Ann. Soc. entomol. Fr. (n.s.), 2002, 38 (1-2) : 101-144. ARTICLE

Heterotricha Loew and allied genera (Diptera : Sciaroidea): offshoots of the stem group of Mycetophilidae and/or Sciaridae ?

Peter CHANDLER

606B Berryfield Lane,
Melksham, Wilts SN12 6EL, UK

Résumé – Les genres Heterotricha Loew et apparentés (Diptera : Sciaroidea) sont-ils des descendants du groupe basal des Mycetophilidae et/ou des Sciaridae ? – L'ensemble des espèces du groupe Heterotricha Loew et de Pterogymnus Freeman sont décrites et leur position systématique est examinée. Pterogymnus est représenté par une espèce de la sous-région chilienne. Neuf genres (dont sept nouveaux) sont rapportés au groupe Heterotricha, qui est présent dans toutes les régions zoogéographiques sauf la Néarctique et comprend 17 espèces actuelles, trois de l'Éocène et probablement Mangas exilis Kovalev du Crétacé. Ces genres ont été parfois attribués aux Sciaridae ou aux Diadocidiidae, mais un réexamen de leurs caractères montre qu'ils ne peuvent appartenir à aucune famille existante des Sciaroidea. Les deux groupes sont apparemment plus proches des formes mésozoïques, attribuées respectivement aux Antefungivoridae ou à la sous-famille Mangasinae des Bolitophilidae (groupe Heterotricha) et aux Mesosciophilidae (Pterogymnus). Ces groupes semblent donc appartenir à une souche basale d'où dérivent Mycetophilidae et Sciaridae, ainsi que peut-être d'autres familles modernes. Après discussion des parentés entre ces groupes et les autres Sciaroidea, et entre les genres eux-mêmes, une phylogénie des Sciaroidea est proposée.

Abstract – Known species of the Heterotricha Loew Group and Pterogymnus Freeman are described, and their systematic position is considered. Pterogymnus includes a single species from the Chilean Region. Nine genera (seven of them newly described) are recognised in the Heterotricha Group, which occurs in all zoogeographic Regions except the Nearctic and includes 17 living species, three from Eocene amber and probably Mangas exilis Kovalev from Cretaceous amber. These genera have sometimes been placed in Sciaridae or Diadocidiidae, but reassessment of their characters shows that they cannot belong to any currently recognised families of extant Sciaroidea. Both groups appear closer to Mesozoic forms presently assigned respectively to Antefungivoridae or subfamily Mangasinae of Bolitophilidae (Heterotricha Group) and Mesosciophilidae (Pterogymnus). These groups are thus considered to belong to the basal stock from which Mycetophilidae, Sciaridae and possibly some other modern families are derived. Following discussion of relationships with other Sciaroidea and between the taxa themselves, a tentative phylogeny of Sciaroidea is suggested.

This study was prompted by the discovery of a living *Heterotricha* species in southern Europe. The genus was originally described from Tertiary fossils in Baltic amber but all known extant species hitherto referred to *Heterotricha* were from the Southern Hemisphere. Examination of available fossil material showed that the new species was more nearly related to them than to any other living species. While the South African species *relicta* Edwards is considered nearest, it is not closely related to the European species and the other living species are more distant relatives. The author later learned of the existence of other undescribed species, belonging to this Group on the basis of similar wing venation, and the living forms are here considered to represent nine distinct genera, with representatives in all main zoogeographic regions except the Nearctic.

Rhynchoheterotricha Freeman was already recognised as a distinct genus from *Heterotricha* because of its long proboscis and lack of macrotrichia on the wing membrane. The South American species referred to *Heterotricha* (7 in Chile and Argentina, 1 in southern Brazil) form a clearly monophyletic group (*Chiletricha* n. gen.), while the single New Zealand species is rather different (*Anisotricha* n. gen.); these regional taxa are evidently closer to each other than to *Heterotricha* itself. *Rhynchoheterotricha* is probably also closer to

---

E-mail: chandgnats@aol.com
Accepté le 27-02-2002.

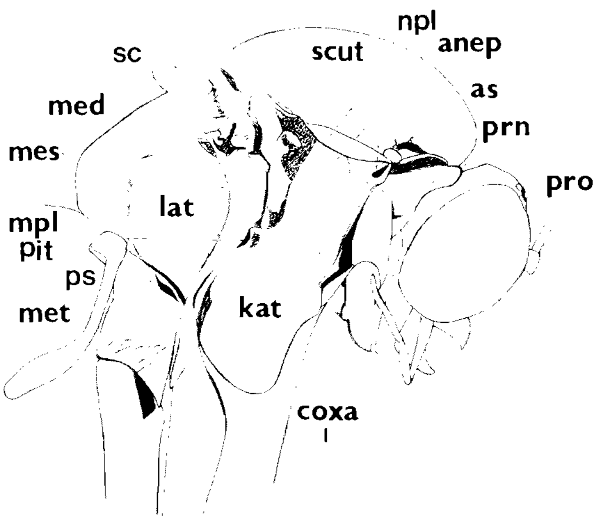


Figure 1
Lateral view of thorax of *Chiletricha spinulosa* n. sp., female, to show pleural morphology; the nomenclature of parts follows McAlpine *et al.* (1981); the equivalent term used by Edwards (1925b) is indicated below:

	McAlpine *et al.* (1981)	**Edwards** (1925b)
pro	proepisrernum	propleura
prn	pronotum	pronotal lobes (anterior, posterior)
anep	anepisternum	anepisternite
mesepisternum		
kat	katepisternum	sternopleurite
mes	mesepimeron	pteropleurite
lat	laterotergite	pleurotergite
met	metepisternum	hypopleurite
med	mediotergite	postnotum
as	anterior spiracle	
ps	posterior spiracle	
mpl pit	(midpleural pit)	
scut	mesoscutum	mesonotum
npl	paratergite [notopleural area]	
sc	scutellum	

them and the three genera may have a common Gondwanaland origin. Whether *relicta* (referred to *Afrotricha* n. gen.) is of similar origin or is of Laurasian origin cannot be deduced in the absence of any clear indication of the antiquity of divergence in the group. Most described species were known only from their type material, but further material of the South American species was fortunately made available by J.P. Duret and the late L. Matile. Papavero (1977) referred to occurrence of *Heterotricha* in Tasmania but the source of this record has not been traced. Two further genera are here described as new from montane habitats in Africa (*Kenyatricha* n. gen.) and Nepal (*Nepaletricha* n. gen.), these being most closely related to each other. Finally, two probably more distantly related new genera from Europe (*Sciarosoma* n. gen.) and Japan (*Sciaropota* n. gen.), first recognised in an unpublished paper by R. Väisänen and T. Saigusa, are also described to ensure complete coverage of the known fauna. However, some further species of this Group from New Zealand await description by Mathias Jaschhof.

They thus represent very widespread and undoubtedly ancient lineages, although only the European genus *Heterotricha* is known in the fossil record. The life history of no genus is yet known and early information on this is unlikely, as most species have been rarely collected. Assignment of the Group to a supra-generic taxon has remained uncertain and it has been included without much conviction in either Sciaridae or Diadocidiidae. Meunier (1904) placed *Heterotricha* in the Sciaridae on venational resemblances, but his suggestion that *Trichosia* Winnertz was a synonym was due to a misidentification and as shown below his *Palaeoheterotricha* represented the *Heterotricha* of Loew. The synonymy of *Palaeoheterotricha* with *Heterotricha* was first suggested by Frey (1942) and was thus listed by Evenhuis (1994), both authors including the genus in Sciaridae. Edwards (1925b) also supported inclusion in the Sciaridae when he described a partial "eye-bridge" (upper part of each eye produced towards the other, found in most Sciaridae) in *H. relicta*. Actually the eyes are only reniform in the *Heterotricha* Group and the upper corners may be obscured in dry specimens because the antennae are strongly upturned.

More recently the presence of a "midpleural pit" (a depression on the hind margin of the mesepisternum at the junction of the anepisternum and katepisternum) was considered more important. Shaw (1948) believed this character to be diagnostic of the Sciaridae. Freeman (1951) retained *Heterotricha* in the Sciaridae on this character; he considered *Pterogymnus* to be possibly related but placed it in the Diadocidiinae because it lacked such a pit. The development of the pit is variable in the *Heterotricha* Group and Colless (1963) noted the presence of such a pit in some Ditomyiidae and Mycetophilidae proper as well as a rudimentary pit (and a partial eye-bridge) in one Australian *Diadocidia* species, discounting the importance of this character in defining the Sciaridae. The aberrant genera *Ohakunea* Edwards and *Colonomyia* Colless, which he discussed, both lacked a midpleural pit. The pleural morphology of the *Heterotricha* Group (fig. 1, *Chiletricha*) is close to the ground plan of the Sciaroidea and it lacks several other apomorphies demonstrated by Shaw (1948) in the Sciaridae. However, most genera share with Sciaridae a strongly developed phragma (lower part of mediotergite) projecting into the abdomen. There are small differences between genera and *Heterotricha takkae* n. sp.

shows a reduction in the pleural sutures, although these are well defined in the fossil species of this genus. *Sciarosoma* and *Sciaropota* show more differences in pleural morphology, without the midpleural pit and the latter with the mesepimeron broad below and phragma weakly developed.

Tonnoir & Edwards (1927) first suggested inclusion of *Heterotricha* in the Diadocidiinae, previously including only the small but almost worldwide genus *Diadocidia* Ruthé, on the basis of the wing venation, e.g. loss of basal part of M, R_4 and sc-r (Sc_2); actually sc-r is present in several genera of the Group. Freeman (1951) placed *Pterogymnus* in the Diadocidiinae, although it differed from *Diadocidia* in the presence of R_4 (ending in R_1 to form an elongate cell) and lack of macrotrichia on the membrane. Hennig (1954), Colless (1963) and Papavero (1977) supported inclusion of *Heterotricha* in the Diadocidiidae, but Hennig suggested a possible relationship between *Pterogymnus* and *Bolitophila* Meigen (Bolitophilidae) because of the presence of R_4.

Material and methods

This study was based principally on pinned adult specimens and a few preserved in alcohol. In some cases, genitalia had previously been macerated and stored in glycerine or mounted in balsam. Where they had not previously been studied, male and female genitalia were macerated in hot KOH and transferred to permanent mounts, in earlier preparations using Euparal but more recently DMHF (dimethyl hydantoin formaldehyde). Where necessary other parts of the body were treated in the same way. The fossil material studied was examined as far as practicable in situ and with the assistance of photographs.

The phylogenetic conclusions suggested here are based on evaluation of character states across the taxa in relation to their distribution in Sciaroidea. These conclusions take into account the works of previous authors, some of which are intuitive or employ traditional cladistic methods, while some of the more recent are based on cladistic computer programmes. The latter method has not been practicable in the present work, but it is recognised that computer analysis of a wider range of characters would be desirable and any conclusions postulated are of necessity tentative.

Most of the material studied was from the Natural History Museum (BMNH, London) or Muséum national d'Histoire naturelle (MNHN, Paris). Some material was also examined from the following institutions: Muséum d'Histoire naturelle de Neuchâtel (MHNN); Cawthron Institute, New Zealand (CINZ, Nelson); Geologisch-Paläontologisches Institut und Museum der Georg-August-Universität (GPIM, Göttingen); Palaeontological Institute, Russian Academy of Sciences (PIRA, Moscow) and the Zoological Museum (ZMH, Helsinki).

Definition of the *Heterotricha* Loew Group

The genera included in this paper (except *Pterogymnus*) are characterised by the following basic wing venation plan, in which they differ from all other known Sciaroidea:

Vein Sc long but ending free; sc-r may be absent but if present on basal half of Sc. Vein R_1 long, reaching costa on apical half of wing. Rs short, vertical to diagonal, originating before middle of R_1, but well beyond h. Vein R_4 absent. Vein R_5 ending shortly before or just beyond wing tip, often downturned apically. Costa ends at or extends a short distance beyond tip of R_5. Crossvein ta (= r-m) variable in length, usually directed diagonally basad from Rs, sometimes more vertical (*Anisotricha* and some *Chiletricha*) or almost obliterated (*Kenyatricha* and *Nepaletricha*), meeting junction between tb and stem of median fork (M_{1+2}), the fork itself (M_1 and M_2) broad and at least a little longer than its stem. Base of M before this junction absent or faintly indicated as a colourless seam, but crossvein tb (= m-Cu of Edwards) long and extending strongly basad to end in the anterior branch of the posterior fork, often nearly parallel with R and replacing base of M functionally; enclosing an area between R and base of CuA referred to here as the "basal cell". Posterior fork narrow basally, broadened apically with both branches (M_4+CuA_1 and CuA_2) reaching costa, but because of junction with tb apparently arising separately from stem vein. Vein CuP arises from stem vein basally and runs close behind CuA_2, ending free. Vein An_1 strong basally, diverging from CuP, ending free well short of wing margin.

The venation of *Palaeoplatyura* (Keroplatidae) (fig. 2) is nearest of extant genera to the ground plan of Sciaroidea, departing from it only in the loss of sc-r. The *Heterotricha* Group thus differs from this ground plan in abbreviation of Sc and An_1 which end free, loss of R_4, loss of sclerotisation of basal part of M and juxtaposition of ta and tb. *Pterogymnus* differs from this ground plan in the same way except that Sc is complete, sc-r absent and R_4 is present but ending in R_1.

Of the genera with the venational characters of the *Heterotricha* Group, *Sciaropota* differs in its more robust body form, with shorter thicker coxae and legs, porrect antennae with short flagellomeres, mesoscutum without clearly differentiated series of setae and the thoracic characters mentioned above. The genera

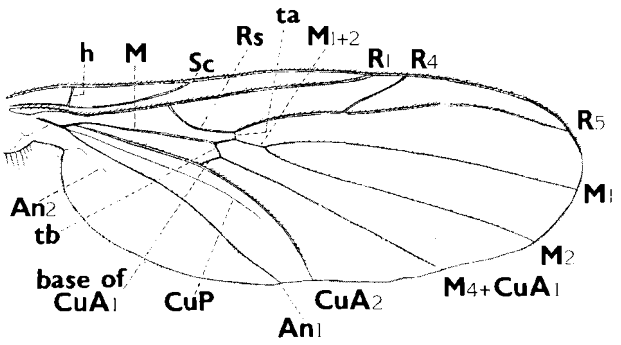


Figure 2

Venation of *Palaeoplatyura* Meunier (Keroplatidae), showing notation of veins, conforming to ground plan of Sciaroidea except in absence of both sc-r and macrotrichia on membrane. The interptetation of veins is compared with that of otber recent authors:

Present paper	**Matile** (1981)	**Vockeroth** (1981)
Sc	Sc_1	Sc
sc-r	Sc_2	sc-r
R_1	R_1	R_1
R_4	R_4	R_{2+3}
R_5	R_5	R_{4+5}
ta	ta	r-m
tb	tb	bm-cu
M_1	M_1	M_1
M_2	M_2	M_2
M_4+CuA_1	M_4+Cu1a	CuA_1
base of CuA_1	m-cu	base of CuA_1
CuA_2	Cu1b	CuA_2
CuP	CuP	CuP
An_1	An_1	A_1
An_2	An_2	A_2

other than *Sciaropota*, however, have many characters in common as indicated in the following description:

Description – Slender bodied gnats with long legs, antennae and wings and the arched thorax, elongate coxae and configuration of tibial spurs characteristic of Sciaroidea. Body mainly dark grey dusted, wings unmarked, legs and halteres yellowish in known species.

Head small, with large ± reniform eyes, strongly emarginate at level of base of antenna and produced dorsomedially but always distinctly separated, without an eye-bridge developed. Three ocelli, the median usually a little in front, outer ocelli separated by a short distance from eye margin. Antenna set near middle of head, long, slender, especially in males (distinctly shorter in respective known females), with 2+14 segments. Scape and pedicel short and adpressed to frons, so that antenna is strongly upturned; basal flagellomere longer than succeeding flagellomeres. Clypeus protruding, usually with strong downturned setae (absent in *Rhynchoheterotricha*, which has the lower part of the head greatly prolonged and *Nepaletricha*). Proboscis short and simple. Palpus slender, elongate, comprising a short palpiger and three longer palpomeres.

Thorax with mesoscutum a little arched, bearing series of acrostichal, dorsocentral and more irregular lateral setae, separated by bare stripes; an incomplete suture extending onto dorsum from humeral area. Scutellum with long setae, including convergent marginals. Prothorax with pronotal lobe bearing setae; small proepisternum bears longer downturned setae. Pleura bare or with setae on metepisternum and/or laterotergite. Mediotergite bare. Anepisternum depressed towards upper margin and anterior spiracle. A shallow narrow depression on hind margin at junction with katepisternum represents "midpleural pit". Katepisternum large, produced ventrally. Mesepimeron broad below wing base, narrowed below level of midpleural pit, then extended vertically or bent anteriorly below to reach upper corner of mid coxa. Laterotergite broad, shallowly depressed or slightly protruding. Metepisternum small, irregularly quadrate. Pleural sutures usually distinct but may be more or less effaced. Mediotergite with lower part (phragma) enlarged and ± projecting into abdomen.

Legs slender, with elongate coxae bearing long setae. Femora slightly enlarged with irregular short setae, longer ventrally. Tibiae cylindrical with short irregular dark setulae and sparse irregular series of short setae. Tibial spurs 1:2:2, well developed. Tarsi slender with short setulae. Claws small, simple; pulvilli absent; empodium usually broad, shorter than or subequal to the claws in length.

Wing long and relatively narrow (shorter and broader in *Afrotricha* and *Sciarosoma*). Most veins bear setae. Wing membrane also usually more or less covered with macrotrichia (entirely absent in *Rhynchoheterotricha*, often ± reduced on basal parts especially in some *Chiletricha* species).

Abdomen elongate, more or less compressed with large tergites; broadly inserted onto thorax.

Male sclerites of segments 1-8 well developed, unmodified with short setae. Genitalia external with tergite 9 partly covering cerci, hypoproct and aedeagus dorsally and articulating with the genital capsule comprising ventrally fused gonocoxites. Tergite 9 widely differs in form generically and specifically. Gonostylus articulating with gonocoxites apically, large and relatively simple but with highly specific form; sometimes one or two accessory lobes of gonocoxites are developed in association with gonostylus. Gonocoxal apodemes usually well developed and may be connected dorsally. Aedeagal complex varying considerably in structure but usually with parameres well developed and these more or less fused to gonocoxal apodemes.

Female (known only in three genera) with sclerites of segments 1-7 and tergite 8 simple but sternite 8 bilobed and variously modified. Sclerites of segments 9 and 10 small and retracted in situ. Tergite 10 and/or sternite 8 bear numerous long (golden yellow) setae. Cerci large, two-segmented, articulating with tergite 10 and bearing short setae. Two ovoid spermathecae (*Chiletricha*) or chitinised spermathecae apparently absent (*Heterotricha*, *Afrotricha*).

Key to genera of the *Heterotricha* Loew group

1. Wing membrane devoid of macrotrichia. Lower part of face flat and bare, but clypeus produced into a long slender extension of the head, on which small mouth parts are borne apically. Laterotergite bare. Metepisternum with short hairs. Male tergite 9 produced into 4 spinose processes apically, gonostylus simple . . . . ***Rhynchoheterotricha*** Freeman
– Wing membrane bearing macrotrichia. Clypeus not produced apically, but prominence above mouth margin usually bearing long curved setae 2
2. Laterotergite bearing long setae. Vein Rs subequal to or shorter than ta (= r-m), more vertical, originating beyond level of junction of ta with M and tb. Male tergite 9 simple, rounded apically or produced medially; gonostylus simple 3
– Laterotergite bare 4
3. Wing elongate. Vein Sc bare. Crossvein ta short and thick, Rs weaker. Median fork distinctly longer than its stem. Metepisternum bare . . . . . ***Heterotricha*** Loew
– Wing shorter and broader. Vein Sc setose. Crossvein ta longer, Rs not weaker. Median fork subequal to its stem. Metepisternum with short hairs . . . . ***Afrotricha*** n. gen.
4. Vein Rs shorter than ta, more vertical, originating beyond level of junction of ta with M and tb. Pleura (other than prothoracic) bare. Male tergite 9 simple, rounded apically or produced medially; gonostylus bilobed 5
– Vein Rs subequal to or (usually) longer than ta, curved and not vertical, originating before level of junction of ta with M and tb 6
5. Antenna upturned (scape and pedicel adpressed to head) and with flagellomeres long and slender (as in all other genera) . . . . ***Sciarosoma*** n. gen.
– Antenna porrect, with flagellomeres short and nearly quadrate . . . . ***Sciaropota*** n. gen.
6. Metepisternum with short fine setae. Crossvein ta short but usually distinct 7
– Pleura (other than prothoracic) bare. Crossvein ta very short or obliterated 8
7. Vein Sc setose and wing with more uniform macrotrichia, including some in basal cell. Male tergite 9 short and transverse without spinose processes. Gonostylus with inner margin bearing lobes but lacking spines . . . . ***Anisotricha*** n. gen.
– Vein Sc bare and wing with costal and basal sectors more or less devoid of macrotrichia. Male tergite 9 medially narrow, produced laterally into spinose processes. Gonostylus usually with internal basal lobe and often bearing spines . . . . ***Chiletricha*** n. gen.
8. Vein Sc setose. Tergite 9 rounded apically, but with blunt submedial process on each side. Gonostylus with setose internal basal lobe and with short setose processes of gonocoxites alongside it . . . . ***Nepaletricha*** n. gen.
– Vein Sc bare. Tergite 9 excavated medially, with blunt setose process on each side of excavation. Gonostylus simple, but with setose processes of gonocoxites ventrad to it (***Kenyatricha*** n. gen.) 9
9. Vein tb longer than part of CuA_1 basal to it. Tergite 9 with pointed lateral process. Gonocoxites with two setose processes adjacent to gonostylus . . . . ***Kenyatricha elgon*** n. sp.
– Vein tb shorter than part of CuA_1 basal to it. Tergite 9 rounded laterally. Gonocoxites with a single process adjacent to gonostylus . . . . ***Kenyatricha mulanje*** n. sp.

Genus *HETEROTRICHA* Loew

Heterotricha Loew, 1850 : 34. Type-species : *Heterotricha hirta* Loew, monobasic.

Palaeoheterotricha Meunier, 1904 : 62. Type species: *Palaeoheterotricha grandis* Meunier, monobasic.

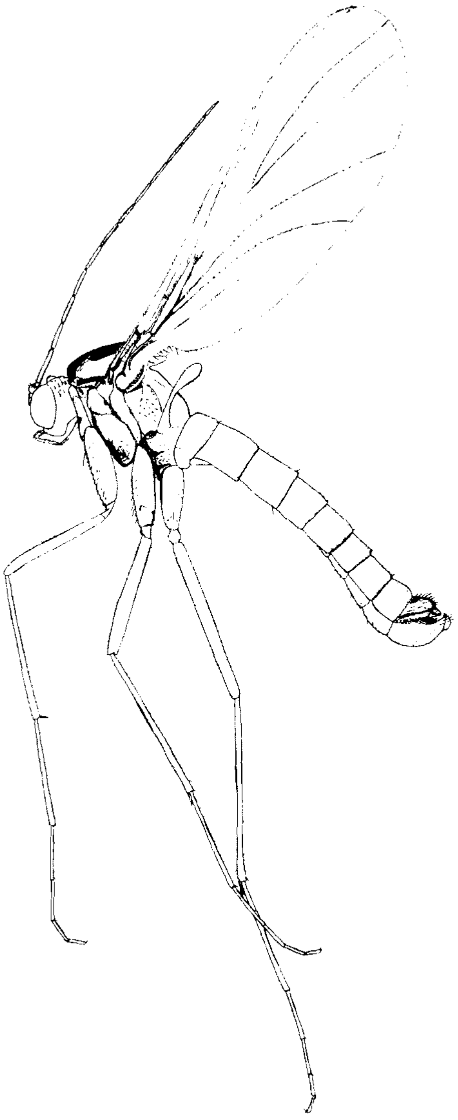


Figure 3
Heterotricha ? *grandis* (Meunier), lateral view of whole insect (K1144)

Description (♂♀) – *Head.* Eyes practically bare, emarginate level with base of antennae, produced a little above antennae but broadly separated dorsally. Antenna with flagellomeres elongate, distinctly shorter overall in female than in male. Outer ocelli separated by about their diameter from eye margin, median a little in front.

Thorax. Pleura other than prothoracic sclerites bare except for laterotergite, which bears some long setae. A diagonal suture between anepisternum and katepisternum, ending near midpleural pit and that between katepisternum and mesepimeron are distinct in fossil species, these sutures effaced in extant species.

Wing membrane largely covered with macrotrichia, with bare areas of varying extent in costal and basal sectors. The abbreviated vein Sc is linked with R by a strong vertical sc-r situated on its basal third. Costa produced only a short distance beyond tip of R_5, which is less downturned than in other long winged genera. Rs subequal to ta, nearly vertical, originating beyond level of junction of ta with M. Vein tb parallel with R so that basal cell is narrow and basal part of M is not indicated.

Male. Tergite 9 broad basally, apically rounded or medially produced (with a blunt bilobed process in extant species), beyond which small cerci protrude. Gonostylus simple, variously shaped apically.

Female (based on extant species). Sternite 8 broadly bilobed by deep median incision. Sternite 9 short, apically bilobed. Tergite 9 short, broad and simple. Tergite 10 short but bearing copious long curved bristling as long as apical segment of cerci. Cerci two segmented, with broad blunt bristly apical segments. Sclerotised spermathecae not apparent.

Discussion – Loew described *Heterotricha* briefly, distinguishing it from *Sciara* on the form of the posterior fork and stated that there were macrotrichia on the wing membrane. Meunier (1899) examined three specimens determined as *hirta* in the part of Loew's collection at Königsberg, two of which he figured (plate 1, figs. 5, 6), showing most of the characters of specimens he subsequently described as *Palaeoheterotricha grandis*. Although the wings are obscure in fig. 6 and the apical part is missing from one wing, and the radial sector of the other wing is obscured in fig. 5, R_1 does clearly end somewhat beyond the base of the median fork and the separate origin of the branches of the posterior fork is clearly shown. Meunier (1904), however, described *Palaeoheterotricha* and placed *Trichosia* Winnertz in synonymy with *Heterotricha*. He then described *hirta* from a single female with setae on the wing veins but not on the membrane, which was incorrectly identified. The female specimen (Z2134, GPIM) from which Meunier (1904) drew up his description of *H. hirta* has been examined and found to correctly belong to *Trichosia* or *Leptosciarella* Tuomikoski (Sciaridae) and is evidently not one of Loew's types of *hirta*. The characters he gave for *Heterotricha* were thus those of *Trichosia*, resulting in some confusion in the literature. It is curious that Meunier overlooked the absence of macrotrichia on the wing membrane in this specimen, but setae are present on the fork veins and some detached ones are scattered on the membrane within the median fork on one wing. This error apparently led Meunier to describe *Palaeoheterotricha* from specimens congeneric with Loew's types of *hirta* and it is concluded, as already indicated by Frey (1942), that it is a synonym of *Heterotricha* although since the discovery of further fossil species of the genus it is unclear whether *hirta* and *grandis* are also synonymous, as discussed below.

