apicomeres lobe of gonocoxite.

Sternite 8 short, also with gonocoxite short; gonapophysis 8 well-developed, long, about half the length of sternite 8, in lateral view the apical part projecting as a roundly pointed process at the apicoventral margin of gonocoxite. Gonapophysis 9 long, about half the length of sternite 8. Orifices of the spermathecal ducts encircled by a ring-like sclerotized rim. Tergite 10 greatly reduced, sternite

10 present as two small sclerotized plates with a seta. Cercus two-segmented. Two sclerotized spermathecae present.

*Diagnostic characters.* – *Sciarotricha* differs from similar *Sciarosoma* by having an eyebridge, by having a well developed and, in lateral view, exposed pleural pit which interrupts the anterior



margin of anepimeron, by having a setose laterotergite and by having m-cu unusually long. The holoptic eyes distinguish *Sciarotricha* also from *Rangomarama*. In addition, *Sciarotricha*, as well as *Sciarosoma*, differs from *Rangomarama* by having the anepimeron posteroventrally extending to metepisternum and posteroventral margin of katepisternum, instead of being abbreviated ventrally of the pleural pit. Furthermore, vein Rs is short, 1/10 of the wing breadth instead of being unusually long, 1/4-1/5 of the wing breadth, and the tibial spurs are long, not rudimentary or absent.

*Sciarotricha* differs from recent Sciaridae (Sciarinae) by having the posteroventral process of anepimeron less horizontal so that its apex anteriorly is at the middle coxa instead of the metepisternum, by having a setose laterotergite, by having a 1+4 segmented palp instead of 1+at most 3 segments, by having a short simple lacinia instead of a long one that is branched in the apical part, by having stM conspicuously shorter than M2, by having a two-lobed gonostylus and by having sclerotized spermathecae. Furthermore, *Sciarotricha* differs by lacking a tegmen.

*Sciarotricha* differs from the fossil genera placed in the Archizelmiridae, *Archizelmira*, *Archimelzira*, *Burmazelmira* and *Zelmiarcha*, e.g. by having an eyebridge and by having vein Rs placed in the basal half of the wing instead of at the middle or in the apical half.

### *Sciarotricha biloba* sp. n.

(Figs 3-7)

*Material examined.* - *Holotype male:* NAMIBIA, Brandberg, Messum Valley, 700 m, 21° 13' 29" S, 14° 30' 98" E, sparsely vegetated river valley, bushy Karoo-Namib shrubland, UV light trap, 3.iv.1999, S. van Noort & S.G. Compton (Type series T 649, NMNW). *Paratypes:* same data as for holotype, 3 males, 10 females (Type series T 649, NMNW), 4 males, 35 females (NRM), 8 males, 100 females (MZH), 1 male, 2 females (BMNH).

*Description.* - Male. Head, Fig. 3. Antennal flagellomeres 4 and 14, Fig. 4A, E. Prefrons with 7 - 12 setae. Maxillary palpomere 2 with 1 - 2 setae. Length/width of flagellomere 4 1.50 - 1.71. Thorax, Fig. 5A, B. Anterior pronotum with 6 - 9 setae. Episternum 1 with 6 - 7 setae. Laterotergite with 2 - 4 setae. Apex of fore tibia, Fig. 4D, apex of hind tibia Fig. 4E. Length of fore basitarsomere/length of fore tibia 0.60 - 0.70. Length of hind tibia/length of scutum + scutellum 1.50 -

1.60. Wing, Fig. 5D. Wing length 1.50 - 1.80 mm, width/length 0.45 - 0.50. c/w 0.15 - 0.20. Abdomen, Fig. 6A. Hypopygium, Fig. 6A, B.

- Female. Head, Prefrons with 8 - 15 setae. Maxillary palpomere 2 with 1 - 2 setae. Length/width of flagellomere 4 1.46 - 1.63. Thorax, similar to male. Anterior pronotum with 7 - 8 setae. Episternum 1 with 4 - 8 setae. Length of fore basitarsomere/length of fore tibia 0.68. Length of hind tibia/ length of scutum + scutellum 1.40. Wing length 1.8 - 2.0 mm, width/length 0.45 - 0.50. c/w 0.15 - 0.30. Abdomen, similar to male. Terminalia, Fig. 7.

*Discussion.* - The species is variable in the presence or absence of the stem of the cubital fork: in two specimens the stem is absent, in one CuA1 and CuA2 meet at a point, in the others there is a distinct stem (Fig. 5D). The ventral lobe of the male gonostylus has curved transverse ridges on its dorsal side which are reminiscent of part of a stridulatory organ. For the distinguishing characters from other Sciaroidea, see under *Sciarotricha* above.

