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Phylogeny of the Sciaroidea (Diptera): the implication of additional taxa and character data

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Abstract

A cladistic analysis of the extant Sciaroidea was made, using re-evaluated morphological characters, with some additional taxa and with or without the Mesozoic Mesosciophilidae in the ingroup. When the new data were incorporated, the conflict between our earlier phylogenies, with extant taxa only and with both extant and fossil taxa in the ingroup, was resolved. The present result is similar to the one we reached earlier with extant + fossil taxa, which showed the Cecidomyiidae as the sister group of all other Sciaroidea, instead of the Cecidomyiidae appearing as the sister group of the Mycetophilidae + Sciaridae. In the new hypothesis, the main clades of the Sciaroidea outside the Cecidomyiidae were as follows: Ditomyiidae + (Diadocidiidae + ((Keroplatidae + (((Bolitophilidae + (((*Mesosciophila* + ((((*Starkomyia* + rest of Sciaroidea))))))). The placement of the recently described, enigmatic New Zealand genus *Starkomyia* Jaschhof was similar regardless of whether the fossil Mesosciophilidae were included fell in the analysis or not. The two still-undescribed Neotropical taxa that we included fell in the Rangomaraminae clade within the Sciaridae. Unlike our earlier result with extant taxa only, and similar to our extant + fossil result, the *Ohakunea* + *Colonomyia* clade now appears as the sister group of the Mycetophilidae-Lygistorrhinidae-Sciaridae lineage.

Key words: Diptera, Sciaroidea, phylogeny

Introduction

Great interest has recently been shown in the study of the interrelationships of taxa in the Sciaroidea. New family-group taxa have been proposed (Jaschhof & Didham 2002, Hippa & Vilkamaa 2005), the systematics of a number of enigmatic groups has been discussed (Matile 1990, Chandler 2002, Jaschhof & Hippa 2003, Hippa & Jaschhof 2004), and new groups have been introduced (Blagoderov & Grimaldi 2004; Jaschhof 2004a, b, c;

zоотаха 1132 Vilkamaa & Hippa 2004). Even the Mesozoic fauna has been included in discussions and analyses (Grimaldi *et al.* 2003, Blagoderov & Grimaldi 2004, Hippa & Vilkamaa 2005). Jaschhof (2004c) described a new taxon, *Starkomyia*, from New Zealand and discussed its phylogenetic position but without making a numerical analysis. This genus, as well as two undescribed Neotropical taxa, have unexpected sets of characters.

After studying these taxa, we considered it necessary to reanalyze our earlier data and to present our parsimony-based opinion of the phylogenetic position of these new taxa. At the same time, we correct some mistakes made while compiling our earlier character matrix (Hippa & Vilkamaa 2005).

Material and methods

For a cladistic reanalysis of the phylogeny of the main groups of the extant Sciaroidea, we added the recently described New Zealand genus *Starkomyia* Jaschhof (*Starkomyia inexpecta* Jaschhof) and two still-undescribed Neotropical taxa in our earlier ingroup (Hippa & Vilkamaa 2005). Because a sister-group relationship between *Starkomyia* and the Mesozoic Mesosciophilidae has been proposed (Jaschhof 2004c), we performed the analysis either with *Mesosciophila* Rohdendorf in the ingroup or without it. We also added two additional ditomyiid genera, *Symmerus* Walker (*Symmerus annulatus* Meigen, Finland) and *Celebesomyia* Saigusa (*Celebesomyia* sp., Malaysia). As before, *Plecia* Wiedemann (Bibionidae) was used as the outgroup.

The character states of the new genera were written into the matrix of Hippa & Vilkamaa (2005), which includes 78 characters coded for the main groups of the Sciaroidea, with the numbering of the characters and their states being exactly the same as in our earlier paper. We gave proper codes for several characters formerly marked as "?", and we corrected a number of miscodings. A number of errors in the original matrix, especially in *Ditomyia*, were corrected using new material. For the present analysis, we added one new character (number 78): *Ocelli present (0), ocelli absent (1)*. Character 37 (*presence or absence of an unsclerotized break on Rs*) was de-activated because difficulties in its interpretation were pointed out to us. Both the characters concerning the aedeagus-tegmen complex (68: *presence or absence of aedeagal teeth*, 69: *presence or absence of tegmen*) were de-activated because our recent studies (Hippa *et al.* 2005a, b) have cast doubts on the interpretation and applicability of these characters. Except for the additional character 78, the characters now used are the same as in Hippa & Vilkamaa (2005). The characters were equally weighted and the multistate characters were used as unordered. For the data matrix, see Table 1.