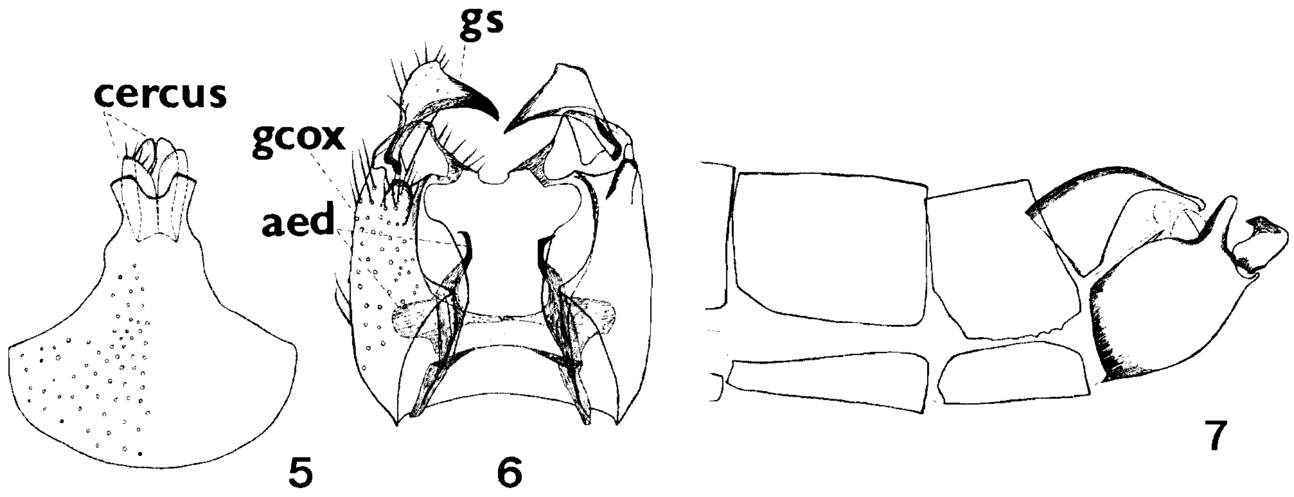
The extant species is described first below and the fossil material examined is then discussed comparatively.

Key to species of *Heterotricha*

1. Antenna relatively shorter, but still longer than head and thorax together in male, about equal to head and thorax together in female. Suture between anepisternum and katepisternum incomplete, that between katepisternum and mesepimeron also effaced. Tergite 9 with narrower median apically bilobed part as long as broader basal part .... ***takkae*** n. sp.
– Antenna with flagellomeres proportionately longer and entire antenna much longer, extending in male to twice or more length of head and thorax together (longer than head and thorax together in only female examined). A complete suture between anepisternum and katepisternum, and between katepisternum and mesepimeron. Tergite 9 shorter and broader but apically produced (Baltic amber species) 2
2. Wing broader, with basal cell relatively broader (fig. 11). Macrotrichia in costal cell and a few in basal cell. Gonostylus sickle-shaped .... ? ***hirta*** Loew
– Wing narrower with basal cell narrower (fig. 3). Macrotrichia not in both cells 3
3. A few macrotrichia in apex of costal cell, absent from basal cell. Gonostylus appears bifurcate ....? ***grandis*** (Meunier)
– Macrotrichia absent from costal cell, some in apical third of basal cell. Gonostylus hatchet-shaped .... ***dolabrata*** n. sp.

Heterotricha takkae n. sp.
(figs. 4-10, 48)

Type material – **Holotype** ♂, Greece, Peloponnese, south west of Lake Takka, 27.iv.1979, swept by shaded



Figures 5-7
Heterotricha takkae n. sp., male genitalia. – 5, tergite 9 and cerci. – 6, dorsal view of genitalia with tergite 9 and cerci removed. – 7, lateral view of segments 7-8 and genitalia. *aed*, aedeagal complex; *gcox*, gonocoxites; *gs*, gonostylus.

two-thirds length of 6, the visible portion of 8 half length of 7 but otherwise normally formed. All sclerites slightly shining black, thinly grey dusted, with short yellow bristling longer on apical margins of tergites. Tergite 9 (fig. 5) articulating with gonocoxites and partly covering them dorsally, broad basally, tapered then bluntly bifid apically with small cerci protruding from apical bifid portion. Gonocoxites brownish yellow, rounded ventrally with simple upturned apically pointed gonostylus (figs. 6-7). Aedeagal complex including apically pointed parameres basally fused to gonocoxal apodemes.

Body 6 mm, wing 5.1 mm.

Female. Similar in most respects. Antenna shorter (fig. 48), about equal in length to head and thorax. Mesoscutum with stripes more broadly separated; acrostichals biserial in front; dorsocentrals irregularly biserial along entire length, becoming pluriserial in front as well as behind. Legs darker; femora and tibiae with dark shades and tarsi blackish. Wing with costa extended a little more beyond R_5 (length of Rs). Haltere with grey shade on knob.

Abdomen relatively a little shorter but proportions of sclerites similar. Ovipositor (figs. 8-10) short, blunt, not much protruding, brownish yellow, but sternite 8 produced in association and broadly bilobed by deep median division, which broadens basally to leave only narrow basal strip entire, bearing long yellow bristling. Tergite 8, however, relatively short and simple, about two-thirds length of 7 (one third when contracted). Tergite 9 well developed, contracted in situ; sternite 9 plate like, apically emarginate with long converging projections from side margins and with thicker shorter lateral projections. Tergite 10 short but bearing copious long curved yellow setae. Cerci large, as long as tergite 9, broadened apically with inner margin reflexed, bearing short pale hair. Chitinised spermathecae absent

Body 5 mm, wing 5.5 mm.

Discussion – The Greek localities included both shaded streams and drier scrub habitats. The Swiss locality is described by Haenni & Dufour (1983), who recorded *Hyperoscelis eximia* (Boheman) (Canthyloscelidae) there, for the first time in Switzerland.

Etymology – The name of the species is derived from that of the type locality.

Heterotricha species in Baltic amber

It has not been practicable to examine certain type material of either *hirta* or *grandis*, but they are provisionally considered as distinct species on the evidence presented below, now that it is known that at least three species of the genus have been found in amber. The Baltic amber fossils, although variously labelled, are probably all Upper Eocene (to Lower Oligocene), i.e. 35-40 million years before the present (Andrew Ross, pers. comm.).

Figure 4
Heterotricha takkae n. sp., male wing.

stream, *A. E. Stubbs* (deposited in BMNH). **Paratypes** : 1 ♀, same data as holotype (also deposited in BMNH); 1 ♀, Greece, Crete, Kritsa, rocky valley, 18.iv.1980; 1 ♀, Greece, Crete, 2 km north east of Plakalona, scrubby hillside, 27.iv.1980; 1 ♀, Greece, Crete, 2 km north of Melambes, by stream, 22.iv.1980, *A. E. Stubbs* (in author's collection).

Other material – 1 ♀, Switzerland, Neuchâtel canton, Jura Mountains, Château de Rochefort, 780 m, Malaise trap, submediterranean thermophilous *Quercus pubescens* forest, 18-20.vi.1982; 1 ♀, same locality, 4-11.vii.1982 (both *C. Dufour*, MHNN); 1♀, Italy, Abetone province, Pistoeisi-Campolino nature reserve, 1500m, 11.vii.2000, Malaise trap (S. Vanin, State Forestry Corps. NRBF collection).

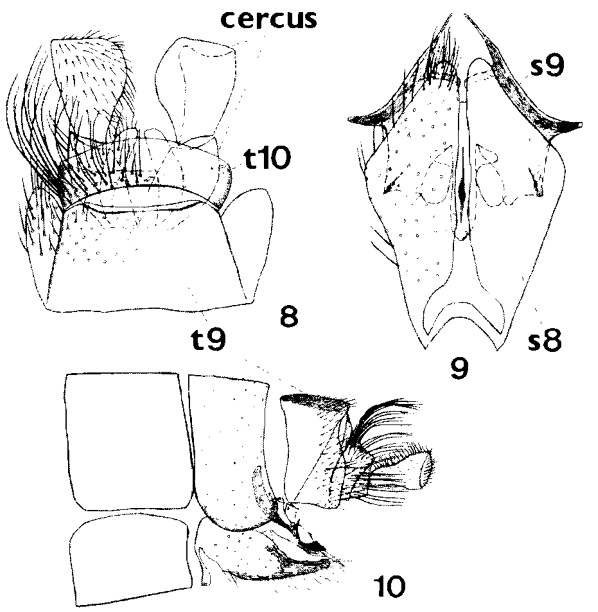
Description – **Male.** *Head* grey dusted with large bare eyes, produced a little above antennae but broadly separated dorsally; ocelli in a nearly straight line between the upper edges of the eyes, outer nearer to eyes than to median but still distinctly separated by about their diameter from eye margin. Antenna with scape and pedicel small and quadrate, dark brown, bearing short pale bristling; flagellum slender, longer than head and thorax together, first flagellomere 1.5 x length of second, flagellomeres 2-5 subequal but all flagellomeres progressively shorter and narrower, flagellomere 12 only half length and width of first, which is yellowish at base, otherwise dark brown, clothed with very short pale hair. Frons and face bare but facial prominence bears long downturned yellowish setae. Proboscis short, brownish yellow; palpus brownish yellow, with palpomeres progressively longer, apical more slender. Occiput bears short pale hair.

Thorax light grey dusted with mesoscutum bearing slightly shining dark brown longitudinal stripes. Median stripe extending from anterior margin is divided medially by a narrow dusted stripe along acrostichal row, the two components tapered and rounded off (occupying anterior three quarters of thorax); separated more broadly, by dusted stripes along dorsocentral rows, from broad lateral postsutural stripes, which are rounded at each end to stop distinctly short of scutellum. Mesoscutum bears short yellow uniserial (irregularly biserial in front) acrostichal row ending level with median stripes; similar uniserial dorsocentrals which become longer and irregularly biserial in front and pluriserial beyond end of acrostichals; longer irregular yellow bristling external to lateral brown stripes. Scutellum clothed with long yellow setae amongst which one pair of longer stouter marginal setae, set close together and convergent apically, may be discerned. Postpronotum brownish yellow; diagonal suture extends from middle of postpronotum to median stripe. Pronotal lobes bear moderately long fine yellow bristling; small ill-defined proepisternum bears longer downturned setae. Pleura and mediotergite otherwise bare, except for irregular short yellow setae in central area of laterotergite. Anepisternum fused with katepisternum as intervening suture is only indicated by a short indistinct incision across posterior third. Narrow lower portion of mesepimeron only separated from katepisternum by narrow depression (rather than suture).

Legs dull yellow. Coxae with long yellow bristling; femora with irregular yellow bristling mainly short but longer ventral series. Tibiae and tarsi with irregular dark setulae and sparse irregular series of short brown setae as long as half tibial diameter or less, best developed on tibia 1. Tibial spurs a little longer than apical tibial width, pairs subequal, dark brown. First tarsomere subequal in length to tarsomeres 2-5 together; fore tarsus especially long, 1.5 x tibial length; mid and hind tarsi progressively shorter relative to their tibiae, hind only slightly longer. Claws very small, subequal in length to broad whitish empodium.

Wing long, narrow but with rounded hind margin and broadest beyond middle (fig. 4). Costa and radial sector dark brown, other veins light brown, membrane hyaline. Vein Sc thick and brown tinted to level of Rs, then pale and tapered to end free close to R_1; sc-r present on basal third. Rs very short, narrow, running almost at right angles to R_1 to meet short but broad ta (r-m) (nearly twice length of Rs) which extends diagonally basad to meet M. Base of R_5 also broad continuous with ta, but then sharply narrowed to same width as R_1, to which it runs close and beyond tip of R_1 parallel with costa, downturned apically; costa only slightly extended beyond tip of R_5. Anterior branch of posterior fork (M_4 + CuA_1) arising little more than length of Rs from origin of posterior branch. All veins bear setae except Sc, Rs, ta, tb, basal portions of branches of posterior fork, and base of CuA_2. Membrane bearing conspicuous but small dense macrotrichia over most of its surface - except basal part before anal lobe, cell c, area between R and tb, and bases of all other cells. Haltere pale yellow, with long stem and small knob.

Abdomen twice length of head and thorax together. Segments 1-3 progressively longer, 3 and 4 subequal in length, then succeeding segments progressively shorter, 7



Figures 8-10
Heterotricha takkae n. sp., female genitalia. – 8, dorsal view of tergites 9-10 and cerci. – 9, ventral view of sternites 8-9. – 10, lateral view. *s*, sternite; *t*, tergite.

The fossil specimens examined vary in condition and are described as far as practicable, with tentative identifications. All have the antenna longer and the pleural sutures more distinct than in *H. takkae.*

Heterotricha hirta Loew
(? *hirta* : figs. 11, 14)

Heterotricha hirta Loew, 1850 : 34 (only hairing of wings indicated for species in addition to brief generic key characters)
Heterotricha hirta Loew; Meunier, 1899 : 163, Pl. 1, figs. 5, 6 (whole insects)

Material examined – 1 ♂, labelled II 2130, Baltic amber, Presd. Rontaler, R. 27/11/98; 1 ♂, labelled 29057, Presented A. Théry 1932 Oligocene Baltic amber and Heterotricha hirta (determined by F.W. Edwards) (BMNH).

Specimen II2130 – Body appears dark coloured, but the body, halteres and femora of this specimen contain much black particulate material, so actual pigmentation of body not discernible.

Head. Outer ocelli less than their diameter from eye margin. Antenna very slender, distinctly more than twice head and thorax (ratio 21:9), with basal flagellomere yellowish at base and as long as height of head, 1.5 x length of second flagellomere, other flagellomeres 6 or more x as long as broad. Apical flagellomere 1.3 x as long as penultimate (broken off on one antenna). Facial prominence with long setae. Palpus slender, about 1.5 x as long as head, apical palpomere a little longer than two preceding palpomeres together.

Thorax with long setae on sides of mesoscutum, other thoracic setae difficult to discern.

Legs. Ratio of tibia 1: tarsus 1 is 2.5:4.5. Tibial spurs nearly twice apical tibial width.

Wing (fig. 11) a little broader than in other species, with basal cell broad relative to other species. Costa hardly extending beyond tip of R$_5$, with hairs a little longer than its width. Most veins setose, stem of median fork setose from the base: Sc, Rs, ta, tb, stem and base of CuA$_2$ bare. Macrotrichia sparse on basal part of wing, only a few present in basal cell but numerous in costal cell. Vein Sc weak beyond level of base of Rs. Crossvein sc-r very faintly indicated. Vein Rs a little shorter than ta, which is thickened. Vein R$_5$ parallel with R$_1$ on basal part, diverging for apical two-thirds of R$_1$. Stem of median fork about twice as long as tb. Veins M$_1$ and M$_2$ parallel, M$_1$ a little divergent from R$_5$ apically.

Abdomen appears attenuated basally (considered an artifact) but broadened in apical part, from segment 7 onwards, covered in long pale bristling (longer than apical tibial width). Tergite 8 broad and short. Genitalia (fig. 14): tergite 9 broadly rounded on apical and lateral margins; cercus simple, rounded apically; gonostylus simple, curved and tapered apically in a sickle shape.

Wing length 3.7 mm, antenna 3.0 mm, body 3.8 mm.

Specimen 29057 – Body entirely greyish brown. Antenna as above specimen, apical flagellomere 1.3 x as long as penultimate. Palpus as long as head, structure as above.

Thorax greyish brown, with brownish setae.

Legs dark coloured, a little longer than body. Tarsus 1 about 1.5 x its tibia in length. Tibia 1 with spurs as long as apex of tibia, 2-3 with spurs 1.5 x long as tibial apex.

Wing as above specimen, with Rs about as long as ta, R$_1$ then more approximated to R$_1$ on most of basal half. Vein Sc close to R$_1$, ending at about level of middle of stem of median fork; sc-r cannot be discerned. Macrotrichia evenly distributed including scattered on middle part of basal cell. Costal hairs 1.5 x width of costa. Haltere dark.

Abdomen is in dorsal view, dark coloured with yellow setae. Genitalia difficult to see; gonostylus may be simply curved as in above specimen).

Wing length 3.5 mm, antenna 2.8 mm.

Discussion – The first specimen resembles the figures of Loew's syntypes of *hirta* by Meunier (1899) in the antenna, wing structure and apparent form of the gonostylus and the second specimen is considered conspecific.

Heterotricha grandis (Meunier)
(? *grandis* : figs. 3, 13)

Palaeoheterotricha grandis Meunier, 1904 : 62.

Material examined – 1 ♂ (intact and well preserved), labelled K1144 and Heterotricha (teste Hennig); 1 ♂ labelled Palaeoheterotricha (teste Hennig), entire insect but amber piece broken in half, with apical part of abdomen, most of antenna and wings in separate piece to remainder; 1 ? sex, only head, thorax, fore legs and part of one wing, labelled Palaeoheterotricha grandis (teste Hennig) (all in GPIM); 1 ♂, labelled 29106, Heterotricha grandis (Meun.) [Palaeoheterotricha] Baltic amb., presented A. Théry Feb. 1932 (BMNH).

Specimen K1144 – An intact well preserved male (fig. 3 is based on it). *Head.* Outer ocelli less than their diameter from eye margin. Antenna with scape dark brown; pedicel, first flagellomere and base of second pale. Flagellomeres are proportionately longer so that entire antenna is much longer than in *takkae*, extending to more than twice length of head and thorax together. Second flagellomere is 0.75 length of first, flagellomere 12 is 0.6 length of first.

Thorax with the three black mesoscutal stripes only narrowly separated. Most setae are detached in the specimen examined but long yellow ones are apparent on the grey areas at the sides of the mesoscutum.

Legs slender, longer than body, brownish yellow. Fore tarsus 1.25 x its tibia.

Wing very similar in form and venation to *takkae*; macrotrichia absent from basal cell, a few in apical part of costal cell. Costa slightly produced beyond tip of R_5. M_1 sinuous, divergent from and then parallel with R_5. Basal cell narrow, vein sc-r at just before half length of cell.

Abdomen more depressed. Visible part of segment 8 is 0.6 length of segment 7. Bristling pale except on genitalia, including tergite 9, which has dense brown bristling over much of its surface. Genitalia only clearly visible in lateral view, shape *in situ* similar to *takkae* with rounded gonocoxites. Tergite 9 appearing shorter and broader but produced apically and downturned over cerci. Gonostylus contracted but appears of similar simple form, possibly internally pointed as in *takkae* but could also be bifurcate as apparently in specimen 29106.

Wing length 3.6 mm.

Specimen 29106 – Generally dark brown, grey dusted in appearance due to presence of an opaque milky halo around specimen. *Head.* Ocelli not clearly visible, but considered to be as in other specimens. Antenna twice length of head and thorax together. Facial prominence with setae. Palpus a little shorter than head, as long as height of eye, apical palpomere slender and as long as two preceding palpomeres together.

Thorax with pale setae distributed as in other species.

Legs brown. Tibial spurs short, not longer than apical tibial width. Tarsus about 1.8 x its tibia, which is subequal in length to first two tarsomeres together.

Wing relatively narrow, with costal hairs 1.5-2 x costal width. Macrotrichia evenly distributed on membrane, sparser basally and not apparent in basal cell. Distribution of setae on veins as in other species, but only present on apical half of stem of median fork. Vein Sc not clearly visible. Rs and ta subequal, ta thicker. R_5 close to R_1 on basal part, then divergent, but parallel with costa apically. Costa produced a little beyond R_5 apically. Stem of median fork 2.5 x tb in length. M_1 sinuous, becoming parallel with R_5 apically.

Abdomen dark brown with pale setae, more brownish on genitalia (in dorsal view obscured by wing, ventrally by milky halo). Segment 7 about as long as segment 6, 8 about two-thirds its length, a little shorter than gonocoxites in ventral view. Genitalia (fig. 13): tergite 9 with rounded lateral margins, with apical part narrower and straight edged; cercus ovate and more tapered apically than in other species; gonostylus narrow basally and appearing broadly bifurcate apically. (Apical part of gonocoxites not visible because end of abdomen surrounded by milky area).

Body length 4.6 mm, wing 3.8 mm and antenna 3.25 mm.

Discussion – The specimens examined agree well with Meunier's description of *grandis* (based on 10 ♂, not examined and possibly lost) and it is concluded that they are conspecific with it. The orientation of the genitalia in specimen K1144 precludes confirmation whether the structure is as in 29106, but the second male is considered conspecific with K1144.

Heterotricha dolabrata n. sp.
(fig. 12)

Type material – **Holotype** ♂, labelled In22225(1) and **Paratype** ♂, labelled In22225(2); both labelled Miocene amber Dr H. Loew Coll. Purchd F.A.B. Lord July 1922 (BMNH). Two specimens in one piece of amber; the holotype is in lateral view with wings and has same genital structure as paratype, which is in dorsal view and lacks wings and the dorsal part of thorax.

Description – **Male.** Outer ocelli less than their diameter from eye margin. Antenna dark brown, more than twice as long as head and thorax together (ratio 12.5:5.5); flagellomeres with hairs as long as their diameter; basal flagellomere

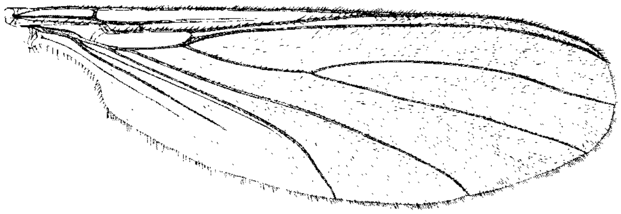


Figure 11
Heterotricha ? hirta Loew (II2130), male wing.

1.5 x long as second, which is about 5 x as long as broad. Apical flagellomere a little longer than penultimate in length. Palpus slender, a little longer than height of head; apical palpomere 1.5 x preceding palpomere in length.

Thorax entirely dark coloured, with mesoscutal stripes indicated as lighter brown areas.

Legs dark brown. Ratio of tibia 1:tarsus 1 is 2.8:4.5. Tibial spur of fore leg 1.5 x apical width of tibia, of mid and hind legs up to twice apical width of tibia.

Wing with costal hairs up to 1.5 x width of costa. Macrotrichia evenly dispersed on membrane but only a few present in apical third of basal cell; setae on veins as in other species. Vein Sc approximated to R_1 and reaching to level of half length of stem of median fork, sc-r present at basal third. Vein Rs short, about half length of ta, which is thicker. Costa extends slightly beyond tip of R_5, venation otherwise as in II2130. M_1 a little divergent from R_5, parallel with M_2 apically. Haltere brownish yellow.

Abdomen shining dark brown with pale setae uniformly distributed on both tergites and sternites, pleural membranes apparent on segments 1-4. Tergites 7-8 progressively shorter, 8 two-thirds length of 7. Genitalia (fig. 12): tergite 9 broad basally, with semicircular apical part of about same length as basal part; cercus small, straight sided but rounded apically; gonostylus narrow basally, then sharply broadened into large triangular hatchet-shaped apical part.

Wing 4.0 mm, body 4.8 mm, antenna 3.2 mm (winged specimen); body 4.5 mm, antenna 3.0 mm (wingless specimen).

Discussion – Although stated to be from Loew's collection, these specimens were evidently not among the syntypes of *hirta* examined by Meunier, which were in separate pieces of amber. The structure of the gonostylus is closest to *takkae* of the fossil material examined.

Etymology – The specific name refers to the form of the gonostylus.

Heterotricha sp. indet.

Material examined – 1 ♂, labelled 22284, Loew coll. and also bearing an old label "Heterotricha" (suggesting that this may be a syntype of *H. hirta*); 1 ♀, labelled In 22081, Mycetophila Dr H. Loew Colln. Purchd. F.A.B. Lord 1922 (BMNH) (unlikely to be a syntype of *hirta* in view of the *Mycetophila* label).

Specimen 22284 – This has the left half of the head and thorax, most of the left antenna (apart from 3 apical segments) and the apical part of the abdomen sheared off, with much dark particulate material associated including the left wing. Abdomen with only segments 1-4 intact, only the left side of tergites 5-6 and part of tergite 7 present so genitalia are missing.

Generally dark coloured. *Head*. Ocelli not visible. Antenna with flagellomeres about 6 x as long as broad, bearing hairs up to the diameter of the flagellomere in length. Apical flagellomere 1.5 x length of penultimate. Facial prominence with long setae. Palpus a little shorter than head, apical palpomere about twice as long as two preceding palpomeres together.

Thorax with long brownish bristling on sides of mesoscutum and on scutellum.

Legs with fore tarsus 1.5 x its tibia in length. Tibial spurs on fore leg 1.5 x tibial length, on other legs twice as long as in II2130.

Wing with quite long costal hairs, about twice the thickness of the costa. Vein sc-r present, on basal third of Sc, which is weak beyond base of Rs. Vein Rs very short and R_5 closely approximated to R_1 basally. Basal cell is consequently narrow and also lacks macrotrichia on the membrane; these otherwise and setae on veins as other species. Vein M_1 divergent from R_5 and parallel with M_2 on apical half. Stem of median fork less than twice as long as tb.

Wing length 3.5 mm, antenna 2.8 mm, body incomplete.

Specimen 22081 – Body including head, antenna and palpus all dark coloured. *Head*. Antenna distinctly longer than head and thorax together; first flagellomere 5 x as long as broad, twice length of scape and pedicel together and 1.5 x as long as second; other flagellomeres shorter, narrower, 4 x as long as broad; apical flagellomere longer, 1.5 x penultimate. Palpus long and slender, longer than head; apical palpomere nearly equal in length to two preceding palpomeres together.

Thorax. Mesoscutum dull brown, without stripes apparent. Thoracic setae short, pale, arranged in acrostichal and dorsocentral rows, the former broadened in front; long pale setae on sides of mesoscutum, scutellum and pronotal lobes as in other species.