### Acknowledgements

We thank Ashley Kirk-Spriggs (Windhoek, Namibia) for material of the new taxon, and Peter Chandler (Melksham, UK) and Mathias Jaschhof (Greifswald, Germany) for important information on certain taxa. Adrian Pont (Oxford, England) kindly checked the English language and commented on the manuscript. PV received financial support from the Ministry of the Environment, Finland.

### References

- Ansorge, J. (1996) Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue palaeontologische Abhandlungen* 2: 1-132.
- Blagoderov, V. A. (1993) Dipterans (Mesoscofilidae) from the lower Cretaceous of Transbaykal. *Paleontological Journal* 27 (1A): 123-130.
- Blagoderov, V. & Grimaldi, D. (2004) Fossil Sciaroidea (Diptera) in Cretaceous ambers, exclusive of Cecidomyiidae, Sciaridae, and Keroplatidae. *American Museum Novitates* 3433: 1-76.
- Blaschke-Berthold, U. (1994) Anatomie und Phylogenie der Bibionomorpha (Insecta, Diptera). *Bonner Zoologische Monographien* 34: 1-206.
- Chandler, P. (2002) *Heterotricha* Loew and allied genera (Diptera: Sciaroidea): offshoots of the stem group of Mycetophilidae and/or Sciaridae? *Annales de la Société Entomologique de France (n.s.)* 38 (1-2): 101-144.
- Freeman, P. (1951) *Diptera of Patagonia and South Chile. Part III - Mycetophilidae*. The British Museum (Natural History), London, 138 pp., plates I-XLIX.