The analysis was made using the computer program NONA, version 2.0 (Goloboff 1999) together with the computer program WinClada, version 1.0 (Nixon 1999). The parameters for the heuristic search with NONA were hold/100000, hold/100, mult*100 and TBR+max*.

Results and discussion

The cladistic analysis produced one most parsimonious cladogram (260 steps CI 31, RI 67), which was fully resolved. The phylogenetic tree (Fig. 1), produced after the addition of five taxa and the correction of some character data, differs from our earlier one of extant groups in some important details. The fundamental difference when compared with our analysis of the extant taxa (Hippa & Vilkamaa 2005: Fig. 1) is that the cecidomyiid clade now appears as the sister group of the rest of the Sciaroidea, instead of having a much more apical position. In this respect, the new result is similar to the earlier cladogram that we obtained with both the extant and the fossil Sciaroidea (Hippa & Vilkamaa 2005: Fig. 2). The basal clades of the Sciaroidea excluding the Cecidomyiidae are similar to those obtained by Matile (1997), except that in our present analysis the Diadocidiidae is the sister group of the Keroplatidae plus the rest of the Sciaroidea, instead of being the sister group of the Keroplatidae alone. Furthermore, in our new cladogram, the Ditomyiidae are not in the same clade as the Keroplatidae, which was the result of a miscoding in our earlier analyses (Hippa & Vilkamaa 2005). Starkomyia appears as the sister group of the clade that includes the Sciaroidea minus the Cecidomyiidae, Ditomyiidae, Diadocidiidae, Keroplatidae, and Bolitophilidae. Jaschhof (2004c) discussed four possible hypotheses for the placement and sister group of *Starkomvia*: 1) it is the sister group of *Freemanomvia* Jaschhof (= Pterogymnus Freeman); 2) it is a living representative of the Mesozoic Mesosciophilidae; 3) it belongs to the Heterotricha group sensu Chandler (2002); and 4) it is the sister group of a clade comprising the *Heterotricha* group sensu Chandler (2002). Ohakunea group, and Sciaridae. The result of our parsimony analysis does not support any of these ideas exactly, but Jaschhof's (2004c) hypothesis 2 is closest to our result. The addition of *Mesosciophila* (Mesosciophilidae) in the present analysis places it as the sister group of the whole clade, including Starkomyia. The Heterotricha group sensu Chandler (2002) remains polyphyletic, but in the present tree, the Ohakunea group (Ohakunea + Colonomyia) is no longer included in a common clade with Afrotricha Edwards and Heterotricha Loew, but appears as the sister group of the lineage Mycetophilidae-Lygistorrhinidae-Sciaridae, just as it did in our earlier extant + fossil analysis.

According to the present analysis, the two undescribed genera that are included belong to the Sciaridae, as redefined by Hippa & Vilkamaa (2005), and appear together as the sister group of *Rangomarama* Jaschhof & Didham. *Rangomarama* is the type genus of Rangomaramidae (Jaschhof & Didham 2002), subsequently assigned subfamily rank in the Sciaridae by Hippa & Vilkamaa (2005). For the present, we leave open the question of whether these new genera should be included in the Sciaridae; until the analysis produces more robust results, these new genera could be included in the Sciaridae, Rangomaraminae, or could be given separate subfamily status.

The various hypotheses of the phylogenetic relationships among the taxa of the Sciaroidea that have been proposed, including our recent one (Hippa & Vilkamaa 2005), show that this group is complex and difficult to analyze. Including additional taxa in the analyses can easily cause alterations in the phylogenies.

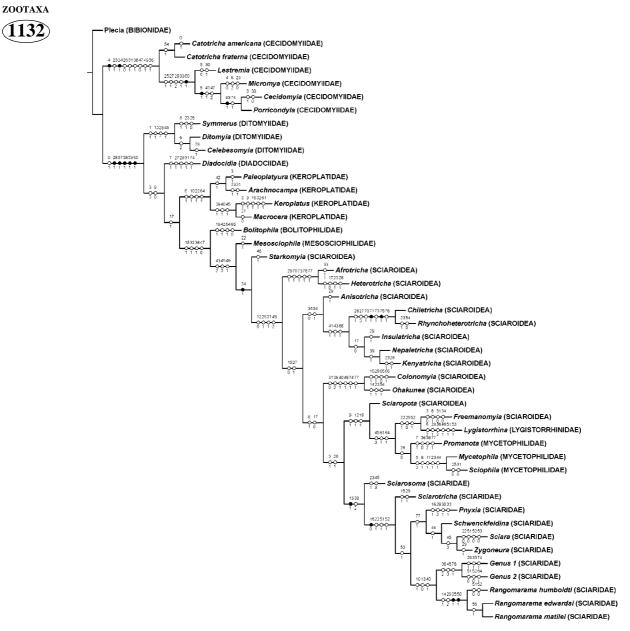


FIGURE 1. Phylogeny of the Sciaroidea. The most parsimonious cladogram (260 steps, CI 31, RI 67) was obtained with the program NONA. Numbers above hatch marks (open = homoplaseous, black = unique) refer to characters; numbers below hatch marks refer to the state indicated. Only unambiguous changes are shown. The current family assignments of the genera are shown.