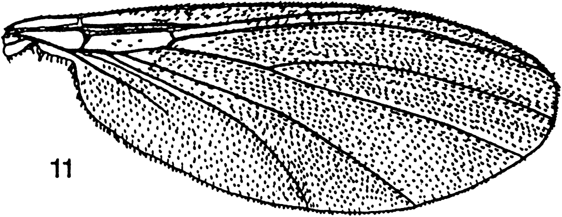
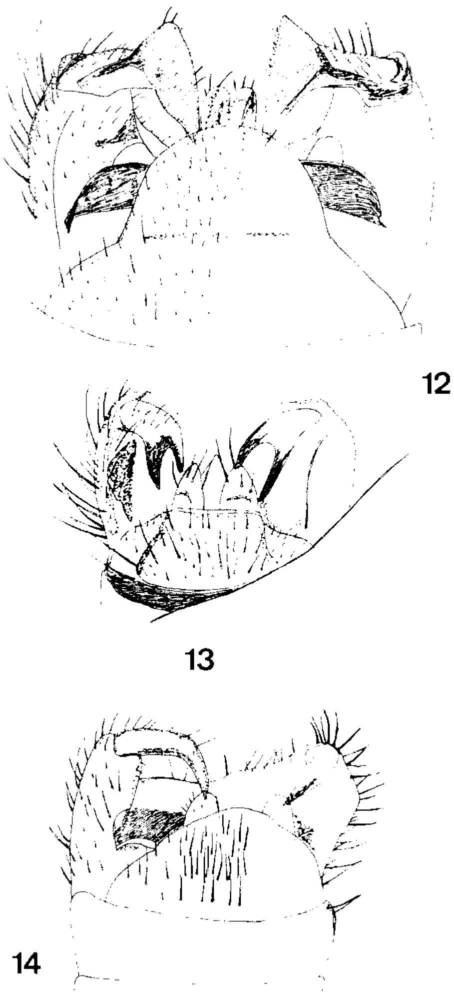


Figure 11
Heterotricha ? *hirta* Loew (II2130), male wing.

correct figure, fig. 4 had been duplicated here



Figures 12-14
Heterotricha ex Baltic amber, male genitalia, dorsal view, showing tergite 9 and cerci in situ. – 12, *H. dolabrata* n. sp. (22225). – 13, ? *H. grandis* (Meunier) (29106). – 14, ? *H. hirta* Loew (II2130).

Legs brown, similar to *takkae*, with short pale setae on coxae and femora. Tarsus 1 is 1.5 x its tibia. Tibial spurs relatively short, on fore leg as wide as tibial apex, others 1.5 x apical width of their tibiae.

Wing relatively broad, with costal hairs only about equal to costal width. Distribution of setae and macrotrichia on wing as other species, but relatively wide basal cell with few macrotrichia. Vein Sc extends distinctly beyond base of Rs, sc-r vaguely indicated. R_5 close to R_1 on most of its length. M_1 divergent from R_5, parallel with M_2 apically, stem of median fork almost twice as long as tb. Crossvein ta and Rs subequal in length, ta much thicker. Haltere pale yellow.

Abdomen cylindrical, appearing shining dark brown on tergites. Pleural membranes broadly expanded on segments 2-7, narrower on 1 and 8. Ovipositor enclosed in a bubble and difficult to discern the structure. Tergite 8 is two-thirds length of tergite 7; tergite 9 short and small, about half length of tergite 8 and distinctly narrower. End of abdomen is obscured but cercus appears to be two segmented, with apical segment rounded apically.

Wing length 4.7 mm, body 4.8 mm and antenna 2.1 mm.

Genus *AFROTRICHA* n. gen.

Type species : *Heterotricha relicta* Edwards, 1925a, by present designation.

Description (♂♀) – *Head.* Eyes large, with a narrow supra-antennal portion 3-4 facets wide, forming an incomplete eye-bridge, separated by width of 2 facets. Ocelli in a flat triangle, separated by nearly twice their breadth from eye margin. Antenna elongate, slightly longer (about 1.5 x head and thorax together) in male than in female. Proboscis short, with slender palpus.

Thorax. Pleura with sutures scarcely indicated, that between anepisternum and katepisternum a curved furrow, indistinct from some aspects; bare except for flat laterotergite which bears long pale hairs and short scattered hairs on metepisternum.

Legs slender but a little shorter than in *Heterotricha.* Empodium broad, almost as long as claws.

Wing (fig. 15) shorter and broader than in *Heterotricha* with more complete covering of macrotrichia, including most of costal cell. Costa with very dense long bristling, giving it a thickened appearance. Vein Sc setose, ending free a little beyond base of ta; sc-r present but weak and pale, situated near base of CuA_1. Vein R_1 ending more apically and Rs originating at about half its length so basal cell larger and longer than in *Heterotricha*. Crossvein ta much longer than in *Heterotricha* (about 3 x Rs), running diagonally basad, so that M is more distant from R_5 than in other genera. R_5 less downturned apically and costa a little more produced than in *Heterotricha*. Vein tb is a little longer than ta and parallel with costa. Base of CuA_1 also a little longer than in *Heterotricha*, so that bases of branches of posterior fork originate further apart.

Male. Tergite 9 large, rounded apically, with a blunt hairy tip; cerci partly enclosed within it apically as in *Heterotricha*. Gonostylus simple, apically pointed internal process giving a shallowly bilobed or notched appearance.

Female. Not examined. Ovipositor (according to figures by Edwards, 1925a) of similar structure to *Heterotricha*. Sternite 8 shorter and broader but also deeply notched medially, with only short bristling. Sternite 9 also shorter and only shallowly notched apically without lateral processes. Cerci relatively smaller with apical segment less broadened apically but long curved yellow bristling on tergite 10 very similar to *Heterotricha*. Spermathecae not chitinised (according to Edwards, *op. cit.*).

Etymology – The generic name is based on occurrence in Africa and relationship to *Heterotricha*.

Discussion – This genus is proposed for a single known species, which is close to *Heterotricha* in the restricted sense adopted here, but which differs significantly in the form and venation of the wings. The close resemblance between the Baltic amber and modern European members of *Heterotricha* and the striking differences from *relicta* which they share suggests that the South African population of the *Heterotricha* Group has long been isolated from that in Europe and generic separation is warranted.

Afrotricha relicta (Edwards) comb. n.
(figs. 15, 17-18)

Heterotricha relicta Edwards, 1925a : 605, fig. 1a-d.

Type material examined – **Lectotype ♂**, South Africa, Cape Province, Montague, x.1917, *E.P. Phillips* (BMNH).

Lectotype designation – *Heterotricha relicta* was described from a male and female, of which only the male syntype has been examined. This specimen is here designated lectotype to enable the new genus to be characterised and has been labelled accordingly.

Description – **Male.** *Head* and thorax dull dark grey dusted. Palpus dark brownish. Antenna with scape and base of first flagellomere yellowish, otherwise dark brown.

Thorax with bristling yellow, distributed as in *Heterotricha takkae*. Legs with coxae and femora yellow, with pale bristling; tibiae brownish, trochanters and tarsi darkened. Halteres yellow with knob darker.

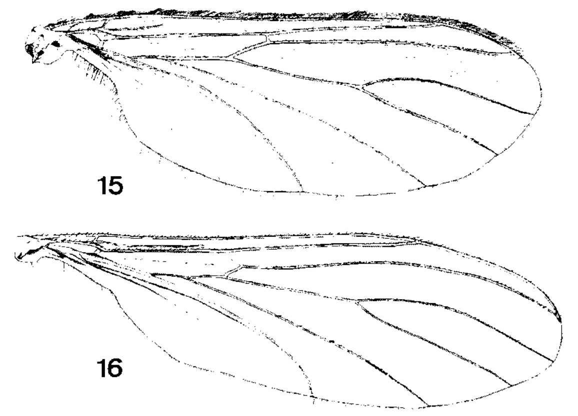
Abdomen blackish, faintly shining, with long yellow hairs. Genitalia, figs. 17-18.

Wing length 3.5 mm.

Female. Not examined (syntype in South African Museum, Cape Town). Antennae are described as slightly shorter than in male.

Genus *CHILETRICHA*, n. gen.

Type-species : *Heterotricha marginata* Edwards, 1940, by present designation.



Figures 15-16
Wings of South African species. – 15, *Afrotricha relicta* (Edwards). – 16, *Rhynchoheterotricha stuckenbergae* Freeman.

Description (♂♀) – *Head* with eyes strongly reniform but widely separated on frons, bearing very short pubescence. Ocelli in a shallow triangle, outer ocelli close to eye margin (further removed in *freemani* n. sp. and *dureti* n. sp.).

Thorax with chaetotaxy similar to *Heterotricha* but laterotergite bare and metepisternum setose as in *Anisotricha* and *Rhynchoheterotricha*. Posterior part of mesepisternal suture between anepisternum and katepisternum distinct, extended less distinctly in front in most species. Mesepimeron constricted behind katepisternum, extended to mid coxa. Mediotergite arched above, with lower part (phragma) strongly enlarged and projecting into abdomen.

Legs long and slender. Empodium broad but distinctly shorter then claws.

Wing membrane mostly covered with macrotrichia but with bare areas of varying extent in costal and basal sectors. Vein Sc bare; sc-r present although often weak, on basal half of Sc and level with or before base of posterior fork. Basal cell broader than in *Heterotricha* with base of M faintly indicated only as seam on membrane, ending close to junction of ta, tb and M_{1+2}. Venation close to *Anisotricha* with base of Rs (as long or longer than ta) originating basad of or close to level of junction of ta with M and costa usually distinctly extended beyond tip of R_5 (except in *freemani* n. sp. and *dureti* n. sp.). Vein R_5 not closely approximated to R_1, but strongly downturned apically.

Male with tergite 9 medially narrow, exposing large cerci, laterally broader and bristly, produced in a long process, which is bare except for strong black internal spines near tip (except in *spinulosa*, where it is expanded apically and bears small spinules). Gonostylus with broad simple lateral lobe and shorter inner lobe bearing strong black spines apically in most species (inner lobe absent in *spinulosa*).

Female with abdominal structure differing from that of *Heterotricha* in proportion and chaetotaxy of parts: tergite 8 is longer, tergites 9 and 10 are smaller without long bristling on tergite 10, while sternite 8 is strongly developed, bilobed medially with a series of short (± spinose) setae on inner margin of each lobe, bearing close set golden yellow bristly hairs on its side margins and on a pair of apically rounded basal ventral lobes; sternite 9 broadly divided medially into two narrow flattened lobes; cerci with large broad basal segment and apical segment longer and narrow, apically rounded.

Etymology – The generic name is based on relationship to *Heterotricha* and the predominant occurrence in the Chilean subregion.

Discussion – This genus is proposed for eight south American species, which are mainly distributed in Chile and Argentina while one species, *marginata* (Edwards), is found in the south of Brazil. The species differ in the proportions of Rs and ta, the degree of extension of the costa beyond R_5 and in the distribution of macrotrichia on the wing membrane. The yellow abdominal markings of *H. marginata* are unique in the *Heterotricha* group but other external characters are very similar. Most species have very similar male genital structure, differing chiefly in the proportions of the parts, but *C. spinulosa* differs strongly and possibly deserves at least subgeneric rank. However, on external characters it is close to *C. nudicostalis* and *C. penae* and it is uncertain if the remaining species of the genus are monophyletic without it.

Key to species of *Chiletricha*

1. Costa ending just beyond or at tip of R_5, which is not strongly downturned apically. Crossvein ta very short, vertical, distinctly less than half length of Rs . . 2
– Costa produced beyond tip of R_5, which is more strongly downturned apically. Cross-vein ta at least half as long as Rs 3
2. Costa slightly exceeding tip of R_5. Distance between R_5 and M_1 less than half that between M_1 and M_2 which are divergent apically. Thoracic stripes indistinct. Female with medial processes of sternite 8 elongate . . . . ***freemani*** n. sp.
– Costa ending at tip of R_5. Distance between R_5 and M_1 more than half that between M_1 and M_2 which are less divergent apically. Thorax with more distinct dark stripes. Female with medial processes of sternite 8 short . . . . ***dureti*** n. sp.
3. Macrotrichia absent from cells c, r_1 and basal cell (basal third of wing membrane lacking macrotrichia except on anal lobe). Rs about twice as long as ta. R_5 close to costa beyond tip of R_1 4
– Macrotrichia present in at least cell r_1 R_5 not closely approximated to costa beyond tip of R_1 5
4. Costa produced nearly half distance to M_1. Tergites with narrow yellow apical bands. An additional spiny process on gonostylus . . . . ***marginata*** (Edwards)
– Costa produced for a third distance to M_1. Tergites entirely dark . . . . ***seminuda*** (Freeman)
5. Macrotrichia present in cell c . Rs only a little longer than ta. Costa produced more than a third distance to M_1 . . . . ***equalis*** (Freeman)
– Macrotrichia absent from cell c. Rs nearly twice as long as ta. Costa produced less than a quarter distance to M_1 6
6. Setae on Rs and R_5 long, those on Rs nearly half its length. Crossvein tb about 2 x base of CuA_1. Gonostylus with internal spinose lobe in medial position . . . . ***nudicostalis*** (Freeman)
– Setae on Rs and R_5 relatively short, much less than half length of Rs. Gonostylus with internal lobe basal or absent 7
7. Crossvein tb about 1.5 x base of CuA_1. Gonostylus with basal spinose lobe . . . . ***penae*** n. sp.
– Crossvein tb 2.5 or more x length of base of CuA_1. Gonostylus without basal lobe, but flanked above and below with lobes of gonocoxites . . ***spinulosa*** n. sp.

Chiletricha marginata (Edwards), comb. n.
(figs. 19, 21)

Heterotricha marginata Edwards, 1940 : 441.

Type material examined – Holotype ♂, Brazil, Santa Catarina, Nova Teutonia, 27°11'S, 52°23'W, 30.x.1937, *F. Plaumann* (BMNH).

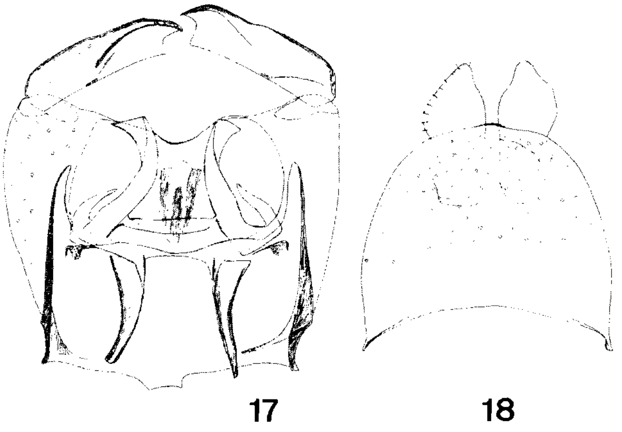
Other material – 1 ♂, locality as holotype, 12.ix.1947, *F. Plaumann* (MNHN); 1 ♀, same locality, 300-500 m, xi.1944, *F. Plaumann* (MNHN) (both 27°11'S, 52°23'W); 1 ♂, Brazil, Nova Teutonia, vii.1941, *F. Plaumann* (BMNH).

Description – **Male.** *Head* grey dusted. Antenna with scape greyish, pedicel and extreme base of first flagellomere yellow, rest of flagellum dark brown; flagellomeres very elongate (basal flagellomere = height of head, 1.3 x second flagellomere). Palpus yellow, slender, elongate (more than 1.5 x head height).

Thorax uniformly grey dusted. A nearly complete suture between anepisternum and katepisternum.

Legs including coxae yellow. Hind legs missing in holotype, present in second male examined; tibial spurs almost twice tibial diameter (said to be less than twice in original description).

Wing (fig. 19) with base of Rs diagonal, nearly twice ta, R_5 strongly downturned and close to costa apically, costa



Figures 17-18
Afrotricha relicta (Edwards), male genitalia. – 17, dorsal view with tergite 9 and cerci removed. – 18, tergite 9 and cerci.

extended nearly or quite halfway to M_1. Macrotrichia absent from cells c, r_1, basal cell and bases of other cells; setae absent from most of Rs, ta, tb, base of CuA_1, stem of posterior fork and bases of fork veins. Haltere with yellow stem, darkened knob.

Abdomen slender, compressed, shining dark brown with narrow yellow apical margins of tergites 1-5, narrowed medially. Genitalia with two internal spinose lobes on gonostylus (fig. 21).

Wing length 4.5 mm.

Female. Coloration of head, antenna, palpus and thorax as male. Antenna with basal flagellomere shorter than head height, about twice length of second flagellomere. Legs as male. Wing with Rs more than twice ta and bearing setae. Halteres missing in specimen examined. Abdomen slender, dark brown with apical yellow band on tergites 1-8, occupying about apical quarter of each tergite, the bands not narrowed medially. Ovipositor similar to that of *C. seminuda*, with apical segment of cerci narrow and more elongate in lateral view. Sternite 8 bears long fine yellow hairs and has short narrow apical processes. Wing length 5.3 mm.

Discussion – Lane (1952) recorded a further two males from the state of São Paolo, Brazil.

Chiletricha seminuda (Freeman), **comb. n.**

(figs. 20, 22, 25)

Heterotricha seminuda Freeman, 1951 : 27.

Type material examined – **Holotype** ♂, Chile, Chiloé, Chiloé I., Ancud, 19.xii.1926, *F. & M. Edwards* (BMNH). **Paratypes** : 2 ♀, Chile, Llanquihue, Puerto Montt, 24.xi.1926; 3 ♀, Chile, Llanquihue, Peulla, 12-13.xii.1926; 2 ♀, Chile, Chiloé, Mechuque Island, 23.xi.1926 (all *F. & M. Edwards*) (BMNH).

Other material – 1 ♂, Argentina, Neuquén, Pucará, Parque Nacional Lanín, Malaise trap, 4.ii.1972; 1 ♀, same data, 22.i.1972, *S. Schajovskoy* (J. P. Duret collection, MNHN); 1 ♂, Chile, Cautin, Los Coigües, L. Villar, 1-15.i.1965; 1 ♀, Chile, Malleco, Rio Blanco, 1100-2000 m, xi.1964, *L. Peña* (MNHN)

Description – **Male.** *Head* dark grey dusted. Antenna more than twice head and thorax together, with pedicel and base of first flagellomere yellow, the latter less than head height, 1.5-1.8 x second flagellomere. Palpus brownish yellow, about head height.

Thorax dark grey dusted. A complete suture between anepisternum and katepisternum.

Legs yellow, hind coxae more brownish.

Wing (fig. 20) with Rs nearly twice ta. R_5 strongly downturned and closely approximated to costa apically, costa extends 0.35 distance to M_1. Macrotrichia absent from cells c, r_1, basal cell and bases of other cells; setae absent from Rs, ta, tb, base of CuA_1 and stem of posterior fork. Haltere entirely yellow.

Abdomen more shining grey. Male genitalia with broad internal lobe bearing long spines on gonostylus (fig. 22).

Wing length 4.1 mm.

Female. Similar in most respects. Antenna proportionately shorter, about 1.5 x head and thorax together, basal flagellomere little more than half head height. Ovipositor (fig. 25) with long curved golden hairs on sternite 8 and protruding cerci with apical segment elongate, bluntly pointed at tip, brownish yellow. Wing length 4.3-4.7 mm.

Discussion – Dr. J.P. Duret informed me that he had 12 ♂, 4 ♀ from various localities, including material from Malleco, Osorno and Maule Provinces, Chile and Chubut Province, Argentina.

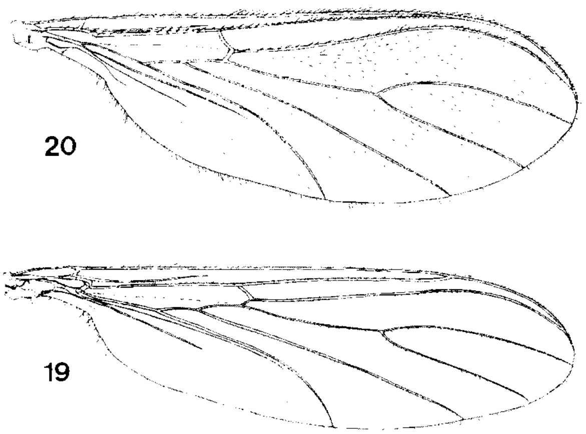
Chiletricha nudicostalis (Freeman) **comb. n.**

(figs. 23, 27)

Heterotricha nudicostalis Freeman, 1951 : 28.

Type material examined – **Holotype** ♂, Chile, Chiloé, Mechuque Island, 23.xii.1926, *F. & M. Edwards* (BMNH) (genitalia missing, evidently detached from Canada balsam mount).

Other material – 1 ♂, Chile, Valdivia, La Union Las Tables, ii.1988, *L.E. Peña* (J.P. Duret collection, MNHN).



Figures 19-20
Chiletricha species, wings. - 19. *C. marginata* (Edwards). - 20. *C. seminuda* (Freeman).

Description – **Male.** *Head* grey dusted. Antenna with pedicel and base of first flagellomere pale yellow, the latter less than height of head (1.3 x second). Palpus brownish yellow, less than head height.

Thorax uniformly slightly shining grey dusted. A complete suture between anepisternum and katepisternum.

Legs including coxae yellow.

Wing (fig. 27) with Rs about 1.7 x ta, R_5 strongly downturned but not closely approximated to costa apically, costa extended only short distance (about 0.15) towards M_1. Macrotrichia absent from cell c, but present in apical two-thirds of cell r_1, 1-2 in basal cell, bases of other cells bare. Rs with long setae on greater part in Valdivia male, only 1 apical seta apparent in holotype; ta, tb, and stem of posterior fork bare. Crossvein tb about 2 x as long as base of CuA_1. Haltere yellow, with knob brownish apically.

Abdomen slightly shining grey dusted. Gonostylus with series of close-set spines, on a medial internal lobe (fig. 23). Wing length 4.3 mm.

Female. Not examined (females identified as this are now considered likely to be *C. spinulosa*).

Discussion – Dr. Duret informed me that he also had 1 ♂ from Osorno, Pucatrihue.

Chiletricha equalis (Freeman) **comb. n.**
(figs. 24, 28, 29-30)

Heterotricha equalis Freeman, 1951 : 28.

Type material examined – Holotype ♂, CHILE: Chiloé, Chiloé I., Castro, 20-22.xi.1926, *F. & M. Edwards* (BMNH).

Other material – 1 ♀, Argentina, Neuquén, Pucará, Parque Nacional Lanín, Malaise trap, 23.xii.1971, *S. Schajovskoy* (J.P. Duret collection, MNHN); 1 ♂, Chile, Malleco, Rio Blanco, 1100-2000 m, xi.1964, *L. Peña* (MNHN).

Description – **Male.** *Head* dark brown, grey dusted, including entire antenna; first flagellomere = head height, 1.5 x second flagellomere. Palpus brownish.

Thorax dark brown, grey dusted. Only posterior half of suture between anepisternum and katepisternum developed.

Legs including coxae brownish yellow.

Wing (fig. 28) with Rs only a little longer than ta, R_5 downturned apically but not closely approximated to costa, costa extended 0.4 distance to M_1. Membrane with macrotrichia more evenly distributed than other species, present in apical two-thirds of cell c, all but extreme base of r_1, apical half of basal cell and most of anal lobe; setae present apically on Rs, apical two fifths of tb but absent from ta, base of M_4+CuA_1 and stem of posterior fork. Haltere yellow with knob brownish apically.

Abdomen dark brown, grey dusted. Male genitalia with long basal lobe of gonostylus bearing spines apically (fig. 24).

Wing length 5.2 mm.

Female. Entirely grey dusted, only apex of pedicel and base of first flagellomere yellowish. Antenna shorter and more slender than in male, but first flagellomere longer, about 1.8 x second. Legs including coxae entirely yellow. Haltere yellow with knob darkened on apical half. Ovipositor (figs. 29-30) differing from other species in proportion of parts. Wing length 5.5 mm.

Chiletricha freemani n. sp.
(figs. 26, 33-34, 45)

Type material – **Holotype** ♂, Argentina, Neuquén, Pucará, Parque Nacional Lanín, 5.xii.1972, Malaise trap, *S. Schajovskoy* (J.P. Duret collection, MNHN). **Paratypes** : 1 ♀, Argentina, data as holotype (J.P. Duret collection, MNHN); 1 ♂, 1 ♀, Chile, Marga-Marga, ix.1929, *F. Jaffuel* (BMNH).

Description – **Male.** *Head* light grey dusted. Outer ocelli about half their diameter from eye margin. Antenna entirely brownish grey, with lighter grey dusting on scape, about 2.5 x head and thorax together, first flagellomere 0.7 head height, 1.4 x second flagellomere. Palpus brownish yellow.

Thorax grey dusted with vague brownish stripes between rows of setae on dorsum. Pleural structure as other *Chiletricha* species, except only posterior half of mesepisternal suture developed as in *equalis*. Metepisternum with short pale hairs.

Legs yellow with thin grey dusting on coxae, most evident on hind coxae, trochanters darkened, tarsi brownish apically.

Wing (fig. 45) clear with sparse macrotrichia on the membrane, absent from cell c and base of radial cells; setae present on apical half of Rs and to base of M_1, M_2 and stalk of median fork, 3 present on apical part of seam representing base of M before ta, absent on ta, base of CuA_1 and base of veins of posterior fork. Crossvein sc-r weak. Rs well developed, curved diagonally so that base of R_5 is well removed from R_1, but R_5 more approximated to costa apically than in female; costa scarcely produced beyond tip of R_5. Crossvein ta short and almost vertical; tb and base of CuA_1 subequal. Haltere yellow.

Abdomen shining black, thinly grey dusted. Male genitalia (figs. 33-34) without a spinose lobe on gonostylus, but spinose lateral processes of tergite 9 as in other species.

Wing length 3.9 mm.

Female. Antenna distinctly shorter and more slender with shorter hair than in male, about 1.5 x head and thorax together, first flagellomere about half head height, 1.5 x second flagellomere. Palpus dark brown. Mesepisternal suture only indicated near posterior margin. Macrotrichia on wing membrane denser apically, absent from cell c but present in apical half of cell r_1. R_5 less downturned apically and further from costa than in male. Abdomen depressed with large ovipositor (fig. 26), curved golden hairs on sternite 8, which has elongate apical processes and cerci short ovoid and brownish. Wing length 4.2-4.3 mm.