- Gagné, R. (1981) *Cecidomyiidae*. In: McAlpine, J. F. et al. (eds), *Manual of Nearctic Diptera*. Vol. 1: 257-292. Research Branch Agriculture Canada. Monograph 27. Ottawa, Ontario.
- Grimaldi, D., Amorim, D.S. & Blagoderov, V. (2003) The Mesozoic family Archizelmiridae (Diptera: Insecta). *Journal of Paleontology* 77(2): 368-381.
- Hardy, D.E. (1981) *Bibionidae*. In: McAlpine, J. F. et al. (eds), *Manual of Nearctic Diptera*. Vol. 1: 217-222. Research Branch Agriculture Canada. Monograph 27. Ottawa, Ontario.
- Hennig, W. (1954) Flügelgeäder und System der Dipteren unter Berücksichtigung des aus dem Mesozoicum beschriebenen Fossilien. *Beiträge zur Entomologie* 4: 245-388.
- Hennig, W. (1968) Kritische Bemerkungen über den Bau der Flügelwurzel bei den Dipteren und die Frage nach der Monophylie der Nematocera. *Stuttgarter Beiträge zur Naturkunde* 193: 1-23.
- Hennig, W. (1973) *Diptera (Zweiflügler)*. Handbuch der Zoologie. 4(2) 2/31: 1-337. Walter de Gruyter, Berlin-New York.
- Hippa, H. and Jaschhof, M. (2004) A re-evaluation of the genus *Colonomyia* Colless (Diptera, Sciaroidea), with the description of two new species. *Insect Systematics & Evolution* 35: 335-352.
- Hutson, A.M., Ackland, D.M. & Kidd, L.N. (1980) *Mycetophilidae (Bolitophilinae, Ditomyiinae, Diadocidiinae, Keroplatinae, Sciophilinae and Manotinae), Diptera, Nematocera*. Handbooks for the Identification of British Insects, Vol. IX, Part 3. 111 pp. Royal Entomological Society of London. London.
- Jaschhof, M. (1998) Revision der "Lestremiinae" (Diptera, Cecidomyiidae, Lestremiinae). *Studia Dipterologica Supplement* 4: 1-552.
- Jaschhof, M. (2000) Catotrichinae Subfam. N.: a re-examination of higher classification in gall midges (Diptera: Cecidomyiidae). *Entomological Science* 3(4): 639-652.
- Jaschhof, M. (2004) The *Heterotricha* group in New Zealand. *Beiträge zur Entomologie*, 54: 3-30.
- Jaschhof, M. & Didham, R.K. (2002) Rangomaramidae fam. nov. from New Zealand and implications for the phylogeny of the Sciaroidea (Diptera: Bibionomorpha). *Studia Dipterologica Supplement* 11: 1-60.
- Jaschhof, M. and Hippa, H. (2003) Sciaroid but not sciarid: a review of the genus *Ohakunea* Tonnoir & Edwards, with the description of two new species (Insecta: Diptera: Bibionomorpha). *Entomologischer Abhandlungen* 60: 23-44.
- Johannsen, O. A. (1910) The fungus gnats of North America. The Mycetophilidae of North America. Part II. *Bulletin of Maine Agricultural Experiment Station* (ser. 2) 180: 125-192, 4 pls.
- Kovalev, V.G. (1986) [Infraorders Bibionomorpha and Asilomorpha]. In: Insects in the early Cretaceous ecosystems of western Mongolia. *Trudy Sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya* 28: 125-154. (In Russian)
- Matile, L. (1990) Recherches sur la systématique et l'évolution des Keroplatidae (Diptera, Mycetophiloidea). *Mémoires du Muséum national d'Histoire naturelle Paris (A)* 148: 1-682.
- Matile, L. (1997) Phylogeny and evolution of the larval diet in the Sciaroidea (Diptera, Bibionomorpha) since the Mesozoic. In: Grandcolas, P. (ed.), The origin of biodiversity in insects: Phylogenetic tests of evolutionary scenarios. *Mémoires du Muséum national d'Histoire naturelle Paris* 173: 273-303.
- Menzel, F. & Mohrig, W. (2000) Revision der paläarktischen Trauermücken (Diptera: Sciaridae). *Studia Dipterologica Supplement* 6: 1-761.
- Meunier, F. (1899) Révision des Diptères fossiles types de Loew conservés au Musée Provincial de Koenigsberg. *Miscellanea Entomologica* 7: 161-165, 169 - 182, pls. 1-4.
- Oosterbroek, P. & Courtney, G. (1995) Phylogeny of the nematoceros families of Diptera (Insecta). *Zoological Journal of the Linnean Society* 115: 267-311.
- Panelius, S., (1965) A revision of the European gall midges of the subfamily Porricondyliinae (Diptera: Itonididae). *Acta Zoologica Fennica* 113: 1-157.
- Shcherbakov, D.E., Lukashevich, E.D. & Blagoderov, V.A. (1995) Triassic Diptera and initial radiation of the order. *Dipterological Research* 6: 75-115.
- Shaw, F.R. (1948) A contribution to the phylogeny of the Mycetophilidae. *Annals of the Entomological Society of America* 61: 189-199.
- Steffan, W. A. (1966) A generic revision of the family Sciaridae (Diptera) of America north of Mexico. *University of California Publications in Entomology* 44: 1-77.
- Steffan, W.A. (1981) *Sciaridae*. In: McAlpine, J. F. et al. (eds), *Manual of Nearctic Diptera*. Vol. 1: 247-255. Research Branch Agriculture Canada. Monograph 27. Ottawa, Ontario.
- Söli, G.E.E. (1997) The adult morphology of Mycetophilidae (s. str.), with a tentative phylogeny of the family (Diptera, Sciaroidea). *Entomologica Scandinavica Supplement* 50: 5-55.
- Söli, G.E.E., Vockeroth, J.R. & Matile, L. (2000) *Families of Sciaroidea*. In: Papp, L. & Darvas, B. (eds) *Contributions to a Manual of Palaearctic Diptera*, Appendix: 49-92. Science Herald, Budapest.
- Tuomikoski, R. (1961) Zur Systematik der Bibionomorpha (Dipt.). I. Anisopodidae und Protorhynchidae. *Annales Entomologici Fennici* 27: 65-69.
- Tuomikoski, R. (1966) Systematic position of *Lygistorrhina* Skuse (Diptera, Mycetophiloidea). *Annales Entomologici Fennici* 32: 254-260.
- Vilkamaa, P. (2000) Phylogeny of *Prosciara* Frey and related genera (Diptera: Sciaridae). *Systematic Entomology* 25: 47-72.
- Vilkamaa, P. & Hippa, H. (1998) *Are the Sciaridae and Cecidomyiidae sister-groups?* In: Ismay, J.W. (ed.), *Abstracts Volume, Fourth International Congress of Dipterology, 6-13th September, 1998: 232-233*. Oxford.
- Vockeroth, R. (1981) *Mycetophilidae*. In: McAlpine, J. F. et al. (eds), *Manual of Nearctic Diptera*. Vol. 1: 223-246. Research Branch Agriculture Canada. Monograph 27. Ottawa, Ontario.
- Wood D. M. & Borkent, A. (1989) *Phylogeny and classification of the Nematocera*. In: McAlpine, J. F. et al. (eds), *Manual of Nearctic Diptera*. Vol. 3. 1333-1370. Research Branch Agriculture Canada. Monograph 27. Ottawa, Ontario.