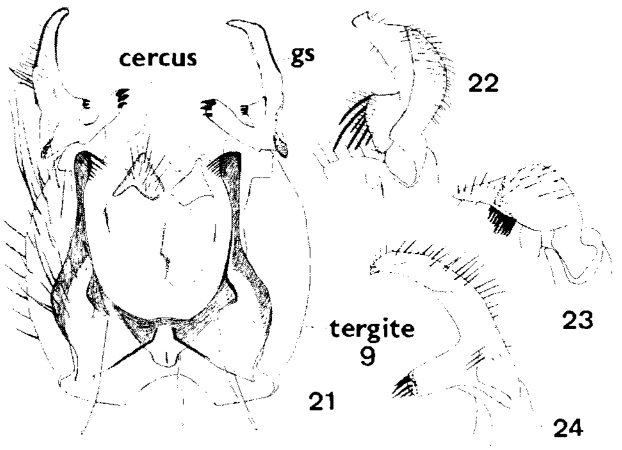
Etymology – The species is named for Paul Freeman, to acknowledge his contribution to knowledge of this genus. This species was mentioned but not described by him as the only specimen then available was damaged.

Chiletricha dureti n. sp.
(figs. 35-36)

Type material – **Holotype** ♀, Chile, Linares, Fundo Molcho, 11-21.xi.1965, *L.E. Peña* (MNHN). **Paratypes** : 1 ♀, Argentina, Neuquén, Pucará, Parque Nacional Lanín, 15.xi.1973; 1 ♀, same locality, 23.xi.1971, *J.P. Duret* (MNHN).

Description – **Female.** *Head* light grey dusted. Antenna entirely brownish grey, about 1.3 x head and thorax together; first flagellomere less than half head height, 1.3 x second flagellomere. Palpus brownish yellow.

Thorax grey dusted with four brown stripes between rows of setae on mesoscutum, more obvious than in *freemani*: two long brown stripes from fore margin either side of acrostichal row, not reaching scutellum; lateral stripes, external to dorsocentral rows, begin behind humeral area and reach scutellum.



Figures 21-24
Chiletricha species, genitalia. – 21, *C. marginata* (Edwards), dorsal view. - 22-24, dorsal view of left gonostylus (after Freeman, 1951, *seminuda* slightly revised). – 22, *C. seminuda* (Freeman). – 23, *C. nudicostalis* (Freeman). - 24. *C. equalis* (Freeman). *gs*, gonostylus.

Mesepisternal suture faintly indicated except near posterior margin. Metepisternum with short pale hairs.

Legs yellow, hind coxa greyish basally.

Wing (fig. 36) clear with sparse macrotrichia distributed similarly to *freemani*, absent from cell c, basal cell and bases of other cells; setae absent from Rs (or only on apical part), present to base of R_5 and M_{1+2}, absent from ta, tb, base of CuA_1 and base of veins of posterior fork. Rs well developed, nearly straight, about 2.5-3.5 x ta, so that R_5 is well removed from R_1 basally and from costa apically; costa ending precisely at tip of R_5. Crossvein ta diagonally basad; tb longer than base of CuA_1. Haltere yellow.

Abdomen shining black, thinly grey dusted similar to *freemani*; sternite 8 with long curved golden hairs, its apical processes short as in most other species (not elongate as in *freemani*) (fig. 35).

Wing length 4.3-4.4 mm.

Male. Unknown.

Etymology – This species is named for José Pedro Duret, to acknowledge his contribution to knowledge of South American Sciaroidea.

Chiletricha penae n. sp.
(figs. 37, 39-41)

Type material – **Holotype** ♂, Chile, Santiago, Cerro el Roble, 28-31.xii.1963, *L.E. Peña* (MNHN).

Description – **Male.** *Head* grey dusted. Antenna with pedicel and base of first flagellomere yellow, the latter about 1.3 x as long as second flagellomere. Palpus brown.

Thorax uniformly grey dusted. Mesepisternal suture represented by a shining ridge, not reaching fore margin.

Legs yellow including coxae.

Wing (fig. 37) clear, radial veins brown; macrotrichia sparsely distributed on membrane, absent from cell c, present in apical two-thirds of cell r_1; basal cell and base of other cells bare; Rs, ta, tb, base of M_{1+2}, bases of other veins and stem of posterior fork bare. Rs diagonal, nearly twice as long as ta; tb about 1.5 x base of CuA_1; R_5 as *nudicostalis*; costa extended 0.2 distance from R_5 to M_1. Haltere yellow, brownish on knob.

Abdomen shining black, thinly dusted. Genitalia (figs. 39-41): gonostylus (fig. 40) with broad elongate blunt-ended lateral lobe and short internal spinose lobe, resembling *equalis*. Tergite 9 (fig. 41), however, has a slender apical lobe with a short comb of spines apically (this lobe broadened with longer spines in *equalis*).

Wing length 4.1 mm.

Female. Unknown.

Etymology – This species is named for Luis E. Peña, who collected this and several other species of this genus.

Chiletricha spinulosa n. sp.
(figs. 1, 31-32, 38, 42-45)

Type material – **Holotype** ♂, Chile, Curicó, El Coigual, 20-26.i.1964, *L.E. Peña* (MNHN). **Paratypes** : 1 ♀, data as holotype; 1♀, Chile, Nuble, Cordillera Chillán, ii.1980, *L.E. Peña* (MNHN).

Description – **Male.** *Head* slightly shining, grey dusted. Antenna relatively short, about 2.7 x head and thorax together. Pedicel and base of first flagellomere brownish yellow, rest dark brown. Palpus yellow.

Thorax slightly shining, grey dusted, with bristling as other species. Mediotergite more strongly shining, especially on apical part. Mesepisternal suture indistinct.

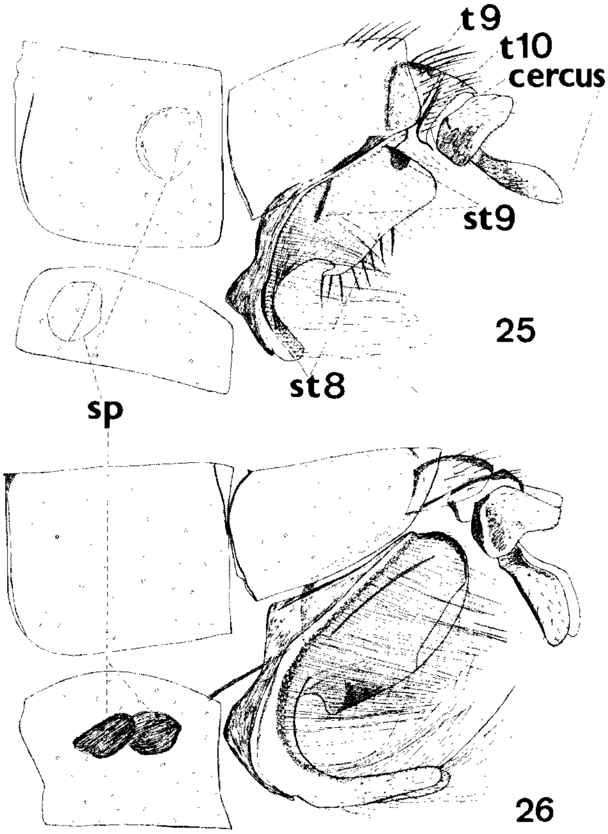
Legs including coxae yellow.

Wing (fig. 38) clear, radial veins not much darker than others, with macrotrichia on most of membrane, absent from cell c, base only of cell r_1 and other cells, a few in apical part of basal cell (on the seam representing the base of M). Rs and ta with some setae near their junction, otherwise bare; tb, base of CuA_1, stem of posterior fork and base of its branches bare. Rs nearly twice as long as ta, tb almost 3 x as long as base of CuA_2. R_5 downturned apically, but not close to costa. Costa extends 0.2 distance from R_5 to M_1. Haltere yellow.

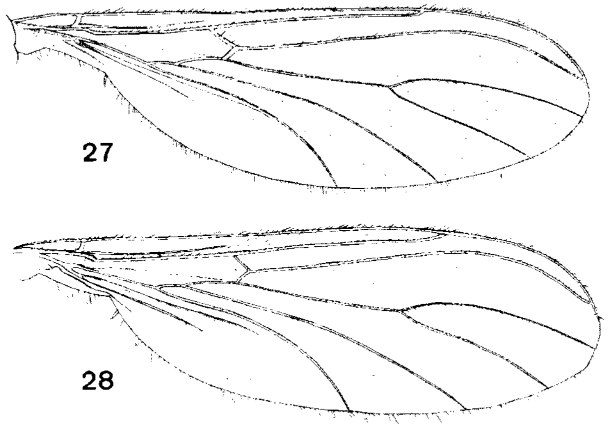
Abdomen shining black. Genitalia (figs. 42-44) broad and spherical with yellowish appendages. Tergite 9 (fig. 44) with median bridge broader than in other *Chiletricha* species; lateral lobe expanded, apical lobe shorter than in other species and apically expanded into two broad lobes, each bearing many internal spinules on apical margins (fig. 45). Gonostylus strap shaped, bristly at tip, without spinose internal lobe; dorsal and ventral expansions of gonocoxites above and below gonostylus.

Wing length 4.5 mm.

Female. Similar to male, but Rs and ta practically bare; considered to be this species rather than *nudicostalis* because of short setae on R_5. Head and thorax uniformly grey dusted. Antenna entirely grey except for apical margin of pedicel and base of first flagellomere yellowish; antenna about 1.25 x head and thorax together, proportionately shorter and more slender than in male, first flagellomere about half head height. Legs and haltere yellow, coxae with grey dusting externally. Abdomen more thinly dusted and distinctly shining black. Ovipositor structure (figs. 31-32) very like



Figures 25-26
Chiletricha species, female genitalia, lateral view of ovipositor and segment 7 (enclosing spermathecae). – 25, *C. seminuda* (Freeman). – 26, *C. freemani* n. sp. *sp*, spermatheca; *st*, sernite; *t*, tergite.



Figures 27-28
Chiletricha species, wings. – 27. *C. nudicostalis* (Freeman). – 28. *C. equalis* (Freeman).

that of *seminuda*, but small differences in proportion of parts and internal processes of lobes of sternite 8 more weakly setose. Wing length 4.6-4.7 mm.

Etymology – The specific name refers to the spinules on the lobes of tergite 9, in contrast to the spines found in most species of the genus.

Genus *ANISOTRICHA* n. gen.

Type-species : *Heterotricha novaezealandiae* Tonnoir, 1927, by present designation.

Description (♂) – *Head* with eyes sparsely pubescent, as widely separated on frons as distance between outer ocelli, but upper part appearing produced a little towards its fellow because of strong emargination of eyes above antennae. Median ocellus slightly in front, outer ocelli about their diameter from eye margins. Antenna more than 2 x as long as head and thorax, with long slender flagellomeres. Short setae on facial prominence. Proboscis short with slender palpus, a little longer than head with last palpomere almost as long as two preceding together.

Thorax with bi-triserial acrostichals, pluriserial dorsocentrals and irregularly distributed long yellow bristling on sides similar to other members of Group. Chaetotaxy of pleura as *Chiletricha* in bare laterotergite and presence of short hairs on metepisternum. Mesepisternal suture distinct posteriorly, upturned and fading anteriorly. Mesepimeron vertical, constricted at angle of katepisternum, level with lower margin of laterotergite and deflected below to base of mid coxa. Mediotergite with phragma enlarged as in *Chiletricha* but less arched above (examined in Palmer Road specimen, fig. 100).

Legs slender, with empodium vety small, only about half as long as claws.

Wing (fig. 47) with membrane largely covered with macrotrichia. Vein Sc setose; sc-r absent. Venation similar to *Heterotricha* but Rs longer than ta and originating basad of junction of ta with M and tb; tb more strongly basad and parallel with costa than in *Chiletricha* and posterior fork originating more basally as in *Heterotricha*. Costa extending more than half distance from R_5 to M_1.

Male with tergite 9 short and transverse without any apical prolongation or processes, leaving most of genitalia exposed dorsally. Gonostylus with emarginate outer and lobed inner margin. Gonocoxites on each side bearing a ribbon-shaped process arising immediately external to base of gonostylus.

Female unknown.

Etymology – The generic name both has a Greek derivation with an equivalent meaning to *Heterotricha* and is also based on the name of the type locality of Aniseed Valley.

Discussion – *Anisotricha* is based on a single species, described from a single male. Further males have been collected recently and Mathias Jaschhof forwarded one of these to me. The third male examined is in poor condition (with genitalia missing) and it is uncertain whether it is conspecific. Although *Anisotricha* has most structural characters in common with the South American species referred to *Chiletricha*, it is considered generically distinct because of the genital characters in which *Chiletricha* shows more resemblance to *Rhynchoheterotricha*. The male genitalia of the holotype (figured by Tonnoir & Edwards, 1927) are not refigured here because the preparation was in unsatisfactory condition when examined, but the Buller specimen has enabled the structural characters to be confirmed.

Anisotricha novaezealandiae (Tonnoir) **comb. n.**
(fig. 47)

Heterotricha novaezealandiae Tonnoir in Tonnoir & Edwards, 1927 : 771, fig. 22 (wing), fig. 231 (♂ genitalia).

Material examined – **Holotype** P, New Zealand, South Island, Nelson, Aniseed Valley, *A. Tonnoir* (CINZ). 1 P, New Zealand, North Island, Buller, St. Arnaud, in mixed mature *Nothofagus* forest, 700 m, 11-18.i.1991, Malaise trap, *L. Nelson* (author's collection); 1 P (congeneric but not certainly conspecific), New Zealand, Palmer Road Springs Junction, 11.xi.1974, *P.M. Johns* (MNHN).

Description – **Holotype male**. Head and body shining black, thinly grey dusted. Antenna dark brown with first two flagellomeres yellowish. Legs and halteres yellow; trochanters, tips of hind femora and tibiae dark, tarsi brownish. Genitalia dark brown with the ribbon shaped processes pale. Tergite 9 less than half length of gonocoxites, broadest laterally, emarginate on anterior edge, produced a little medially on posterior margin, otherwise simple in structure. Gonostylus with concave outer margin, inner margin produced into two blunt digitate lobes, the apical of these longer; a long curved apically pointed ribbon shaped dorso-internal process set on gonocoxites (apparently of gonocoxal origin) at base of each gonostylus. Wing (fig. 47) length 3.5 mm.

Female. Unknown.

Genus *RHYNCHOHETEROTRICHA* Freeman

Rhynchoheterotricha Freeman, 1960: 75. Type-species : *R. stuckenbergae* Freeman, 1960 : 77, by original designation.

Description (♂) – *Head* with eyes slightly emarginate, but not produced dorsomedially, more widely separated above than below antenna, with very short sparse pubescence. Ocelli close together, outer more than twice their diameter from eye margin. Antenna very long and slender, about two-thirds body length, with first flagellomere 1.5 x long as second. Lower part of face greatly elongated, forming a slender "proboscis" as long as front tibia. Small mouthparts including short palpus carried at tip of this projection.

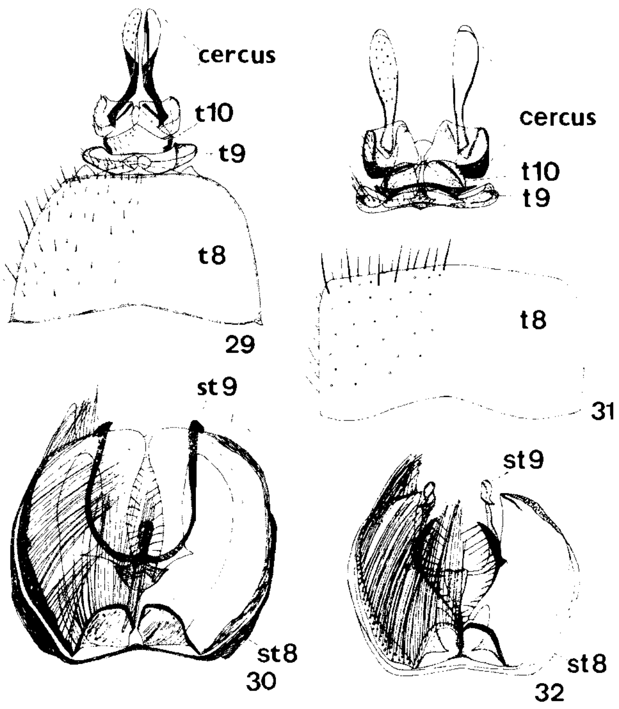
Thorax with pleura bare except prothorax and metepisternum, which has short hairs. Posterior part of mesepisternal suture present, extended less distinctly in front. Katepisternum angled behind, mesepimeron constricted behind it. Mediotergite with phragma enlarged as in *Chiletricha*.

Wing membrane with complete covering of microtrichia, devoid of macrotrichia but setae present on the veins. Vein Sc ending free; sc-r weak, situated before level of base of CuA$_1$. Rs subequal to ta; both are diagonal with Rs originating at same level as junction of ta with M. Costa produced a short distance beyond tip of R$_5$, which is downturned apically, but not approximated to costa after tip of R$_1$.

Male tergite 9 short and broad with two pairs of apically spinose processes on apical margin. Gonostylus simple.

Female unknown.

Discussion – The formation of the elongate "proboscis" in consisting mainly of an elongation of the head only resembles *Gnoriste* Meigen (Mycetophilidae, Gnoristinae) among those Sciaroidea that have this type of adaptation to feeding at flowers. Some genera of Sciaridae (especially *Eugnoriste* Coquillett) have the head partly extended but not forming the greater part of the proboscis. In other such Sciaroidea with an elongate proboscis (Lygistorrhinidae and some Keroplatidae) the mouthparts themselves are variously developed to form the greater part of the proboscis. The only known species of *Rhynchoheterotricha* was recorded as visiting *Erica* flowers, the only biological information yet published on any member of this Group.



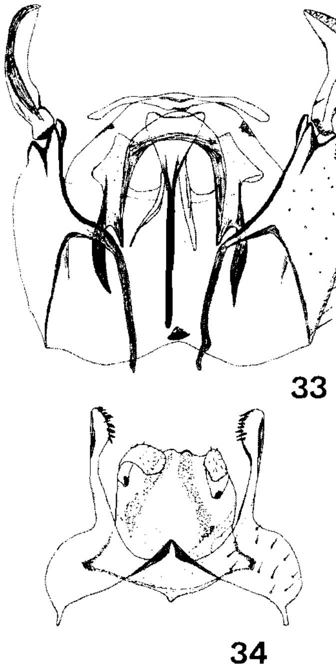
Figures 29-32
Chiletricha species, female genitalia. – 29-30, *C. equalis* (Freeman). – 31-32, *C. spinulosa* n. sp.. – 29, 31, dorsal view of tergites 8-10 and cerci. – 30, 32, ventral view of sternites 8 and 9. *s*, sternite; *t*, tergite.

Rhynchoheterotricha stuckenbergae Freeman
(figs. 16, 48, 50-51)

Rhynchoheterotricha stuckenbergae Freeman, 1960 : 77.

Material examined – **Paratypes** : 1 ♂, South Africa, W. Cape Prov., Du Toits Kloof, Pearl. dist. 27.ix.1959, on *Erica* species, *P. J. Stuckenberg*; 1 ♂, South Africa, Cape Prov., Worcester, ix.1938, *R. E. Turner* (BMNH).

Description – **Male**. *Head* (fig. 48), antenna, proboscis and



Figures 33-34
Chiletricha freemani n. sp., male genitalia. – 33, dorsal view with tergite 9 and cerci removed. – 34, tergite 9 and cerci.

body entirely dark, grey dusted, but abdomen more shining black. Legs brownish yellow. Haltere pale yellow. Bristling of body and coxae pale, setae and setulae of femora, tibiae and tarsi dark. Antenna with first flagellomere a little more than height of head without proboscis. Face above proboscis bare but facial part of proboscis bears short pale hairs. Wing, fig. 16. Setae absent on Rs, ta, base of CuA$_1$, stem of posterior fork and bases of veins of posterior fork. Male genitalia, figs. 50-51.

Wing length 4 mm.

Female. Unknown.

Discussion – In addition to the paratypes examined, only the holotype (data as first paratype, in the Natal Museum, South Africa) is known.

Genus *NEPALETRICHA* n. gen.

Type-species : ***Nepaletricha mystica***, n. sp., by present designation.

Description (♂) – *Head* with eyes produced only a little towards each other dorsally, widely separated by greater than width of ocellar tubercle. Outer ocellus less than its diameter from eye margin. Antenna slender, longer than head and thorax, with scape and pedicel adpressed to head; first flagellomere very elongate, nearly as long as next two flagellomeres together. Face bare. Proboscis a third head height; palpus slender, as long as head.

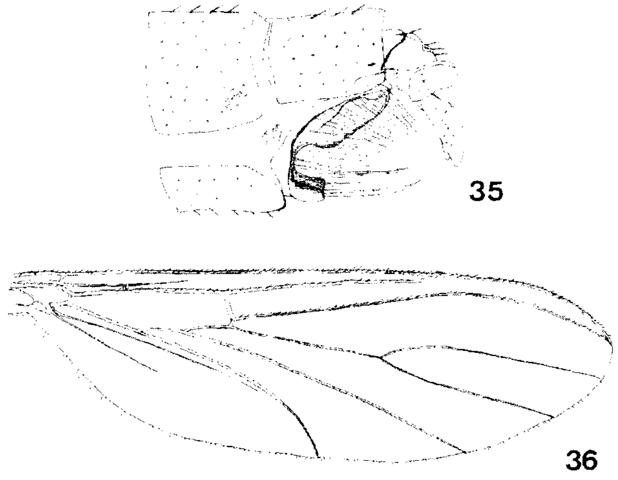
Thorax with uniserial acrostichal and dorsocentral rows; two pairs of scutellars; some strong intraalars. Pleura (except prothorax) and mediotergite entirely bare. Mesepisternal suture distinct, transverse; upper part of katepisternum below this suture constricted and depressed. Mesepimeron vertical, strongly narrowed below. Laterotergite only slightly convex. Mediotergite with phragma enlarged below (exposed in holotype as abdomen had been removed).

Legs long and slender. Tibiae about 1.5 x their femora, tibial spurs on tibiae 2-3 subequal, more than twice apical tibial width in length. Legs weakly bristled throughout; bristling on tibiae and tarsi a little longer than leg width.

Wing (fig. 52) broad, with macrotrichia scattered over whole membrane. Vein Sc long, reaching halfway to tip of R$_1$ but ending free; sc-r absent. R$_1$ ends at 0.7 wing length; R$_5$ basally parallel with R$_1$, ending near wing tip; costa extends halfway from R$_5$ to M$_1$. Crossvein ta very short, almost vertical, stalk of median fork about as long as the fork; basal part of M faintly indicated; tb extends diagonally basad, meeting M$_3$+CuA$_1$ about its length from base of posterior fork; CuA$_2$ basally diverging gently from CuA$_1$, then sharply downturned. Setae long on costa and radial veins, shorter on Sc, stalk of median fork and fork veins; ta, tb, base of CuA$_1$ and CuA before fork bare.

Abdomen relatively short and thick with broad rectangular tergites and sternites; segment 7 only a little shorter than 6; segment 8 shorter and contracted into 7.

Male genitalia with tergite 9 broadly rounded, with a slender bare process on each side of apical margin, cerci enclosed within it. Gonostylus apically curved with a terminal spine and with a basal internal lobe bearing long setae



Figures 35-36
Chiletricha dureti n. sp., female. – 35, lateral view of genitalia. – 36, wing.

Figures 37-38
Chiletricha species, wings. – 37, *C. penae* n. sp. – 38, *C. spinulosa* n. sp.

apically; flanked below by a pair of blunt gonocoxal lobes on each side of medial emargination of gonocoxites.

Female unknown.

Etymology – The generic name is based on occurrence in Nepal and relationship with the *Heterotricha* Group.

Discussion – This genus is described for a single species from Nepal, known from a single male. This is very distinct from other known species in structure of genitalia, although with some characters in common with the following genus *Kenyatricha* (e.g. gonocoxites with setose lobes adjacent to gonostylus) and the wing venation (especially ta reduced, bringing radius and media into close proximity).

Nepaletricha mystica n. sp.
(figs. 52, 54-55)

Type material – **Holotype** ♂, Nepal, 27°57'N 84°59'E, Malaise trap 5.10, 100', 30.v.1967 (*Canadian Nepal Expedition*: glued to side of a pin, the legs distorted due to previous preservation in alcohol) (MNHN).

Description – **Male.** *Head* dark brown, thinly grey dusted with dark bristling. Scape light brown, antenna otherwise light dull yellowish. Proboscis and palpus brown; proboscis a third head height; palpus slender, as long as head.

Thorax slightly shining brown with yellowish humeral area and sutures. Mesoscutum with narrow dark furrows along acrostichal and dorsocentral rows (most setae broken off from holotype).

Legs long and slender, uniformly dark brownish yellow with coxae more brownish.

Wing (fig. 52) broad, slightly brownish. Haltere yellow.

Abdomen slightly shining dark brown with long dark bristling uniformly distributed. Genitalia (figs. 54-55) short, more or less spherical, brownish yellow.

Wing length 4.1 mm, body length 3.3 mm.

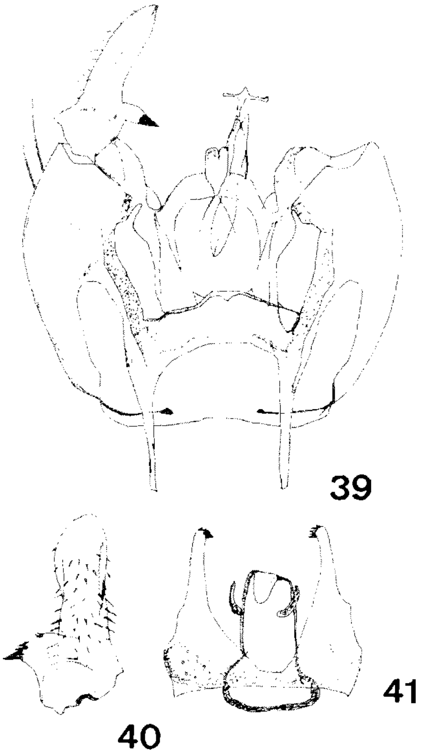
Female. Unknown.

Etymology – The specific name refers to another secret of the Himalayas, revealed by the Canadian Expedition, showing that the *Heterotricha* group exists on the borders of the Oriental Region.

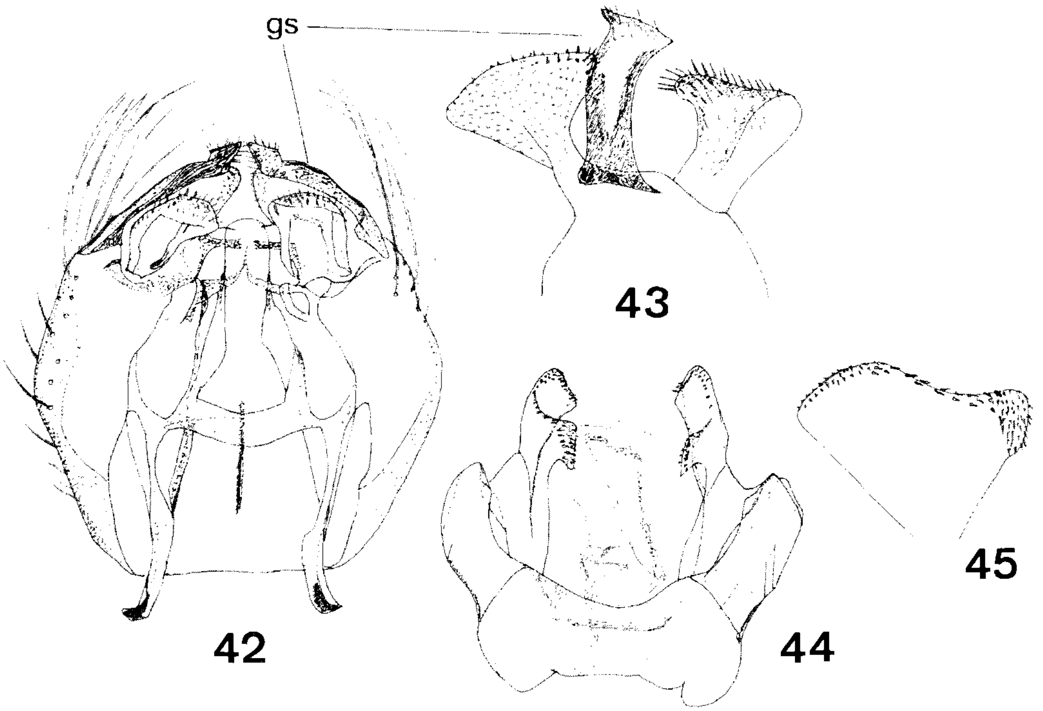
Genus *KENYATRICHA* n. gen.

Type-species : *Kenyatricha elgon* n. sp., by present designation.

Description (♂) – *Head* with eyes reniform around bases of antennae, produced a little towards each other dorsally, the inner edge level with outer ocellus, which is less than its width from eye margin. Scape and pedicel short, subequal,



Figures 39-41
Chiletricha penae n. sp., male genitalia. – 39, dorsal view without tergite 9 and cerci. – 40, internal view of left gonostylus. – 41, dorsal view of tergite 9 and cerci.



Figures 42-45
Chiletricha spinulosa n. sp., male genitalia. – 42, dorsal view without tergite 9 and cerci. – 43, external view of right gonostylus, to show accessory gonocoxal lobes. – 44, dorsal view of tergite 9 and cerci. – 45, internal view of left lobe of tergite 9. *gs*, gonostylus.

adpressed to head; flagellum elongate with long slender flagellomeres [based on *K. mulanje*]. A group of strong downturned setae on facial prominence above mouth margin. Proboscis short, simple; palpus long, slender.

Thorax with irregular rows of acrostichal, dorsocentral and lateral setae on mesoscutum. Mesepisternal suture distinct, curved upwards posteriorly. Katepisternum tounded below. Mesepimeron strongly narrowed below. Laterotergite flat or only slightly bulging below. Pleura (except prothorax) and mediotergite entirely bare. Mediotergite with phragma enlarged (visible in situ in holotype of *K. elgon*).

Legs long, slender, with long setae on coxae and below femora. Tibiae 1.5 x femora, with short bristling only subequal to tibial width. All tarsi with an irregular series of strong setae, a little longer than tarsal width, below.

Wing with macrotrichia over most of membrane, though largely absent from basal third to half of wing. Vein Sc ends free level with base of Rs; sc-r absent. R_1 ends at 0.7-0.75 wing length; R_5 parallel with it basally, but downturned apically and ending near wing tip. Costa extends a third distance from R_5 to M_1. Crossvein ta obliterated; base of M very faint; tb and M_{1+2} meet at junction with Rs and R_5; tb diagonal, parallel or converging with R basally. Vein Sc bare; fork veins, m-stalk and tb with short setae, Rs and base of CuA_2 bare.

Abdomen elongate, laterally compressed.

Male genitalia: tergite 9 emarginate medially, on each side an apically setose lobe; gonocoxites emarginate ventrally, with one or two setose lobes apically, situated ventral to gonostylus, which is setose basally with a flattened asetose lobe apically.

Female unknown.

Etymology – The generic name is based on occurrence of the type-species in Kenya and relationship with the *Heterotricha* Group.

Discussion – As discussed under *Nepaletricha*, this genus is closest to it in structure of genitalia and wing venation, crossvein ta being further reduced. The two included species differ strongly from each other in most aspects of genital structure and may deserve subgeneric rank, but they are considered to represent a monophyletic group. Their type localities are rather widely separated Afrotropical montane habitats and it is possible that the genus is distributed elsewhere on the East African mountains.

Figures 46-47
Wings. – 46, *Chiletricha freemani* n. sp. – 47, *Anisotricha novaezealandiae* (Tonnoir).

Kenyatricha elgon n. sp.
(figs. 53, 56-58)

Type material – Holotype ♂, Kenya, Mount Elgon (site 7), 2280 m, 7.ix.1984, *Ficus* sp., *D. Lachaise* (MNHN).

Description – Male. *Head* dark brown, with dark bristling. Scape and pedicel dark yellowish brown, [flagellum of both antennae missing in holotype]. Proboscis short; palpus long, slender, yellow.

Thorax entirely shining dark brown; [dorsal setae, including 2 pairs of scutellars are broken off in holotype].

Legs long, slender, entirely yellow with dark bristling.

Wing (fig. 53) light yellowish brown, with macrotrichia over most of membrane, though largely absent from basal third. Crossvein tb diagonal, almost converging with R basally, longer than base of CuA$_1$. Costa and radial veins with long setulae. Haltere with long slender stem, light brown.

Abdomen shining dark brown, with long dark bristling uniformly distributed; laterally compressed with segments 6-8 broadened, segments 7 and 8 progressively shorter and contracted. Genitalia (figs. 56-58) also shining dark brown except yellowish appendages; tergite 9 with setose lobes broad apically, tergite also produced to a point laterally; gonocoxites with short medial process and two setose lobes ventral to gonostylus.

Wing length 4.0 mm.

Female. Unknown.

Etymology – The specific name is the type-locality, a noun in apposition.

Kenyatricha mulanje n. sp.
(figs. 59-63)

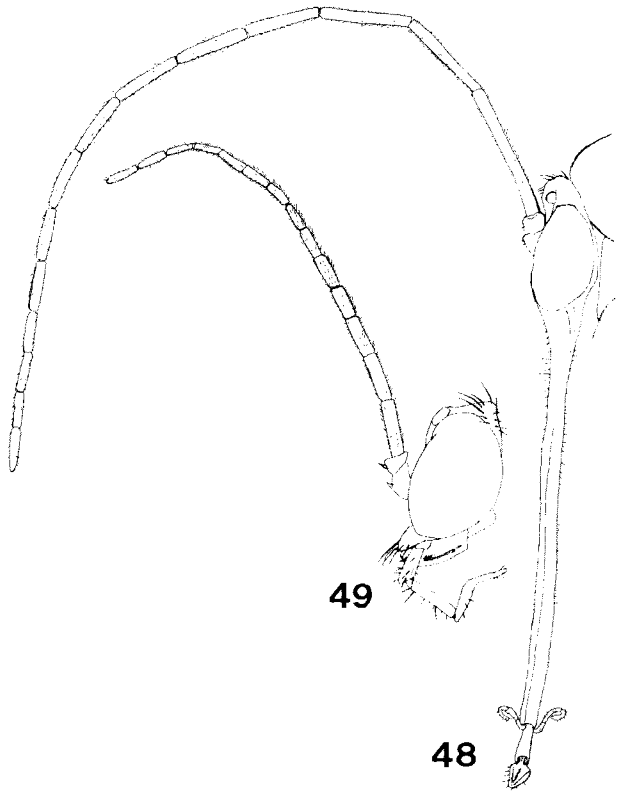
Type material – Holotype ♂, Malawi, "Monts Mulanje", Lichenya Hut, 1840 m, 7.xii.1982, *Y. Cambefort* (MNHN). **Paratype** : 1 P, same data as holotype.

Description – **Male.** *Head.* Antenna dark with short pale hairs on flagellum, which is long and slender, nearly as long as body; first flagellomere longer than head. Proboscis and palpus dark brown.

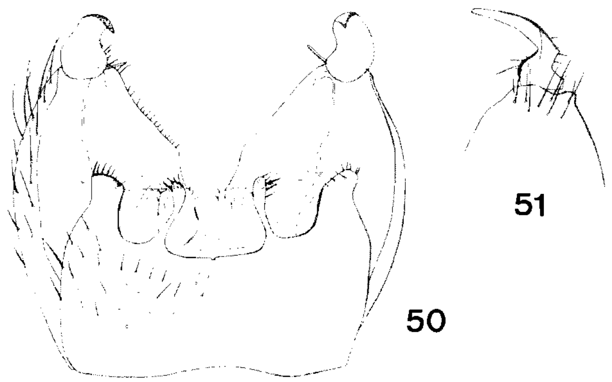
Thorax slightly shining dark brown, grey dusted, with irregularly biserial rows of acrostichals and dorsocentrals, relatively short and pale yellowish, becoming longer posteriorly; long yellowish setae on sides of mesoscutum, on scutellum and prothorax.

Legs long, slender, yellow, with pale setae on coxae and femora, dark setulae on tibiae and tarsi.

Wing (fig. 63) clear, with costa and radial veins (except Rs), tb and base of CuA$_1$ before junction with tb dark brown, other veins yellowish. Macrotrichia absent from basal half of wing, including all of cell c, basal parts of cells



Figures 48-49
Lateral view of heads. – 48, *Rhynchoheterotricha stuckenbergae* Freeman. – 49, *Heterotricha takkae* n. sp.



Figures 50-51
Rhynchoheterotricha stuckenbergae Freeman, male genitalia. – 50, dorsal view. – 51, lateral view of gonostylus.

r_1 and r_5, basal cell, basal half of other cells and all of wing behind CuA_2. Stem of median fork a little longer than fork. Vein tb diagonal, in line with R_5. CuA as in *K. elgon* except that base before tb is a little longer than tb (distinctly shorter in *K. elgon*). Haltere brown, with yellow stem.

Abdomen slightly shining dark brown, grey dusted, clothed with moderately long pale setae. Genitalia (figs. 59-62) dark brown; tergite 9 (fig. 62) with short curved setose lobes; gonostylus (fig. 61) simple, broad and setose basally, with a flattened apical lobe; a curved strongly setose lobe articulating with gonocoxites ventral to it.

Wing length 4.1-4.4 mm.

Female. Unknown.

Etymology – The specific name is the type-locality, a noun in apposition.

Genus *SCIAROSOMA* n. gen.

Type-species : *Sciarosoma borealis* n. sp., by present designation.

Description (♂) – *Head.* Eyes broadly emarginate above antennal bases, more widely separated above than antennal diameter. Ocelli with median a little in front, outer less than its diameter from eye margin. Antenna with scape and pedicel short; flagellomeres elongate, covered with long hairs. Proboscis short, simple, with palpus relatively short, less than half head height, with three palpomeres subequal in length, basal thicker.

Thorax. Mesoscutum with long setae: biserial acrostichals, pluriserial dorsocentrals and many long lateral setae; prothorax also with long setae. Scutellum with many short setae. Pleura (except prothorax) and mediotergite bare. A distinct transverse suture separating anepisternum and katepisternum. Midpleural pit absent. Katepisternum large, broadly triangular below; mesepimeron strongly narrowed below, constricted around its posterior margin and narrowly deflected to reach mid coxa. Mediotergite with phragma projecting strongly into base of abdomen (fig. 67).

Legs slender, with long pale setae on coxae and ventral margins of femora; legs otherwise covered with short dark setulae. Tibial spurs 2.5 x apical tibial width; tibial setulae long and dense, stronger setae shorter than tibial diameter; rows of stronger anteroventral and posteroventral setae present on tarsi. Claws small, empodium shorter.

Wing (fig. 64) with macrotrichia over most of membrane except basal cell, which only has a few near its apical margin; setae on most veins, except Sc and Rs, as in *Sciaropota*. Vein Sc free, ending faintly near level of base of Rs; sc-r absent. Rs vertical. R_1 long, ending level with the tip of CuA_1. R_5 downcurved apically, ending just beyond wing tip; costa extends a short distance towards M_1. Crossvein ta distinctly longer than Rs, directed strongly basad, almost in line with R_5 and tb, basal cell consequently narrow. Stalk of median fork about two-thirds length of its fork. Veins of posterior fork close together basally, base of CuA_1 before junction with tb very short.

Abdomen elongate and slender, broadly inserted on thorax.

Male genitalia: tergite 9 relatively short, almost bandlike, setose, with cerci projecting beyond it (see comments below). Gonocoxites wide, setose with small apical appendages on ventral margin. Gonostylus comprising two separate setose lobes, articulating with each other and lateral margin of gonocoxites. Aedeagal complex with parameres broadly fused with gonocoxal apodemes.

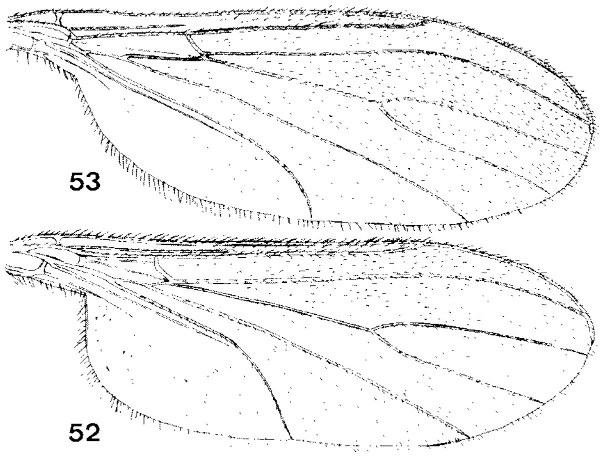
Female unknown.

Etymology – The generic name, coined by R. Väisänen and T. Saigusa, indicates some resemblance in body structure to Sciaridae.

Discussion – This genus, like *Sciaropota* described below, differs from other members of this Group with bare pleura by Rs being shorter than ta and vertical in position, while ta is directed strongly basad, so the venation more closely resembles that of Sciaridae. It resembles other members of the group more in the upturned slender antennae.

Sciarosoma borealis n. sp.
(figs. 64-67)

Type material – Holotype ♂, Russia, Karelia, Kivach, old spruce forest, Malaise trap, 11-17.vi.1991, *A. Polevoi* (label in Russian; preserved in alcohol with genitalia and abdominal segments 2-5 separate, seg-



Figures 52-53
Wings. – 52, *Nepaletricha mystica* n. sp. – 53, *Kenyatricha elgon* n. sp.

ments 6-9 missing) (ZMH). **Paratypes** : 1 ♂, Czech Republic, Bohemia mer., Šumava Mts, Kyselovský les., 48°42'N, 14°03'E, peat bog, Yellow pan traps, *M. Barták & J. Roháček*; 1 ♂, Czech Republic, Bohemia mer., _umava Mts, Nová Hurka, peat bog, 18.v-16.vi.1999, Malaise trap, *M. Barták & Š Kubik* (author's collection).

Other material (not examined). 1 ♂, Finland, Pielisjarvi (=Lieksa), Koli (63°3'N, 28°33'E), 5.vii.1965, *R. Tuomikoski* (ZMH); 1 ♂, Finland, Rovaniemi, Pisavaara (66°17'N, 35°5'E), 13.vii.1965, *R. Tuomikoski* (Kyushu University collection, Japan); 1 ♂, Norway, Østmarka Nature Reserve, Tappenberg, 30.v-27.vi.1991, *B. Økland* (A. Polevoi collection).

Description – Male. *Head* dark. Antenna all dark; scape and pedicel short; flagellomeres about 3 x as long as broad, covered with long pale hairs. Palpus slender, dark grey.

Thorax shining dark grey with all hairs and setae whitish. Mesoscutum shining without distinct stripes, with long pale setae: biserial acrostichals, pluriserial dorsocentrals and many long lateral setae; prothorax also with long pale setae.

Legs yellow with long pale setae on coxae and ventral margins of femora; legs otherwise covered with short dark setulae. Tibial spurs yellow, 2.5 x apical tibial width.

Wing (fig. 64) clear, slightly yellowish, with macrotrichia over most of membrane. Haltere with stem yellow, darker grey on knob.

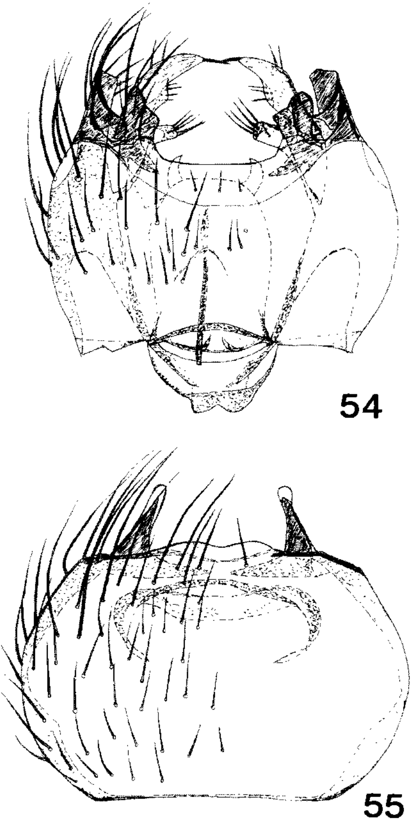
Abdomen entirely dark grey with pale setae. Genitalia (figs. 65-66) yellowish. Tergite 9 (fig. 66) simple, very short and band-like, a little emarginate medially. Gonocoxites bearing three pairs of blunt ventral apical appendages, a slightly curved narrow submedial, a broader less sclerotised appendage lateral to this and a short process laterally below gonostylus. Gonostylus (fig. 65) comprising two separately articulating setose lobes, dorsal one with an apical tooth, ventral blunt-tipped.

Wing length 4.0 mm, width 1.5 mm.

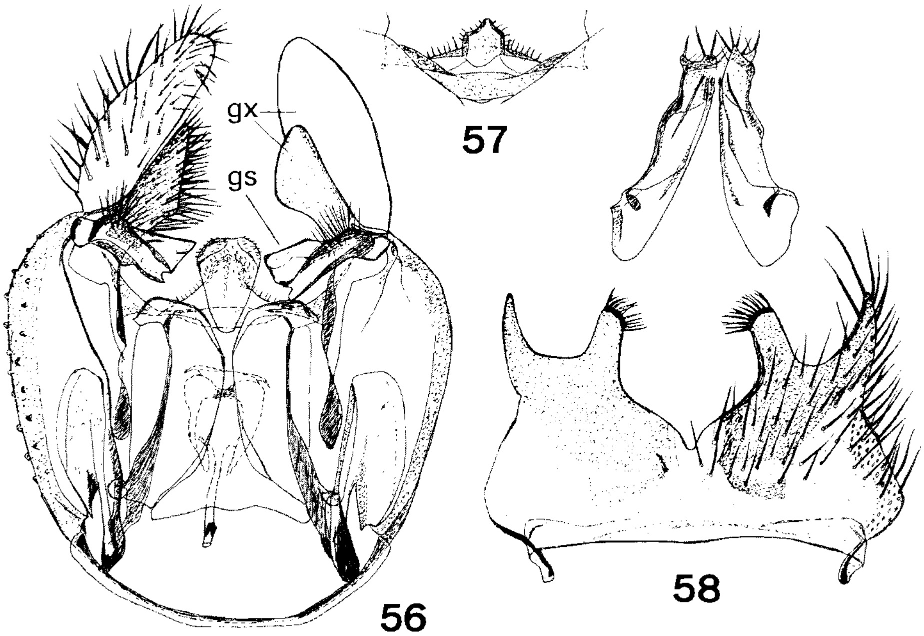
Female. Unknown.

Etymology – The specific name refers to the mainly boreal distribution of the known specimens.

Discussion – Both the above Finnish specimens were netted in old boreal coniferous forests with good quantities of dead wood and lignicolous fungi. Tuomikoski (1966a) stated that A.W. Mikkola had collected two males of a probable *Heterotricha* species at the end of vi.1964 in Finland at Sotkamo, Aarreniemi but the whereabouts of these specimens is unknown. The Norwegian specimen was collected with a trunk-window trap mounted on a fruiting body of *Fomitopsis pinicola* on a dead spruce (*Picea abies*) (B. Økland, pers. comm. to A. Polevoi).



Figures 54-55
Nepaletricha mystica n. sp., male genitalia. – 54, ventral view of gonocoxites and gonostylus (tergite 9 and cerci removed). – 55, dorsal view of tergite 9 (cerci beneath *in situ*).



Figures 56-58
Kenyatricha elgon n. sp., male genitalia. – 56, dorsal view of gonocoxites and gonostylus with tergite 9 and cerci removed. – 57, ventral view of sternal process of gonocoxites. – 58, tergite 9 with cerci separated above. *gs*, gonostylus; *gx*, gonocoxal lobe.

Genus *SCIAROPOTA* n. gen.

Type-species : *S. japonica* n. sp., by present designation.

Description (♂) – *Head* ovoid. Eye broadly and deeply emarginate above antennal base, but not extended dorsally, with short scattered hairs. Three ocelli, outer less than its diameter from the eye margin. Antenna with 2+14 segments, relatively stout and porrect; flagellum stout with ± quadrate flagellomeres, the last three progressively more tapered. Proboscis short and simple; palpus slender.

Thorax with short bristling on mesoscutum, scutellum and proepisternum, but acrostichal, dorsocentral and sublateral series on mesoscutum not clearly differentiated. Pleura (except prothorax) and mediotergite bare. A well-marked transverse suture dividing anepisternum from katepisternum, which is very large and almost triangular. Midpleural pit absent. Mesepimeron constricted in middle, but not much narrowed below, where it is in contact with upper corner of mid coxa. Laterotergite slightly bulging. Metepisternum irregularly rectangular, anterior margin parallel with mid coxa; hind margin convergent with it, so that it is two-thirds its dorsal length ventrally. Scutellum rather short and not much projecting. Mediotergite with phragma weakly developed, small and hardly projecting into abdomen.

Legs with coxae stout and relatively short, femora stout, tibiae relatively stout and dilated, longer than first tarsomeres; uniform irregular setulae on all parts; series of short tibial setulae, shorter than tibial diameter. Claws with small ventral tooth near base.

Wing broad, bearing macrotrichia over most of membrane. Vein Sc abbreviated but ending well beyond base of Rs, sc-r absent. Veins C, R and its branches and CuA_1 stronger than other veins. Vein R_1 strongly curved apically and costal cell much broader than in other genera of this Group. R_4 absent. Costa slightly produced beyond tip of R_5. Branches of posterior fork arising separately. Vein An_1 abbreviated.

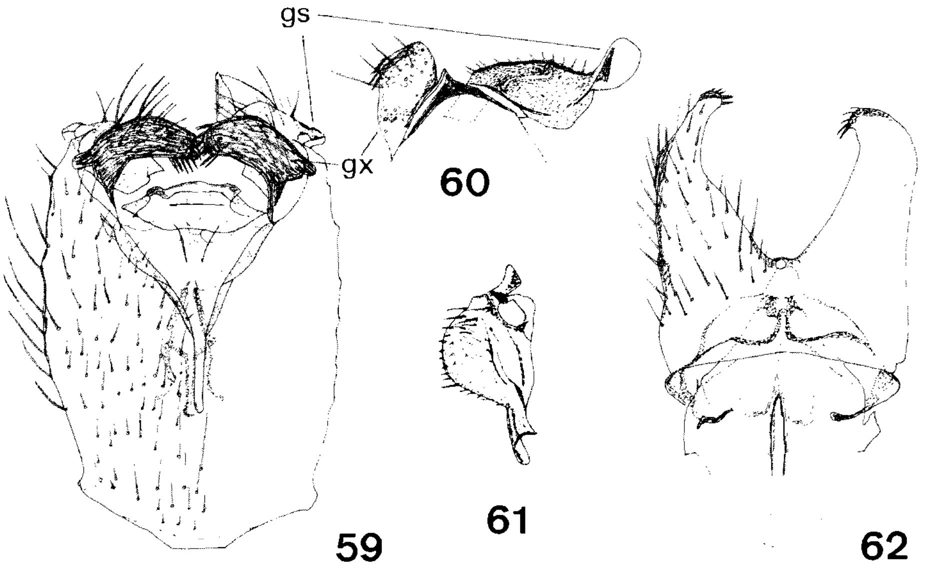
Abdomen broadly inserted on thorax; sternites well developed without fold lines.

Male. Tergite 8 narrowed, tergite 9 small and rectangular, produced medially. Gonostylus deeply bilobed, ventral setose process articulating with ventral margin of gonocoxites. Aedeagal complex with parameres well developed and fused with gonocoxal apodemes basally.

Female unknown.

Etymology – The generic name coined by R. Väisänen and T. Saigusa (literally from the Greek = phantom drinker) refers to resemblance to Sciaridae.

Discussion – Only the type-species has been exami-



Figures 59-62
Kenyatricha mulanje n. sp., male genitalia. – 59, ventral view. – 60, external view of right gonostylus and accessory lobe of gonocoxites. – 61, internal view of left gonostylus. – 62, dorsal view of tergite 9 and cerci. *gs*, gonostylus; *gx*, gonocoxal lobe.

ned. A second species from Taiwan is known to Prof. T. Saigusa (pers. comm. to R. Väisänen). The remarks under *Sciarosoma* about differences from other genera apply, this genus differing strongly from all other genera described here in the more robust form, thoracic and antennal structure.

Sciaropota japonica n. sp.
(figs. 68-71)

Type material – **Holotype** ♂, Japan, Honshu, Nagano, Misuzuko, 20.viii.1962, *K. Hara* (BMNH).

Description – **Male.** Body, legs and appendages all dark brown to black, thinly dusted, with all bristling brownish yellow, only tibial spurs yellow.

Head dark, with short bristling. Antenna about as long as head and thorax together. Proboscis short and dark, palpus slender and dark.

Thorax dark brown, subshining, with short bristling on mesoscutum, scutellum and proepisternum.

Legs dark with short dark setulae irregularly distributed; tibial setae short, only up to a quarter tibial width in length, series of stronger setae on apical margin of tibiae. Tibial spurs pale yellow, on fore tibia 1.5 x and on other tibiae twice apical tibial width. First tarsomere of fore leg two-thirds its tibia in length, of other legs 0.6 their tibia in length.

Wing (fig. 69) broad, yellowish with darker yellow veins, costa and radial veins browner. Macrotrichia over most of membrane except basal part. All veins setose except on basal part and h, Sc, stem of posterior fork and An_1. Vein R_1 ends at two-thirds wing length, R_5 downturned apically. Rs short, vertical, ta about twice its length. Median fork only a little longer than its stem. Haltere black, paler basally.

Abdomen including genitalia entirely dark, subshining with short setae; all pregenital segments with tergite and sternite well developed, segments 2-4 subequal, 5-8 progressively shorter; tergite 8 narrowed medially, about a third length of tergite 9, sternite 8 twice as long in middle. Tergite 9 (fig. 71) short, broad, setose, with median protuberance. Gonocoxites broad and setose, medially emarginate. Gonostylus (fig. 70) deeply bilobed, dorsal lobe pointed apically, ventral lobe rounded and setose.

Wing length 4.0-4.2 mm, maximum width 1.8 mm; body length 6 mm, hind leg length 5.5 mm.

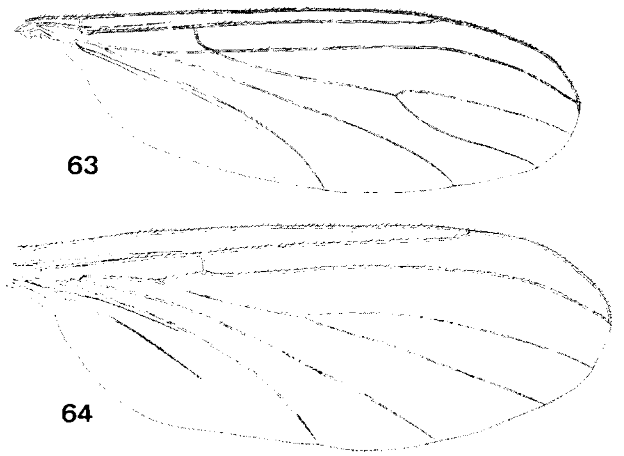
Female. Unknown.

Etymology – The specific name indicates occurrence in Japan.

Genus *PTEROGYMNUS* Freeman

Pterogymnus Freeman, 1951 : 11. Type-species: *Pterogymnus elongatus* Freeman, 1951 : 12, by monotypy.

Description (♂♀) – *Head* small, dorsally flattened. Eyes large, strongly emarginate above, diverging strongly from level of insertion of antennae and twice as wide apart above



Figures 63-64
Wings. – 63, *Kenyatricha mulanje* n. sp. – 64, *Sciarosoma borealis* n. sp.

antennae as below. Three ocelli, the median set a little in front of the outer, which are separated from eyes by about their own diameter or less. Face with rounded densely setose protuberance. Antenna upturned with 2 + 14 segments; scape and pedicel short, adpressed to frons, flagellomeres elongate. Proboscis short, simple. Palpus with short palpiger and three longer palpomeres.

Thorax with prothorax reduced in conjunction with elongate fore coxa. Mesoscutum compressed, strongly humped behind head, with sparse bristling on dorsum and pronotal lobes. Pleural structure similar to *Heterotricha* Group but midpleural pit absent. Pleura (other than prothorax) bare except for short hairs on metepisternum. Mesepisternal suture is complete and transverse. Katepisternum with straight anterior edge, rounded posteriorly. Laterotergite is slightly convex. Mediotergite bare, with phragma small and ventrally directed, not projecting into abdomen.

Legs slender with fore coxa very elongate. Fore and hind tibiae bearing a-d and p-d series of short setae, on apical half of fore tibia and apical two-thirds of hind tibia, those on fore tibia spinose. Pulvilli absent, empodium very short and broad, much shorter than simple claws.

Wing (fig. 72) with macrottichia absent, but with uniform microtrichia on membrane. Vein Sc long, reaching costa; sc-r absent. Vein R_4 present, ending in R_1 to form elongate radial cell. Rs longer than ta. Median fork broad, its branches diverging. Venation otherwise as in *Heterotricha* Group. Costa extends more than half distance from R_5 to M_1, R_5 downturned apically but distant from costa.

Abdomen slender, with sclerites of segments 1-8 in male and 1-7 in female normally developed.

Male tergite 9 simply bilobed apically, gonocoxites with broadly rounded lateral lobes; small simple gonostyli are set internally to these lobes.

Female sternite 8 deeply bilobed as in *Heterotricha* Group; cercus elongate, two segmented.

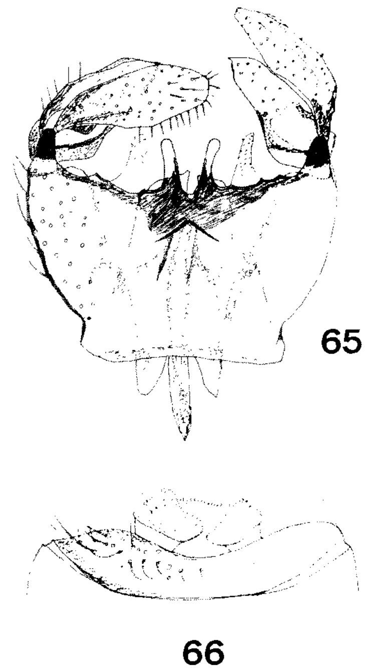
Pterogymnus elongatus Freeman
(figs. 71-77)

Pterogymnus elongatus Freeman, 1951: 12.

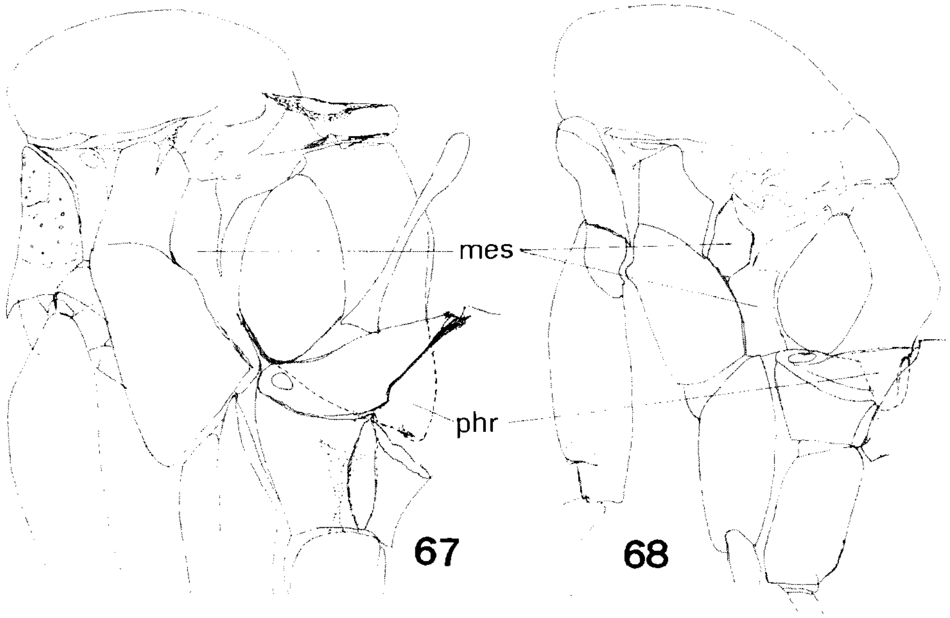
Material examined – Holotype ♀, Chile, Llanquihue prov., Casa Pangue, 4-10.xii.1926, *F. & M. Edwards* (BMNH). 1 ♂, Chile, Osorno prov., Osorno, N. W. Volcan, 22.i.1980, *L.E. Peña*; 1 ♂, Argentina, Neuquén, Pucará, Parque Nacional Lanín, 23.xi.1971, *J.P. Duret*; 1 ♀, same locality, 5.xii.1972, *S. Schajovskoy* (all in J.P. Duret collection, MNHN).

Description – **Male.** *Head* shining brownish black. Antenna with scape and pedicel dark brown; flagellum yellow on two basal segments, succeeding segments progressively darker. Antenna much longer than in female, more than twice head and thorax together, first flagellomere as long as head height, all flagellomeres with very long hair, especially dorsally where length of hairs equals or exceeds half length of the respective flagellomere.

Thorax shining brownish black. Mesoscutum with weak sparse short dark bristling, two rows of acrostichals



Figures 65-66
Sciarosoma borealis n. sp., male genitalia. – 65, ventral view of gonocoxites and gonostyli. – 66, tergite 9 and cerci (after manuscript by R. Väisänen & T. Saigusa).



Figures 67-68
Lateral view of thorax. – 67, *Sciarosoma borealis* n. sp. – 68, *Sciaropota japonica* n. sp. *mes*, mesepimeron ; *phr*, phragma.

converging posteriorly. A row of long dark setae on side margin, from middle of notopleural area to wing base. Also about four long curved setae in series on each posthumeral lobe arching over scutellum. Four long scutellars but many shorter finer setae on hind margin of scutellum below them. Metepisternum with short hairs.

Legs yellow, trochanters dark on apical margin, tarsi darkened apically, tibial spurs black.

Wing venation in Argentine male similar to that of Chilean holotype but Chilean male differs in some respects: Rs 3 x ta, R_4 more diagonal and set further from tip of R_1, R_5 more approximated to R_1 near R_4 so that cell r_1 distinctly broader basally, cell r_1 much shorter than cell r_4. Haltere yellow.

Abdomen all shining brownish black in Chilean male, apical third of tergites 2-5 yellow in Argentine male. Genitalia figs. 74-76.

Wing length 4.5-4.6 mm.

Female. Head (fig. 73) and thorax shining brownish black, mouthparts yellow. Antenna coloured as in male, longer than head and thorax together but much shorter than in male. Wing venation of holotype as in fig. 72; the Argentine female has R_4 closer to tip of R_1 and cell r_1 is thus longer and subequal to cell r_4, Rs is longer relative to ta, while R_5 is more parallel to R_1 basally and closer to costa apically. Abdomen shining brownish, with segments 2-7 paler yellowish on almost their posterior half. Ovipositor with sternite 8 deeply bifurcate, with tapered lobes bearing strong setae apically. Tergites 8-10 short, simple, quadrate. Cerci articulating with tergite 10 are elongate, two segmented. Wing length 5 mm.

DISCUSSION

Relationships between taxa of Sciaroidea

The principal venational character shared by the *Heterotricha* Group, *Pterogymnus* and *Diadocidia* is the loss of the basal part of M as a sclerotised vein. This loss is accompanied by the juxtaposition of the crossveins linking the radial to the median and the median to the posterior (cubital) sectors of the venation. This condition, however, is also found in Ditomyiidae and most Keroplatidae (although the base of M is well developed in the ground-plan of the latter family). The orientation of the crossvein linking the median and posterior sectors, however, differs in these groups. This crossvein was interpreted by Edwards (1925b) as m-Cu and Vockeroth in McAlpine *et al.* (1981) as bm-cu but Hennig (1954) believed the anterior branch of the posterior (cubital) fork to be a fusion of M_4 and CuA_1 and termed it crossvein tb. This interpretation was

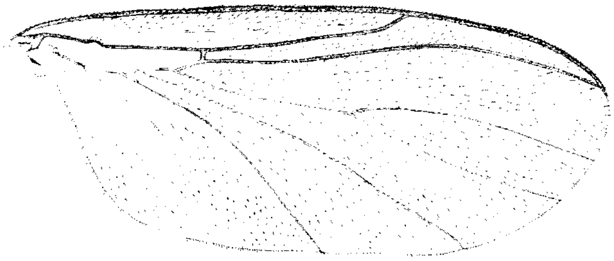


Figure 69
Sciaropota japonica n.sp., wing.

based on a postulated evolutionary series in which the crossvein originated as the petiole of the fork formed in primitive Diptera by M_{2+3} and M_4+CuA_1.

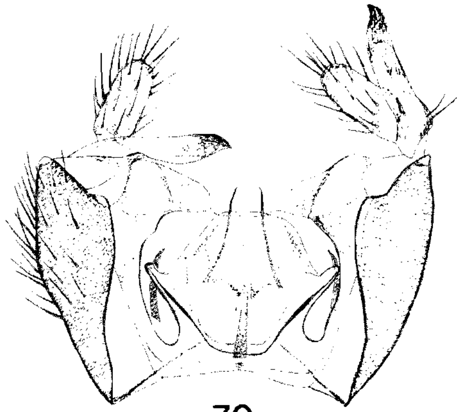
In the ground plan of the Bibionomorpha to which Sciaroidea belongs, crossvein tp (= m-m of McAlpine *et al.* 1981), the discal cell and vein M_3 are obliterated so that ta (= r-m of most authors including Edwards) and tb meet M as crossveins, the base of M remaining strong. Crossvein tb thus primitively met M vertically, basad of its junction with ta as it does in Bolitophilidae (fig. 79, the short vertical vein, which may be obliterated in some species of *Bolitophila*, is here considered to be tb, contrary to the interpretation in fig. 25 of Matile (*op. cit.*) where the more strongly sclerotised portion of M between this vein and ta is labelled as tb) and two of the three genera of Keroplatidae in which ta is not obliterated by the radio-medial fusion (*Arachnocampa* Skuse and *Palaeoplatyura* Meunier). The base of M is sclerotised although weak in these groups. In some Bibionidae tb has become distal to the junction of ta with M but in most Sciaroidea, where it is identifiable, it meets M at or very close to the junction with ta.

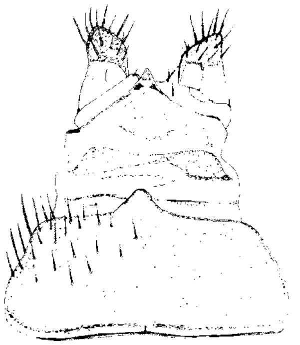
Bolitophila has the complete complement of veins corresponding to the ground plan of the Sciaroidea (fig. 2) but has An_1 abbreviated and tb is far removed basad of ta. *Arachnocampa* possesses sc-r but lacks R_4; its inclusion in the Keroplatidae was based on larval characters and Matile (1990) did not cite any adult characters to indicate the monophyly of the family. A third genus of Keroplatidae, *Asynaphleba* Matile, lacks the radio-medial fusion but has ta and tb adjoining, with the base of M lacking; its position relative to other Keroplatidae requires clarification, as does that of *Palaeoplatyura*. Matile (*op. cit.*) has postulated that *Arachnocampa* represents the sister group of other Keroplatidae, so the primitive position of ta and tb in this genus is presumed to be the ground plan condition of the Keroplatidae.

The basal part of M has become weaker or lost in most Keroplatidae (fig. 80), although it is present as a seam in some genera such as *Platyura* Meigen. Its loss in the Keroplatidae appears to be connected with the development of the radio-medial fusion and must be a convergent condition to the loss of this part of M in other Sciaroidea.

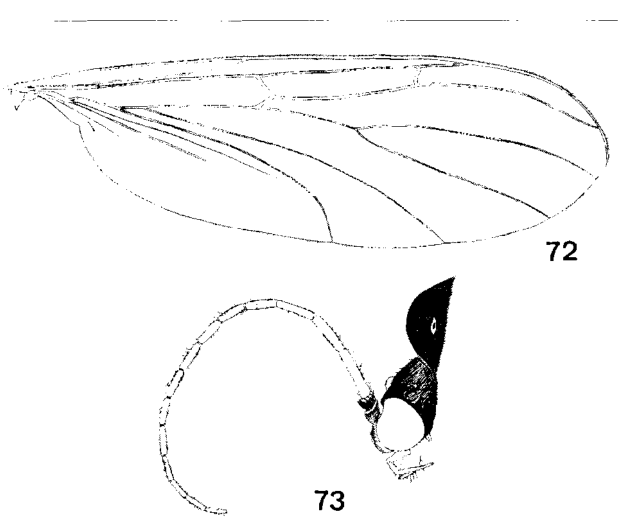
I concur with Amorim (1991) in supporting the conclusion of Edwards (1925b) that where the posterior branch of the radius is forked in Bibionomorpha (other than Pachyneuridae), the intermediate radial vein is R_4 in view of its origin beyond ta (= r-m) and not R_{2+3} as interpreted by Vockeroth (1981) and other authors. R_{2+3} when present in other Nematocera, whether simple (as in Anisopodidae) or forked (as in Pachyneuridae), has an origin from Rs basal to this crossvein.

The venational characters of Sciaroidea are listed in figure 102, where the plesiomorphous condition considered to be in the ground plan of the superfamily





Figures 70-71
Sciaropota japonica n. sp., male genitalia. – 70, dorsal view of gonocoxites and gonostylus, with tergite 9 and cerci removed. – 71, dorsal view of tergite 9 and cerci.

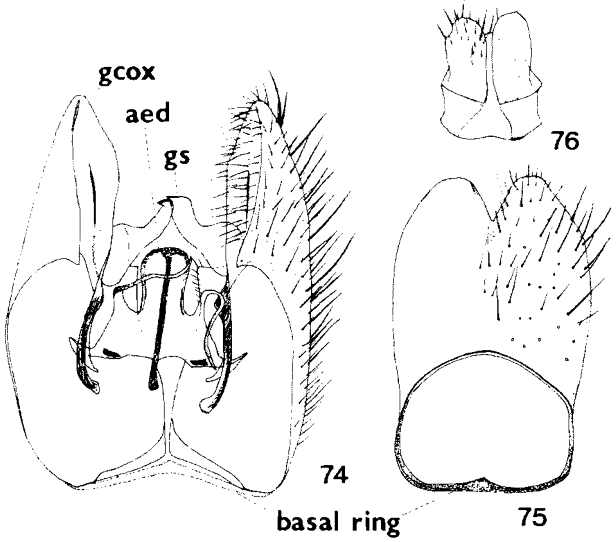


Figures 72-73
Pterogymnus elongatus Freeman, female. – 72, wing. – 73, lateral view of head and antennae, with humped anterior part of thorax.

is first listed, followed by the derived or apomorphous conditions found within the group. The distribution of these characters across the extant taxa of Sciaroidea is shown in this figure. It is evident that most apomorphies are reduction from the ground plan condition and several of these have evidently occurred by convergence in different groups. This has led to difficulty in determining the phylogeny of the taxa within the superfamily. Few structural characters of the adults other than of the venation are useful in this respect, as most plesiomorphous characters are widely distributed through the group and strongly apomorphous characters are either autapomorphous in particular subordinate taxa (e.g. eye-bridge of Sciaridae, filamentous mouthparts of Lygistorrhinidae) or have developed independently in more than one family (e.g. narrow insertion of abdomen in many Keroplatidae and Mycetophilidae, chaetotactic characters of pleura and legs in several families).

The loss of sclerotisation of the base of M and juxtaposition of crossveins ta and tb could be considered to indicate a relationship between the groups with this character state (Ditomyiidae, fig. 81; *Diadocidia*, fig. 82; *Heterotricha* Group (figs. 83-84) and *Pterogymnus*, fig. 85). Among these groups, *Diadocidia* and some Ditomyiidae (*Australosymmerus* Freeman) have tb vertical but most Ditomyiidae have tb running diagonally basad while the *Heterotricha* Group and *Pterogymnus* have it running more strongly basad, becoming nearly parallel with the costa, to meet the anterior branch of the posterior fork nearer its base. This condition is not found in any other extant Sciaroidea although present in most of the Jurassic genera described by Rohdendorf (1938, 1946, 1964). Hennig (1954) interpreted this type of venation, predominating in an earlier radiation of the Sciaroidea, as an evolutionary stage in the development of the venation characteristic of most modern members of the group (i.e. the families Mycetophilidae, figs. 86-88 and Sciaridae, fig. 89) in which there is no "medio-cubital" crossvein. Thus the strong longitudinal vein in Mycetophilidae sensu stricto and Sciaridae, which was considered by Edwards (1925b) and Vockeroth (1981) to be the base of M, is tb which has replaced M in position and function, meeting the stem of the posterior fork near the wing base rather than running to its anterior branch and accounting for the apparent loss of the "m-Cu" crossvein. If this vein were indeed the base of M it would need to have been secondarily strengthened from the ground plan condition of Sciaroidea.

Matile (1981, 1990) accepted Hennig's conclusions, which supported the view that the Mycetophilidae sensu stricto (Mycetophilinae, Sciophilinae and probably Manotinae of Edwards), Lygistorrhinidae and Sciaridae constitute a monophyletic group, from which the other taxa accorded subfamily rank by Edwards (1925b) and many other authors must be excluded. Thus he recognised Bolitophilidae, Ditomyiidae, Diadocidiidae and Keroplatidae following Hennig and also Lygistorrhinidae following Thompson (1975).



Figures 74-76
Pterogymnus elongatus Freeman, male genitalia. – 74, dorsal view of gonocoxites and gonostylus, with tergite 9 and cerci removed. – 75, tergite 9. – 76, cerci (enclosed under tergite 9 in situ). *aed*, aedeagus; *gcox*, gonocoxites; *gs*, gonostylus.

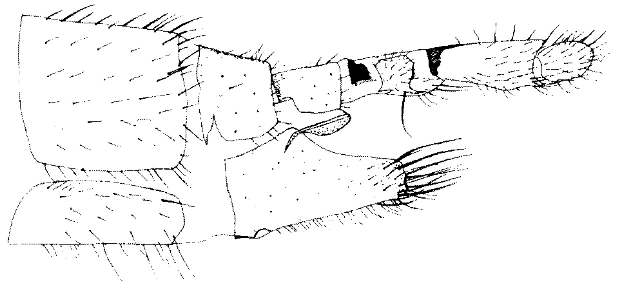


Figure 77
Pterogymnus elongatus Freeman, female genitalia, lateral view.

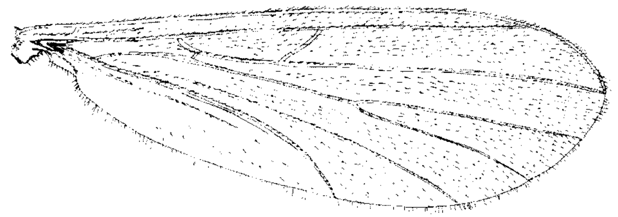


Figure 78
Taxicnemis species, Oltra, New Zealand, wing.

Heterotricha was unplaced in this arrangement and *Pterogymnus* was included in the Diadocidiidae.

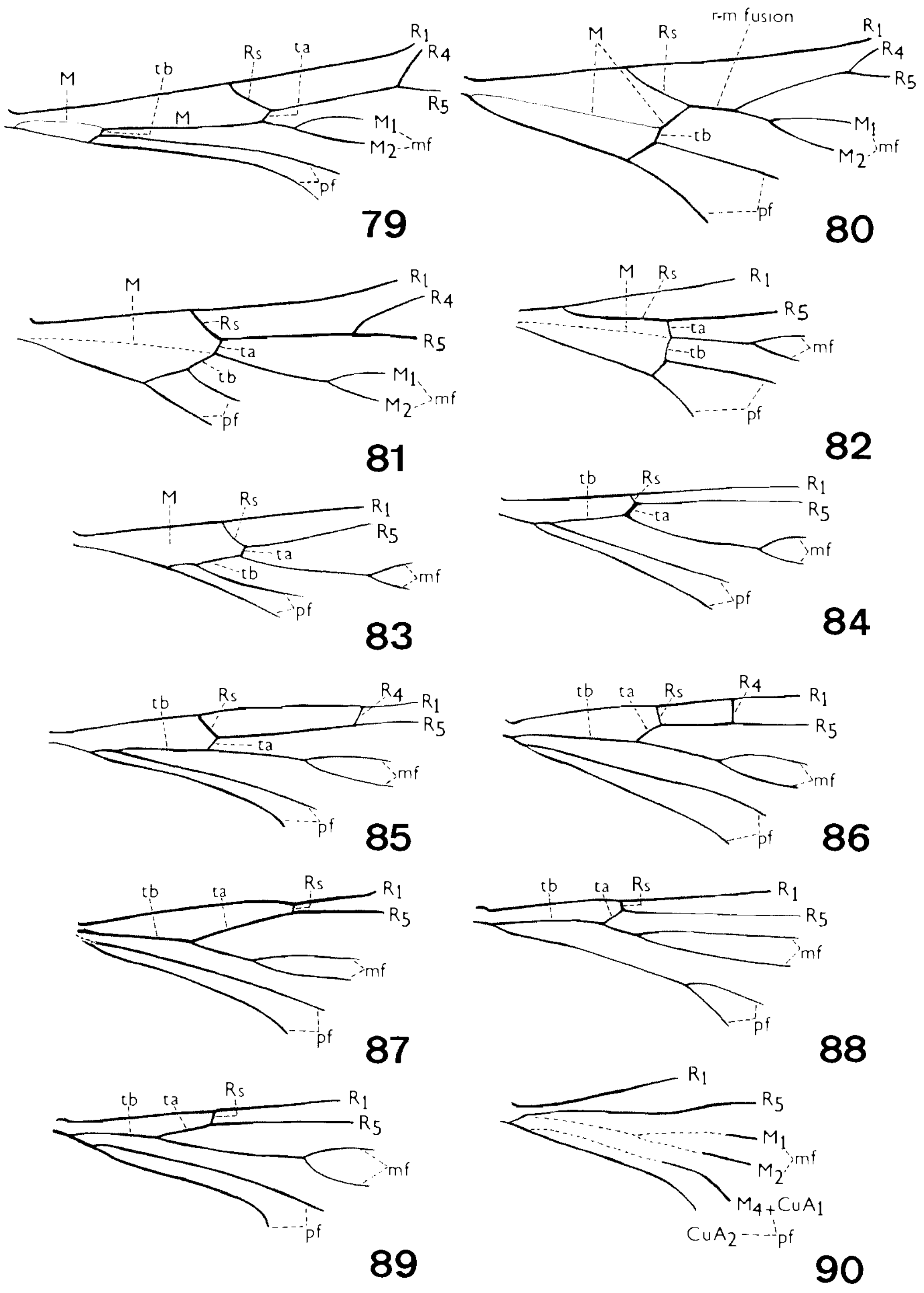
Other views on the position of the Sciaridae have been postulated. Wood & Borkent (1989) included Cecidomyiidae in Sciaroidea, based on two larval synapomorphies (cardo fused with anterior margin of head capsule, metathoracic spiracle absent). They suggested that the Sciaridae and Cecidomyiidae were sister groups, together forming the sister group of other Sciaroidea. This was based on similar development of an eye-bridge and loss of some chromosomes, but no synapomorphy of other Sciaroidea was suggested. Other families were included within Mycetophilidae, although it was recognised that they were paraphyletic and two larval apomorphies linking Sciaridae with Mycetophilidae except Ditomyiinae were mentioned (mandibles heavily sclerotised and flattened, spiracles of 8th abdominal segment absent). The absence of these characters in Cecidomyiidae was considered to be due to reversals.

On the other hand, Blaschke-Berthold (1994) suggested Cecidomyiidae to be the sister group of Sciaroidea as constituted here, although the Sciaroidea without Cecidomyiidae were characterised only by lengthened coxae and a "tibial organ" at the tip of the fore tibia. Sciaridae were then considered the sister group of remaining Sciaroidea on larval characters and two autapomorphies in genital structure (sternite 8 of female lengthened; an area of minute teeth on the tegmen or "genital plate" of the male aedeagus). The remaining families, grouped as Mycetophilidae were said to have one synapomorphy (spermathecae opening directly into roof of genital chamber). Diadocidiinae and Ditomyiinae were then separated in turn and the remaining families included in Mycetophilinae, on basis of larval characters (the first propneustic, the second peripneustic and the last with spiracles of 8th abdominal segment absent as in Sciaridae). Menzel & Mohrig (2000) accepted this classification, dismissing the conclusions of Wood & Borkent on the basis that the loss of chromosomes and development of eye-bridges were due to convergence, but did not refer to the views of Matile on the position of the Sciaridae.

Matile (1990) also dismissed the possibility that Sciaridae and Cecidomyiidae were sister groups because of the peripneustic larvae of the latter. I strongly support this view, as the Cecidomyiidae are clearly an older more diverse group, which had lost characters retained by Sciaridae (e.g. tibial spurs) in their ground plan. Although most Cecidomyiidae have reduced venation, *Catotricha* Edwards has venation almost identical with *Heterotricha*, suggesting a comparable sequence in reduction from the ancestral venation of Bibionomorpha. Cecidomyiidae may be the sister group of the Sciaroidea excluding them, but it is here considered preferable to regard them as a distinct superfamily Cecidomyioidea.

The base of M has evidently been lost by convergence in the ancestral stock of Cecidomyiidae and the possibility that it has been lost independently more than once in Sciaroidea cannot be discounted. Indeed this is likely to have occurred in Ditomyiidae, as the peripneustic larvae and pupal thoracic horns of this family are persuasive of a basal position in the superfamily as postulated by Matile.

Matile cited four synapomorphies of Sciaroidea other than Ditomyiidae, all larval characters including loss of 8th abdominal spiracles apart from reduction of vein R_4. Characters of the early stages cannot be demonstrated for any of the genera dealt with in this paper, but on the basis of a combination of adult characters it is considered likely that they fall in this group. He then considered Diadocidiidae and Keroplatidae together as the sister group of the remainder, on the basis of the closure or loss of the larval abdominal spiracles. However, it was noted that the mycetophilid genus *Speolepta* Edwards had lost these spiracles by convergence and it cannot be discounted that this is also true of these families; they could have been lost in *Diadocidia* because of the tube-



Figures 79-90

Arrangement of veins in basal sector of wing from R_1 to CuA in Sciaroidea, to demonstrate fate of M, ta and tb in respective taxa. – 79, *Bolitophila* Meigen (Bolitophilidae). – 80, ground plan of Keroplatinae (Keroplatidae). – 81, *Symmerus* Walker (Ditomyiidae). – 82, *Diadocidia* Ruthé (Diadocidiidae). – 83, *Chiletricha* n. gen. – 84, *Heterotricha* Loew. – 85, *Pterogymnus* Freeman. – 86, ground plan of Mycetophilidae, e.g. *Drepanocercus* Vockeroth. – 87, *Promanota* Tuomikoski (Mycetophilidae, Manotinae). – 88, Mycetophilidae, derived type with R_4 lost and long stalked posterior fork, e.g. *Phronia* Winnertz. – 89, *Sciara* Meigen (Sciaridae). – 90, *Lygistorrhina* Skuse (Lygistorrhinidae). *mf*, median fork; *pf*, posterior fork.

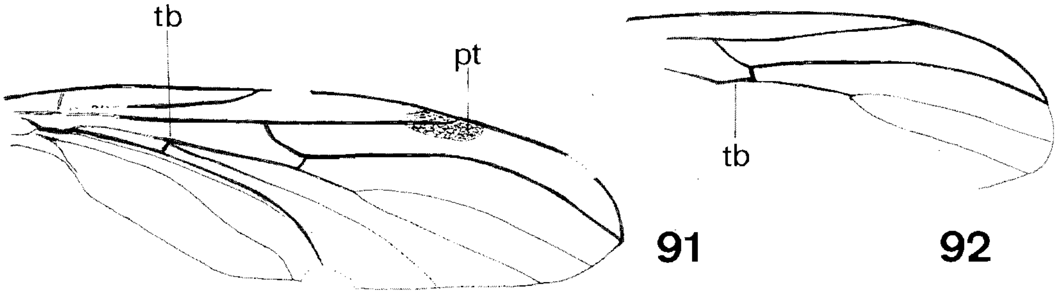
living habit of the larva, as they otherwise differ markedly in adult and larval structure from Keroplatidae. The monophyly of the remaining families was based on the longitudinalisation of tb, because of his interpretation of this vein in *Bolitophila* as discussed above and the structure of larval mandibles. The development of larval antennae in *Bolitophila* was concluded to be apomorphous as these were already reduced in Bibionidae. Lygistorrhinidae were associated with Mycetophilidae sensu stricto on development of laterotergites and the narrow thoraco-abdominal insertion, contrasted with the Sciaridae.

The meeting of crossveins ta and tb at their junction with M, coupled with the loss of the base of M, could then be considered a synapomorphy not only of the taxa mentioned above but of all Sciaroidea other than Bolitophilidae and Keroplatidae, although as discussed it is likely that the Ditomyiidae have developed this condition by convergence. This supports the phylogeny of Matile except that his placement of Diadocidiidae (restricted here to *Diadocidia* alone) may be wrong and that Bolitophilidae do not share the loss of the base of M and form of tb found in the other families. Also, the position of the Lygistorrhinidae and some Manotinae, which have this region of the venation effaced, is uncertain and requires further study. Two of the four genera of the Manotinae, i.e. *Eumanota* Edwards (1933) and *Promanota* Tuomikoski (1966b) (fig. 87), have the base of the median fork and its stem complete and linked with a long diagonal ta and tb running straight to the wing base; these characters suggest that the inclusion of the subfamily in the Mycetophilidae is probably correct. Tuomikoski (1966b) also came to this conclusion on the basis of other apomorphous characters, such as bulging laterotergites, narrow insertion of abdomen and tibial setulae in rows. He considered that the long ta (resembling the Leiinae within Mycetophilidae in this respect) might be derived from the loss of the true Rs, the apparent Rs being actually R_4.

Thompson (*op. cit.*) demonstrated that the characters by which Lygistorrhinidae had been linked to Keroplatidae by Tuomikoski (1966c) were either due to symplesiomorphy or to erroneous assumptions, and restored its family rank. He did not come to an alternative conclusion as no synapomorphy with any other taxon was found. Matile (1990) gave a detailed discussion of Lygistorrhinidae and supported Thompson's conclusions. Grimaldi & Blagoderov (2001) restricted their discussion to relationships within Lygistorrhinidae, but a Cretaceous amber fossil mentioned by them as awaiting description may shed light on the position of the family. The apparent course of the effaced part of the venation in *Lygistorrhina* Skuse (fig. 90) suggested that its derivation might be from the ground plan condition of the Sciaridae, if it had lost Rs and the long "R_5" incorporated elements of ta and tb. However, Matile (1990) and Grimaldi & Blagoderov (2001) have indicated the presence of Rs in a basal position in the Eocene Baltic amber fossil genus *Palaeognoriste* Meunier and some modern species, which would argue against this. Although most Lygistorrhinidae have Sc abbreviated as in Sciaridae, *Palaeognoriste* and some *Lygistorrhina* species have it complete to the costa suggesting that this abbreviation has occurred by convergence as it has in many Mycetophilidae. Søli (1997), using Matile's classification as a model, included *Bolitophila*, Lygistorrhinidae and Sciaridae as outgroups in his phylogenetic study of Mycetophilidae and placed Lygistorrhinidae and Sciaridae together as the sister group of Mycetophilidae.

Among families with ta and tb adjoined the Ditomyiidae have the greatest number of plesiomorphous characters, including a long R_4 ending in the costa and An_1 reaching the margin, but have vein Sc abbreviated and sc-r lost. An_1 also reaches the margin in Diadocidiidae (as well as Bolitophilidae and the ground plan of Keroplatidae); in this family vein Sc reaches the costa but sc-r is absent and R_4 is lost. Both of these families as well as Keroplatidae and Bolitophilidae have retained plesiomorphous characters not found in the known Jurassic Sciaroidea (none of which are presently assigned to modern families), which have not only lost the basal part of M but have tb running strongly basad as in the *Heterotricha* Group and *Pterogymnus*. Among these Jurassic groups the Pleciofungivoridae with R_4 long and ending in the costa are the most plesiomorphous; they differ from the Ditomyiidae in Sc reaching the costa and although the form of An_1 is unclear it apparently does not reach the margin. There are no apparent autapomorphous characters in their venation so their relationships with the other Jurassic groups, which have either lost R_4 or have it ending in R_1, cannot be assessed until better material is available.

The medio-cubital liaison is evidently a ground plan condition of the Sciaroidea, being found in all modern groups except Mycetophilidae and Sciaridae and those in which this region of the venation is effaced. It is found in all known Jurassic taxa assigned to this group except some genera of Antefungivoridae (Pleciomimidae sensu Rohdendorf) and one species misplaced as *Pleciomima* Rohdendorf by Rohdendorf (which also lacked R_4 and had a long stemmed posterior fork). The relationship of the latter forms is uncer-



Figures 91-92
Wings of Mangasinae. – 91, Mangasinae gen. sp. Kovalev. – 92, *Mangas exilis* Kovalev. *pt*, pterostigma.

tain but they may be near the stem of the Cecidomyiidae. Matile (1981) supported Hennig's view that several of Rohdendorf's families and genera were probably polyphyletic, because he had given little attention to the basal sector, fate of tb or development of An_1, but accepted that their assignment to the Sciaroidea was probably correct. The lack of information on structural characters other than the venation precludes any certain conclusion in many cases.

Hennig (1954) had suggested that forms closely related to *Heterotricha* existed in the Jurassic. This view was based on a combination of the symplesiomorphy already discussed (tb joining vein M_4+CuA_1) and a synapomorphy (loss of R_4). Vein sc-r was omitted from all Rohdendorf's illustrations of Jurassic Sciaroidea and Matile considered that he had not sought its presence. These *Heterotricha*-like forms include some Antefungivoridae, in which Sc usually ends in the costa (e.g. *Paralycoriomima* which has venation like *Heterotricha* except for Sc being complete) but at least in *Lycoriomimodes karatavica* (Rohdendorf, 1946) and *Eoboletina* Rohdendorf (placed questionably in Mesosciophilidae by Blagoderov, 1994) vein Sc is apparently abbreviated as in *Heterotricha*. These forms could represent a taxon including the ancestor of the *Heterotricha* Group but their most obvious difference from most members is the shorter broader wings with more widely spaced veins, probably a plesiomorphous condition in the Sciaroidea, found in *Afrotricha* and *Sciaropota* among the extant forms.

Kovalev (1986) described a more probable Cretaceous representative of the *Heterotricha* Group as *Mangas exilis*. *Mangas* Kovalev was proposed as the type of a subfamily Mangasinae in Bolitophilidae, distinguished from Bolitophilinae by the absence of R_4, so if *M. exilis* does belong to the *Heterotricha* Group this is an available family group name. The named species *M. exilis* was described from the impression of an entire insect from the Lower Cretaceous of Mongolia. Kovalev's figure showed the head with complete upturned antennae, nearly as long as the body, with long slender flagellomeres, parts of the long slender fore and hind legs, an elongate abdomen with genitalia showing simple gonostyli and parts of both wings. It was noted by Kovalev that vein tb was not visible in *M. exilis*, but that it was visible in an undescribed form assigned to Mangasinae from the Neocomian of Transbaikalia, where it is the same as in modern Bolitophilidae; only the wing of this second species was preserved. The venation was said to be close to Antefungivoridae (as Pleciomimidae) except that they had the fork M_{1+2} shorter (more than 3 x its stem in *Mangas*); which were also very small, with a shorter abdomen and similar venation was likely to be a parallel development.

Kovalev's material was examined with the following conclusions:

– *Mangas exilis* Kovalev, ♂ holotype, labelled 3149/1508 (PIRA). The visible part of the venation (fig. 92) is as *Heterotricha* with tb and the basal part of CuA identifiable by analogy to its venation, contrary to Kovalev's statement. The origin of the posterior fork could not be discerned, nor could vein Sc, suggesting that it is abbreviated as in *Heterotricha*. The body is as figured by Kovalev; abdominal segments 6-8 appear a little darker, evidently the reason for the statement by Kovalev that 2-3 distal segments are more sclerotised. Tergite 9 is not discernible, but the gonostyli are simple, apically truncated. There is nothing to indicate that *M. exilis* is not allied to *Heterotricha*.

– Mangasinae gen. sp. Kovalev, labelled sp. near *Mangas*, 1989/3631 (PIRA). This is the wing only (fig. 91), agreeing well with Kovalev's figure. The venation is as *Bolitophila*, except for the absence of R_4. It therefore differs from the *Heterotricha* Group in the presence of a pterostigma, Sc reaching the costa, base of M distinct, with tb short and linking M to CuA_1 well basad of ta, and An_1 complete to the wing margin. It is therefore concluded that this wing is correctly referable to Bolitophilidae, but that *Mangas exilis* cannot be demonstrated to be closely related to it or to be a bolitophilid, in the absence of any evidence of these venational characters.

Another Mesozoic group (Mesosciophilidae) with tb and the posterior fork as in the *Heterotricha* Group, has Sc complete to the costa and R_4 present and ending in R_1, the venation thus on the same plan as *Pterogymnus*. Hennig considered that this taxon might be ancestral to the Mycetophilidae + Sciaridae but Matile (1981) speculated that if sc-r was actually absent (as in *Pterogymnus*) they could only be an "extinct" sister group of the Mycetophilidae + Sciaridae. The Mesosciophilidae are known mainly from several genera from the Middle and Upper Jurassic, but Blagoderov (1994) added *Mesosciophilopsis*, which had R_4 more basal and sc-r present, from the Lower Cretaceous (Neocomian) of Siberia. If the tibial spurs of *Mesosciophilopsis* are actually 1:1:1 as described, this could be an autapomorphy of the genus. *Pterogymnus* could be a surviving member of this group but no other modern forms clearly share such a relationship.

Matile (1981) reconstructed the evolutionary stages in venation from primitive Diptera to the principal groups of modern Sciaroidea, in which the *Pterogymnus* venation with Rs shortened and R_4 ending in R_1 was the immediate precursor of the condition in Mycetophilidae and Sciaridae, which differ from it in the approximation of the veins of the posterior fork to first become sessile and then arise from a common stem. Vein R_4 when present in Mycetophilidae ends in R_1, forming a radial cell, evidently a ground plan condition of the family and present in some genera of Mycomyinae, Sciophilinae and Gnoristinae. R_4 is absent in Sciaridae; the presence of a short R_4 ending in the costa was earlier thought to characterise *Cratyna* Winnertz, but this is now considered teratological in the specimens concerned (Menzel & Mohrig, 2000).

The short stalked condition of the posterior fork in most Sciaridae (fig. 89) and some Mycetophilidae (figs. 86-87) would thus be the plesiomorphous condition for these taxa. Apart from the Manotinae (fig. 87), in which the posterior fork is sessile, there are several genera of Mycetophilidae included in the Sciophilinae sensu lato which have a very short stalked or sessile posterior fork, e.g. *Ectrepesthoneura* Enderlein (itself paraphyletic, being based on symplesiomorphous venation), *Drepanocercus* Vockeroth (fig. 86) and *Taxicnemis* Marshall (with CuA weak basally, fig. 90). Søli (1997) found *Drepanocercus* and *Paratinia* Mik (the latter with a longer stalk) together to represent the sister group of other mycetophilid genera studied by him. In one genus, *Loicia* Vockeroth (1980), the anterior branch arises separately from near the base of tb, but the junction is near the wing base, only just beyond the level of crossvein h. The venation of *Loicia* otherwise resembles *Pterogymnus* except in the more basal position of R_4 and presence of sc-r. *Taxicnemis* differs in Sc being abbreviated and sc-r absent and its venation could resemble the stem group of Sciaridae before loss of R_4. *Taxicnemis* and *Loicia* have macrotrichia on the membrane and were placed in Sciophilinae, a polyphyletic group based on this plesiomorphous character. Matile & Duret (1994) noted the limited systematic value of this character, which is often not of generic importance (e.g. in Macrocerinae or Sciaridae). More work is required on the phylogeny of the Mycetophilidae before the significance of the venation in *Loicia* and *Taxicnemis* can be assessed. At present, it seems likely that the origin of M_4+CuA_1 in *Loicia* is the result of a secondary fusion.

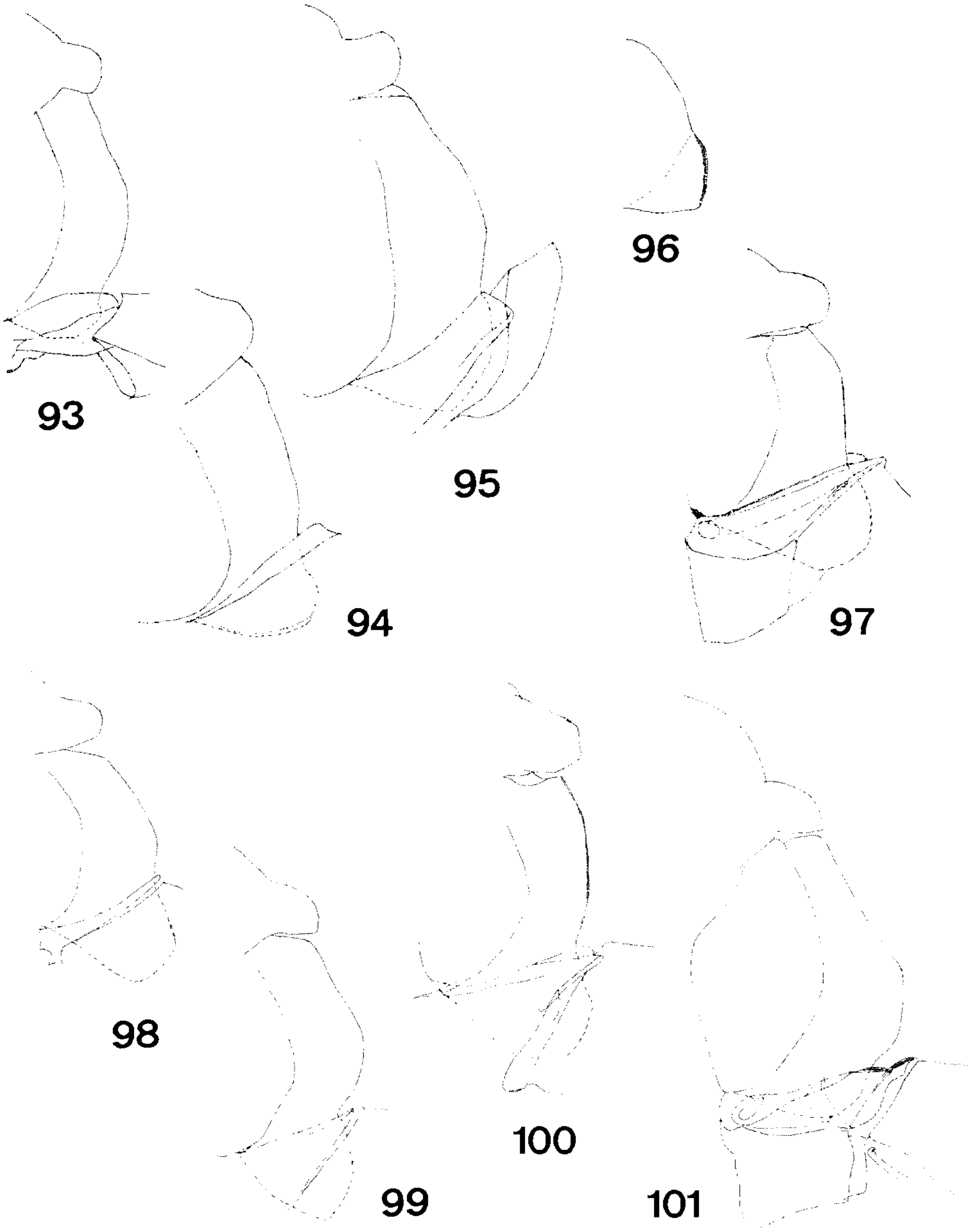
Some discussion of *Ohakunea* and *Colonomyia*, both found in the Australasian and Chilean Regions, is also necessary as they have been considered as possibly related to the *Heterotricha* Group. They have not been dealt with in detail here because their wing venation is reduced and does not fit the ground plan of this Group as defined above. Characters in common with this Group are that veins Sc and An_1 end free and R_4 is absent; macrotrichia are present on the membrane except in one species of *Colonomyia*. Both have a radial sector formed as in Sciaridae, with ta very long and parallel with the costa and a sessile posterior fork, but they have an incomplete eye-bridge and lack a well-developed midpleural pit. *Colonomyia* also has the basal part of the median fork and its stem faint or absent. *Azana* Walker, currently placed in Sciophilinae, also has a radial sector as in these genera and the venation reduced further with M unbranched.

Colless (1963) considered that the more complex male genital structure, especially additional structures identified as basal processes of the gonocoxites (i.e. gonocoxal apodemes) or parameres, excluded them from Sciaridae. Matile also excluded them from Sciaridae because of the narrow thoraco-abdominal insertion not partially enclosing the mediotergite (although the phragma is distinctly projecting in *Ohakunea*) and considered them sister groups, based on reduction of the venation, within the *Heterotricha* Group. *Ohakunea* has the pleural structure similar to *Heterotricha* with a vertical mesepimeron and the antennae are upturned. *Colonomyia* has the antennae more porrect, but still with a slender flagellum; the katepisternum is expanded posteriorly to meet the laterotergite, cutting off the mesepimeron as in some Lygistorrhinidae and Ditomyiidae.

In the *Heterotricha* Group with the exception of *Sciaropota*, the scape and pedicel are adpressed to the frons and the antenna is consequently strongly upturned. This condition is also found in *Bolitophila*, *Pterogymnus*, Manotinae and many genera of Sciophilinae and Gnoristinae. The insertion of the antennae does not appear to have been considered in phylogenetic discussion of the Sciaroidea. The porrect or slightly upturned condition is presumed to be the ground plan of the Bibionomorpha and is found among Sciaroidea in Ditomyiidae, Diadocidiidae, Keroplatidae, Lygistorrhinidae, Sciaridae and most Mycetophilidae. It is possible that the upturned condition is a synapomorphy of the groups concerned, which would require that the porrect condition has developed by reversal in Mycetophilidae, and possibly Lygistorrhinidae and Sciaridae. Possible phylogenies within Mycetophilidae recently suggested by Søli (1997), which cut across traditional subfamily limits, include genera with both conditions in several clades, e.g. in fig. 46 this reversal would have occurred in at least five clades and in fig. 45 in at least six clades. Tozonil & Amorim (1998) have proposed a phylogeny of Mycetophilidae in which the traditional subfamilies are accepted, with Sciophilinae and then Gnoristinae in basal positions but the details of their analysis are yet to be published. It is equally unclear whether the porrect condition in *Sciaropota* is also a reversal or a symplesiomorphy with other families.

All genera dealt with here conform to the primitive condition of the mesepisternum according to Shaw (1948), with an unequal division such that the katepisternum is much larger than the anepisternum. In this they agree with Bolitophilidae, Sciaridae and the ground plan condition of Ditomyiidae and Keroplatidae. Most also agree with the primitive condition of the mesepimeron, which is narrowed below but reaches the mid coxa and the laterotergite, which is relatively shallow and not enlarged anteriorly. These conditions are in the ground plan of most families of Sciaroidea but in many Mycetophilidae and some other groups as indicated above, the mesepimeron is cut off below by enlargement of the katepisternum, laterotergite or both, which then meet below. In Sciaridae the ventral extension of the mesepimeron is relatively broad and still separates the laterotergite from katepisternum but the latter is strongly enlarged posteriorly, so that the mesepimeron is deflected away from the mid coxa, only meeting the upper corner of the metepisternum. The mesepimeron is not significantly constricted by posterior development of the katepisternum in *Heterotricha* (as in *Bolitophila*, *Arachnocampa* and *Pterogymnus*). In most genera there is a constriction behind the katepisternum and a slight anterior deflection to the upper angle of the mid coxa, e.g. in *Chiletricha*. In *Sciarosoma* there is a stronger constriction and deflection immediately above the mid coxa, possibly a stage in development of the sciarid condition. In *Sciaropota* (fig. 68) the mesepimeron is broader below as in Sciaridae, but it still meets the mid coxa as well as the metepisternum since the katepisternum is not enlarged behind.

The isolation of Sciaridae from other Sciaroidea has also been postulated on the phragma (lower projection of the mediotergite) projecting strongly into the abdomen, coupled with a broad abdominal insertion on the thorax. This resembles the condition in Cecidomyiidae, which also have the phragma projecting strongly into the abdomen but this is here considered a parallel development. The plesiomorphous condition for Sciaroidea is presumed to be that found in Bolitophilidae (*Bolitophila*, fig. 93), Ditomyiidae (*Symmerus*, fig. 94) and Diadocidiidae (*Diadocidia*, fig. 95), where the phragma is small and slightly projecting, being most developed in the last. It is also weakly developed in some Mycetophilidae, but in most Mycetophilidae and in Keroplatidae it is reduced and not projecting. In *Pterogymnus* (fig. 101) and *Sciaropota* (fig. 68) it is also weakly developed, but in other members of the *Heterotricha* Group it is enlarged and distinctly projecting into the first abdominal segment (confirmed by maceration in *Heterotricha* (fig. 98), *Chiletricha* (fig. 99), *Anisotricha* (fig. 100) and *Sciarosoma* (fig. 67); also apparent in *Rhynchoheterotricha*, *Nepaletricha* and *Kenyatricha*). The *Heterotricha* Group, except *Sciaropota*, thus closely resembles the condition in Sciaridae (fig. 97 is typical; in *Sciara* Meigen itself, fig. 96, the phragma is more truncated) and this is a possible synapomorphy. It is



Figures 93-101
Outline of mediotergite in lateral view to show degree of development of phragma (indicated by dotted line where it is concealed *in situ*). – 93, *Bolitophila* Meigen (Bolitophilidae). – 94, *Symmerus* Walker (Ditomyiidae). – 95, *Diadocidia* Ruthé (Diadocidiidae). – 96, *Sciara* Meigen (Sciaridae). – 97, *Schwenkfeldina* Frey (Sciaridae). – 98, *Heterotricha* Loew. – 99, *Chiletricha* n. gen. – 100, *Anisotricha* n. gen. (Palmer Rd specimen). – 101, *Pterogymnus* Freeman.

thus possible that the *Heterotricha* Group (except *Sciaropota*) and Sciaridae constitute a monophyletic group, on the basis of this character. If this is the case, the migration of the junction of tb with CuA onto the stem must have occurred independently in Sciaridae and Mycetophilidae.

On the basis of the assumptions made above concerning the relationships between the *Heterotricha* Group and *Pterogymnus* and other living Sciaroidea, it is concluded that they cannot be included in any of the presently recognised families, It is believed that they are representatives of taxa which have had a separate evolutionary history at least since the Cretaceous. If the diversity of this group had been known to Edwards

(1925b), when he proposed the subfamily classification on which currently recognised families are based, it is likely that he would have accorded subfamily status and family status would have followed. However, new families are not proposed here for two reasons: (1) family group names based on fossils may later be found to apply to them, e.g. Mangasinae for the *Heterotricha* Group and Mesosciophilidae for *Pterogymnus* (on the other hand, it is possibly unwise to include Mesozoic fossils in the same family as modern genera, particularly as only *Pterogymnus* and the *Heterotricha* Group among modern Sciaroidea apparently resemble closely the Jurassic Sciaroidea in venation); (2) it is possible that the genera included in this paper do not constitute monophyletic groups with respect to other currently recognised families of Sciaroidea.

Further conclusions on the phylogeny of the Sciaroidea will require a detailed analysis of characters over a wide range of taxa, such as Søli (1997) has attempted for Mycetophilidae and is beyond the scope of this paper, of which the main aims are to extend knowledge of the extant taxa of this remarkable group and to suggest potential future lines of enquiry. However, preliminary suggestions of relationships between taxa of Sciaroidea, based on the above discussion, are suggested in fig. 103 in order to put relationships between the genera of the *Heterotricha* Group and *Pterogymnus* into context; the numbers against branches of this cladogram relate to the apomorphous character states listed in the figure and discussed below.

Relationships between genera of the *Heterotricha* Group

Without any knowledge of the immature stages it cannot be certain whether the *Heterotricha* Group as defined here is monophyletic, although the enlargement of the phragma in most genera may suggest that they are paraphyletic with respect to the Sciaridae. The females are as yet known for only three of the nine genera, i.e. *Heterotricha*, *Afrotricha* and *Chiletricha*. On the basis of the female abdominal structure of these genera, with a rather complex truncated ovipositor with deeply bilobed and strongly setose sternites 8 and 9, it is concluded that they are closely related. This structure differs strongly from Sciaridae in which the ovipositor is often attenuated with sternite 8 lengthened and apically bilobed but otherwise unmodified.

The males of the *Heterotricha* Group also have a more sclerotised aedeagal complex, than is found in Sciaridae, with parameres present and basally fused with the gonocoxal apodemes as in the ground plan of Mycetophilidae. In Sciaridae the parameres are absent and the aedeagal complex, mainly comprising the characteristic tegmen and bifurcate aedeagal apodeme, is consequently not fused with the gonocoxal apodemes. On structural characters of the male, it is considered likely that the other entirely southern hemisphere genera *Rhynchoheterotricha* and *Anisotricha* are also closely related to the genera with known females and similar female structure may be anticipated. *Kenyatricha* and *Nepaletricha* are probably close to each other, based on characters of the venation and male genitalia. There are also indications from the latter that they may be more distantly related to the southern hemisphere genera. The relationship of *Sciarosoma* and *Sciaropota* to the remainder and to each other is less clear.

The characters that have been considered in attempting to assess the relationships between genera in this group are listed in fig. 103, where character states belonging to the probable ground plan of Sciaroidea (plesiomorphies) are first indicated as (p), followed by one or more derived characters (apomorphies), indicated as (a). It is unclear whether the presence of setae on laterotergite or metepisternum is a derived character in this Group, as it cannot be conclusively demonstrated whether any pleural sclerites were setose in the ground plan of the Sciaroidea. Here Søli (1997) is followed in treating absence of setae on meso- and metathoracic pleura as the primitive condition. Specific comments on character states are given below:

Characters

1. – It is unclear if the porrect condition of the antennae in *Sciaropota* is primitive or a reversal. The shortened flagellomeres is a derived character in Sciaroidea, but widely developed by convergence and is probably associated with the more robust form of the body and legs in this genus.

4. – This character is considered the most likely indication of relationship between the *Heterotricha* Group and Sciaridae. However, if this is a derived character in Sciaroidea the more strongly developed phragma in Cecidomyiidae must have developed by convergence.

8. – Vein sc-r has evidently been lost by convergence in many Sciaroidea.

9. – This is a possible synapomorphy of *Afrotricha* and *Heterotricha* although it is associated with a very different development of ta (r-m) in each case (see 10a below). Its similar orientation in *Sciarosoma* and *Sciaropota*, which resemble Sciaridae in this respect, especially in *Sciarosoma* where ta is more strongly basad, is also probably by convergence.

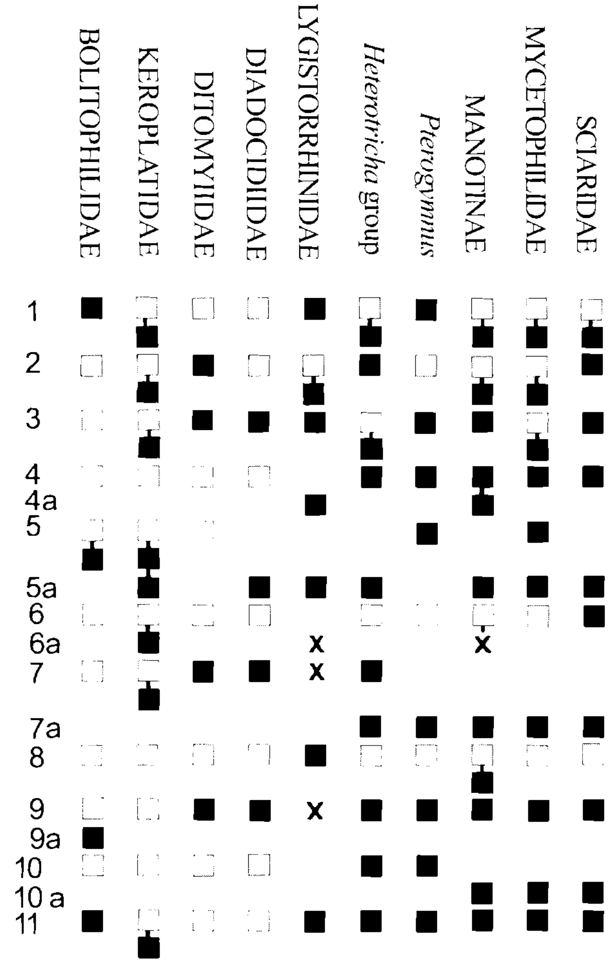


Figure 102

Venational characters in principal extant taxa of Sciaroidea. Explanation of symbols: open squares = plesiomorphies; closed squares = apomorphies; open and closed suqares linked = apomorphous state developed in some members of taxon only; X = vein or portion of vein concerned not identifiable due to reduction. The character state considered plesiomorphous (p) is listed first, followed by the corresponding derived or apomorphous (a) conditions. If there are two apomorphies related to the same character the second is indicated by the letter a following the number of the character.

1 Macrotrichia present on membrane (p), absent (a).
2 Sc reaching costa (p), abbreviated (a).
3 sc-r present (p), absent (a).
4 Rs long, diagonal (p), transformation through short and more sharply angled to vertical position (a).
4a Rs lost (a) (in Manotinae Rs may always be lost, if the apparent Rs is actually R_4).
5 R_4 present, ending in costa (p), R_4 ending in R_1 (a).
5a R_4 absent (a).
6 Crossvein ta vertical to diagonal (longer but still diagonal where present in Manotinae) (p), longitudinal in line with tb (a).
6a Crossvein ta obliterated by radio-medial fusion (most Keroplatidae) (a).
7 Basal part of M distinct (p), reduced to unsclerotised seam (a)
7a Basal part of M entirely absent (a).
8 Stem of median fork (M_{1+2}) present (p), absent (a).
9 Crossvein tb joining m basal to junction with ta (p) (applies to ground plan of Keroplatidae, in most of which ta is obliterated), tb joining m at junction with ta (a).
9a Crossvein tb meeting M strongly basad of ta (a).
10 Crossvein tb vertical (p), extended diagonally basad posteriorly, but still joining anterior branch of posterior fork (M_4+CuA_1) basally (a).
10a Crossvein tb longitudinal, joining basal part of CuA before fork (a0).
11 An_1 extending to wing margin (p), abbreviated (a).

basad and nearly parallel with R and C is perhaps equivalent to a stage in development of that in Sciaridae. The short-thick ta and weak Rs is evidently a synapomorphy of the species retained in *Heterotricha*. A very short or obliterated ta is a probable synapomorphy of *Nepaletricha* and *Kenyatricha*.

11. – The condition found in *Sciaropota* and Sciaridae of the mesepimeron not being strongly narrowed below is in the latter associated with posterior enlargement of the katepisternum so the mesepimeron is directed away from the mid coxa.

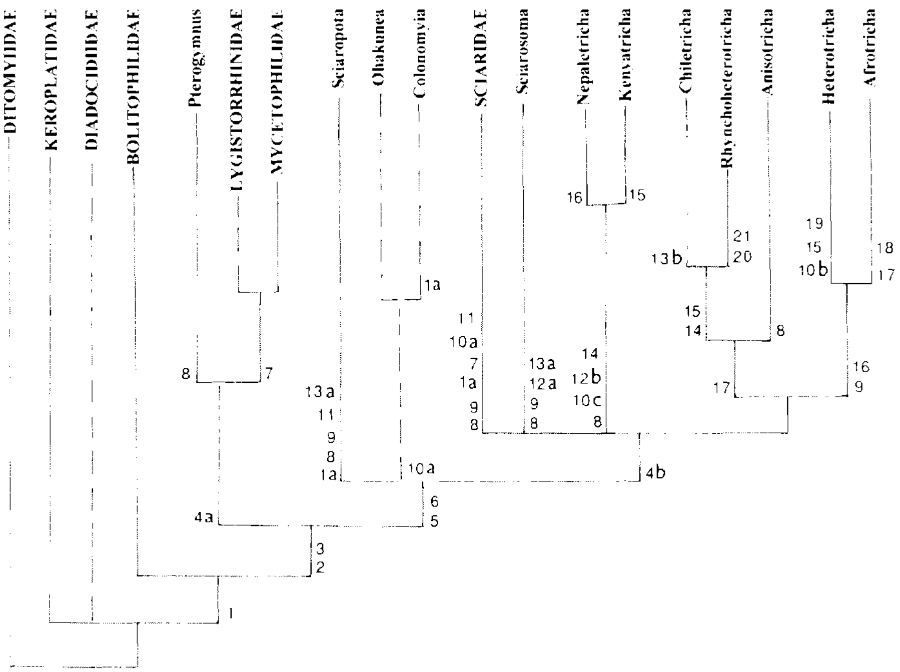


Figure 103
Postulated relationships between the genera of the *Heterotricha* Group, *Pterogymnus* Freeman and other taxa of Sciaroidea.
Characters considered in assessing relationships between the genera of the *Heterotricha* Group, *Pterogymnus* Freeman and other taxa of Sciaroidea. The character state considered plesiomorphous (p) is listed first, followed by the corresponding derived or apomorphous (a) conditions. If there is more than one apomorphy related to the same character this is indicated by a, b, c following the number of the character.

1	Antenna porrect (p), antenna with scape and pedicel adpressed to frons and flagellum upwardly directed (a).
1a	Possible reversal to the porrect condition.
2	Vein tb meets M basad of junction of ta with M (p), veins tb and ta aligned (a).
3	Vein An_1 reaching wing margin (p), An_1 abbreviated.
4	Mediotergite with phragma small and projecting weakly into base of abdomen (p).
4a	Phragma weak and ventrally directed, not projecting into abdomen (a).
4b	Phragma large and projecting strongly into base of abdomen (a).
5	Vein R_4 present, ending in costa (p).
5a	R_4 ending in R_1 (a).
5b	R_4 lost (a).
6	Vein Sc reaching costa (p), Sc abbreviated (a).
7	Vein tb meeting CuA beyond fork (p), tb meeting CuA basal to fork (a).
8	Vein sc-r present (p), absent (a).
9	Vein Rs short and vertical (a), long and curved (p).
10	Vein ta (r-m) diagonal and not noticeably thickened (p).
10a	Vein ta extended strongly basad, becoming parallel with R and C (a).
10b	Vein ta short and thick, coupled with weak Rs (a).
10c	Vein ta very short or obliterated.
11	Mesepimeron ± vertical, narrowed below to mid coxa (p).
11a	Mesepimeron more constricted behind katepisternum and lower part deflected anteriorly to mid coxa (a).
11b	Mesepimeron not strongly narrowed below (a).
12	Gonocoxites ventrally excavated medially, without elaboration (p).
12a	Gonocoxites with submedial lobes on apical margin ventrally (a).
12b	Gonocoxites with setose lobes laterally, adjacent to gonostylus (a).
13	Gonostylus simple (p).
13a	Gonostylus bilobed (a).
13b	Development of spinose or setose inner lobes of male gonostyli (a).
14	Male tergite 9 with apical margin simple and unornamented (p), male tergite 9 bearing spinose or setose processes (a).
15	Vein Sc setose (p), Sc bare (a).
16	Laterotergite bare (p), setose (a).
17	Metepisternum bare (p), setose (a).
18	Vein R_5 parallel with costa apically, ending much closer to M_1 than to R_1 (p), R_5 relatively short, not ending much closer to M_1 than to R_1 (a).
19	Basal cell (formed by loss of M) with macrotrichia densely distributed (p), with macrotrichia sparse or absent (a).
20	Proboscis carried simply on normally developed head (p), proboscis borne on a long tubular extension of the head (a).
21	Macrotrichia distributed over much of membrane (p), macrotrichia absent from wing membrane (a).

12 and 13. – Characters 12a and 13a are among the genital characters of *Sciarosoma* that are more complex with respect to the ground plan of Sciaridae, but likely to be autapomorphous for the genus. As indicated above it is not clear whether character 13b, which applies to most species of *Chiletricha*, is in the ground plan of the genus. A comparable lobe in *Nepaletricha* may have developed by convergence.

14. – Although there are four spinose or setose processes of tergite 9 in *Rhynchoheterotricha*, but only two in *Chiletricha*, this departure from the ground plan of the Sciaroidea does seem to indicate a closer relationship between these genera. It is unclear if the marginal processes in *Nepaletricha* and *Kenyatricha* also indicate a common origin.

10. – The condition in *Sciarosoma* of ta extended strongly

15. – The loss of setae on vein Sc appears to have occurred independently in different lineages of *Heterotricha* Group.

16 and 17. – The laterotergite is setose only in *Heterotricha* and *Afrotricha*. The presence of setae on the metepisternum may be a synapomorphy of *Rhynchoheterotricha*, *Chiletricha* and *Anisotricha*, but presence of short setae in *Afrotricha* may be due to convergence.

18. – This is tentatively considered an autapomorphy of *Afrotricha*, although it may be associated with the possibly plesiomorphous condition of the broader wing shape. However, *Sciaropota* and *Sciarosoma*, which also have the wing broad, have R_1 shorter and R_5 ending much closer to R_1.

19. – This is not a ground plan character of Sciaroidea, as it relates only to taxa which have lost the base of M. The tendency for the loss of macrotrichia from the basal cell (formed by loss of M) is present in all genera except *Afrotricha*, which retains the plesiomorphous state. A few macrotrichia are present in this cell in *Sciarosoma* and in some fossil species of *Heterotricha*.

20. – This is an autapomorphy of *Rhynchoheterotricha*, resembling *Gnoriste* (Mycetophilidae) by convergence.

21. – This is another autapomorphy of *Rhynchoheterotricha* within the *Heterotricha* Group, although often occurring by convergence in other Sciaroidea and there is a tendency towards progressive loss of macrotrichia in some other genera, especially *Chiletricha*.

Acknowledgements – I am grateful to Alan Stubbs for referring to me his catches from mainland Greece and Crete, which included recent *Heterotricha* material and to Jean-Paul Haenni (Muséum d'Histoire Naturelle, Neuchâtel) for enabling examination of the Swiss material and for taking me to the locality where it was collected, during my visit to Switzerland in 1997. I am indebted to the authorities of the Geologisch-Paläontologisches Institut und Museum der Georg-August-Universität, Göttingen and Andrew Ross (Natural History Museum, London), for enabling me to examine the amber material of *Heterotricha*; the Palaeontological Institute, Russian Academy of Sciences for loan of the Mangasinae material; the Cawthron Institute, Nelson, New Zealand and the Natural History Museum, London for the opportunity to study type material of the previously described extant species. Andrew Ross also arranged for the amber specimens in BMNH to be photographed to facilitate their study.

Dr. José Pedro Duret very kindly enabled me to study his recently collected material of the South American species, including the previously unknown male of *Pterogymnus*; his collection has since been deposited in the Muséum National d'Histoire Naturelle, Paris. The late Loïc Matile kindly enabled examination of further material from the Duret collection and other relevant material from the Paris collections, including previously unknown genera from other parts of the world; he also provided a French translation of Kovalev's account of Mangasinae.

Rauno Väisänen kindly permitted the inclusion of the two new genera and species covered in an unpublished manuscript by himself and Prof. Toyohei Saigusa and the manuscript names proposed by them have been used for these taxa. I am also grateful to Alexei Polevoi and Jan Ševčík for passing to me specimens of *Sciarosoma* from Karelia and the Czech Republic respectively. I also thank Pekka Vilkamaa and Heikki Hippa for useful discussion during the 1998 Oxford Congress, which encouraged the completion of this paper.

REFERENCES

Amorim D. de S. 1991 – A phylogenetic analysis of the basal groups of Bibionomorpha, with a critical examination of the wing vein homology. – *Revista Brasileira de Biologia*, **52** : 379-399.

Blagoderov V.A. 1994 – Dipterans (Mesosciophilidae) from the Lower Cretaceous of Transbaykal. – *Palaeontological Journal*, **27** (1A) (1993) : 123-130.

Blaschke-Berthold U. 1994 – Anatomie und Morphologie der Bibionomorpha (Insecta, Diptera). – *Bonner Zoologische Monographie*, **34** : 5-206.

Colless D.A. 1963 – New species of *Obakunea* Edwards and a related new genus with notes on the relationships of *Heterotricha* Loew (Diptera). – *Proceedings of the Linnaean Society of New South Wales* (1962), **87** : 303-308.

Edwards F.W. 1925a – Mycetophilidae and Bibionidae (Diptera) in the collections of the South African Museum. – *Annals of the South African Museum*, **19** : 601-616.

Edwards F.W. 1925b – British Fungus-Gnats (Diptera, Mycetophilidae). With a revised Generic Classification of the Family. – *Transactions of the Entomological Society of London*, **1924** : 505-670.

Edwards F.W. 1933 – Diptera Nematocera from Mount Kinabalu. – *Journal of the Federated Malay States Museum*, **17** : 223-296, pl. 12.

Edwards F.W. 1940 – New Neotropical Mycetophilidae (IV) (Diptera). – *Revista Entomologica, Rio de Janeiro*, **11** : 440-465.

Evenhuis N.L. 1994 – *Catalogue of the Fossil Flies of the World*. Leiden : Backhuys Publishers, 600 p.

Freeman P. 1951 – Mycetophilidae. *In* : *Diptera of Patagonia and South Chile*, 3. London : British Museum (Natural History), 133 p.

Freeman P. 1960. – A new genus and species of Sciaridae (Diptera, Nematocera) from South Africa. – *Annals of the Natal Museum*, **15** : 75-77.

Frey R. 1942 – Entwurf einer neuen Klassifikation der Mückenfamilie Sciaridae. – *Notulae Entomologicae*, **22** : 5-44.

Grimaldi D., Blagoderov V. 2001 – A new genus of Lygistorrhinidae from Vietnam (Diptera: Sciaroidea), and phylogenetic relationships in the family. – *Studia dipterologica*, 8 : 43-57.

Haenni J.-P., Dufour C. 1983 – Première capture en Suisse d'un représentant de la famille relique des Canthyloscelidae (Diptera, Nematocera). – *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **56** : 187-189.

Hennig W. 1954 – Flügelgeäder und System der Dipteren unter Berucksichtigung der aus dem Mesozoikum beschriebenen Fossilien. – *Beiträge zur Entomologie*, 4 : 246-388.

Kovalev V.G. 1986 – [Infraorders Bibionomorpha and Asilomorpha]. *In* : [Insects in the early Cretaceous ecosystems of western Mongolia].–

Trudy Sovmest. Sov.-Mongol. Palaeontol. Exped., **28** : 125-154 (in Russian).

Lane J. 1952 – Some new Brazilian Mycetophilidae (Diptera, Nematocera). – *Dusenia*, **3** : 131-139.

Loew H. 1850 – Ueber den Bernstein und die Bernsteinfauna. – *Programm der Königlichen Realschule zu Meseritz*, **1850** : 1-44.

Matile L. 1981 – Description d'un Keroplatidae du Crétacé Moyen et données morphologiques et taxinomiques sur les Mycetophiloidea (Diptera). – *Annales de la Société Entomologique de France* (n.s.), **17** : 99-123.

Matile L. 1990 – Recherches sur la systématique et l'evolution des Keroplatidae (Diptera, Mycetophiloidea). – *Mémoires du Muséum National d'Histoire Naturelle*, Paris, (A), **148** : 1-680.

Matile L., Duret J.P. 1994 – Le genre *Colonomyia* Colless découvert en région neotropicale (Diptera, Mycetophiloidea). – *Revue Française d'Entomologie* (*Nouvelle Série*), **16** : 143-147.

McAlpine J.F. *et al.* 1981 – *Manual of Nearctic Diptera*. Volume 1, 674 p. Research Branch Agriculture Canada Monograph No. 27, Ottawa.

Menzel F., Mohrig W. 2000 – Revision der paläarktischen Trauermücken (Diptera: Sciaridae). – *Studia dipterologica Supplement*, **6** (1999) : 761 p. Ampyx-Verlag Halle (Saale).

Meunier F. 1899 – Révision des Diptères Fossiles Types de Loew conservés au Musée Provincial de Koenigsberg. – *Miscellanea Entomologica, Revue Entomologique Internationale*, 7 (10-11) : 161-165; 7 (12) : 169-182, pls I-II.

Meunier F. 1904 – Monographie des Cecidomyiidae, des Sciaridae, des Mycetophilidae et des Chironomidae de l'ambre de la baltique. *Annales de la Société scientifique de Bruxelles*, **28** : 19-92.

Papavero N. 1977 – *A Catalogue of the Diptera of the Americas south of the United States, 19A. Family Diadocidiidae*. 3 p. Museu de Zoologia, Universidade de São Paulo.

Rohdendorf B. 1938 – [Dipterous insects of the Mesozoic of Karatau. 1. Brachycera and part of the Nematocera]. – *Trudy Paleontologi Eskogo Instituta Akademie Nauk SSSR*, 7 : 29-67 (in Russian).

Rohdendorf B. 1946 [Evolution of the wing and phylogenesis of the nematocerous Diptera Oligoneura (Diptera, Nematocera)]. – *Trudy Paleontologicheskogo Instituta Akademie Nauk SSSR*, **13** : 1-108 (in Russian).

Rohdendorf B. 1964 – [The Historical Development of the Diptera]. – *Trudy Paleontologicheskogo Instituta Akademie Nauk SSSR*, **100** : 1-311. (in Russian; English translation, 1974, University of Alberta Press, xv + 360 pp].

Shaw F. 1948 – A contribution to the phylogeny of the Mycetophilidae. – *Annals of the Entomological Society of America*, **41** : 189-199.

Søli G.E.E. 1997 – On the morphology and phylogeny of Mycetophilidae, with a revision of *Coelosia* Winnertz (Diptera, Sciaroidea). – *Entomologica Scandinavica, Supplement*, **50** : 1-139.

Thompson F.C. 1975 – Notes on the genus *Lygistorrhina* Skuse, with the description of the first Nearctic species (Diptera: Mycetophilidae). – *Proceedings of the Entomological Society of Washington*, 77 : 434-445.

Tonnoir A.L., Edwards F.W. 1927 – New Zealand Fungus Gnats (Diptera, Mycetophilidae). – *Transactions of the New Zealand Institute*, 57 : 747-876, pls 58-80.

Tozoni S.H.S., Amorim D. de S. 1998 – A phylogenetic analysis of the Mycetophilidae (Bibionomorpha) based on morphology of head, thorax, legs, abdomen, and wing. 230-231. *In* : Ismay, J.W. (ed.). *Fourth International Congress of Dipterology Abstracts Volume*. 275 p.

Tuomikoski R. 1966a – *In* : Finnische Entomologische Gesellschaft. Referat. Ausserordentliche Versammlung 17.iii.1965. – *Annales Entomologici Fennici*, **32** : 207-208.

Tuomikoski R. 1966b – On the sub-family Manotinae Edw. (Dipt., Mycetophilidae). – *Annales Entomologici Fennici*, **32** : 211-223.

Tuomikoski R. 1966c – Systematic position of *Lygistorrhina* Skuse (Diptera, Mycetophilidae). – *Annales Entomologici Fennici*, **32** : 254-260.

Vockeroth J.R. 1980 – New genera and species of Mycetophilidae (Diptera) from the Holarctic Region, with notes on other species. – *The Canadian Entomologist*, **112** (6) : 529-544.

Vockeroth J.R. 1981. – 14. Mycetophilidae. 223-246. *In* : McAlpine *et al.* (q. v.).

Wood D.M., Borkent A. 1989 – Phylogeny and classification of the Nematocera. **114** : 1333-1370. *In* : McAlpine, J.F. & Wood, D.M. (eds), *Manual of Nearctic Diptera*. Volume 3, vi + 1333-1581. Research Branch Agriculture Canada Monograph No. 32, Ottawa.