In Fig. 1 we have indicated the family assignment of the included sciaroid genera, based on recent contributions (Chandler 2002; Jaschhof & Hippa 2003; Hippa & Jaschhof 2004; Jaschhof 2004a, b; Hippa & Vilkamaa 2005). A number of groups (*Starkomyia, Heterotricha* + *Afrotricha, Anisotricha* + *Chiletricha* + *Rhynchoheterotricha* +

Insulatricha + *Nepaletricha* + *Kenyatricha*, *Colonomyia* + *Ohakunea*, *Sciaropota*, *Freemanomyia*) are still without a family affiliation and await a better understanding of the phylogeny of the Sciaroidea.

TABLE 1. Data matrix for phylogenetic analysis. Characters 37, 68 and 69 (the shaded columns) were excluded from the analysis (see the text). A=0/1 polymorphism.

	000000000111111111122222222223333333333
	01234567890123458800000000000000000000000000000000000
Plecia	000100000100000010010010010000000000000
Sciara	0001002000010100000010001111001-0101020010213000100000001110010010-11000000010
Zygoneura	00010020000101000000011001111101-0101020010213000101110001110010010-11000000010
Schwenckfeldina	00010020000101000000011001111001-0101020010212000101110001110010010-100000000
Pnyxia	10010020000101001000011001111211-1101020010202000101110001110010010-100000000
Rangomarama edw	10010010001-0010000001100A111201-01110-110020200011111001111001010101
Rangomarama hum	10010010001-0010000001100A111201-01110-1100202000110010001110010010-100000000
Rangomarama mat	10010010001-0010000001100A111201-01110-AA00202000111110011110010010-10000000000
Colonomyia	10000010001-00001000010001011001010201-020-100100000001110010001-00007010010
Ohakunea	1000001000000101000010101010102010020-1001000010011100100100000000
Sciaropota	1001001001001001010010001111001-0101010000202000100000001110010010-100000000
Sciarotricha	0001000000001010000011001111101-01010200002A2000101100001110010010-0000000000
Sciarosoma	10010010000001001000010101111001-0101020000203000100000001110010010-10000000020
Nepaletricha	100000?00000000000100001001001-00010-101010200010001
Kenyatricha	100000?0000000000001010111001-00010-101010200010001
Chiletricha	1000000000000000110001000101001-0001010010
Insulatricha	10000000000000000010000101101-0001010010
Rhynchoheterotricha	1000000000000000110001010101001-0001010010
Anisotricha	100000000000000110010001011101-000101000020200010001
Afrotricha	100000?000??000111000100100101-1101010000202000100000001110010??0-??101100010
Heterotricha	110000?000000011000010101101101-0101010000202000100000001110010??0-??101100010
Freemanomyia	11000010110010001010011100011000101000020300010010000011101101-0-07000000000
Mesosciophila	1??00?00??00100?1??00110?0?0100010001?1000020300010000000?????10??????????
Promanota	11010011011-1001101001001001001-0100-200002030001000000011101101-0-00000000010
Mycetophila	11010000111-1001111001010101001-0101010000213-101000000011101101-0-0000000000
Sciophila	11010000111-100111100101000010001010101
Lygistorrhina	1001002-011-10011010011000111101-0102020-1-01011100011101101-00000000
Symmerus	11010000111-10001000010101000000001000000
Ditomyia	11010020011-000010000100001010000001000000101-1000000
Celebesomyia	11010020011-000010000100001010000001000000101-1000000
Keroplatus	10010010011-10011110011000101000100011-1100001-1000000
Paleoplatyura	100100100?1-100?1??00110001010000001?00001000-100000000
Macrocera	10000010001-100011100010000101000000011-11000001-1000000
Arachnocampa	10000010001 - 10001110011100101001 - 0001000001000 - 100000000
Diadocidia	1000000100001000010000111101-0001100000100-1000000
Bolitophila	100000000001001111101000010100010001010000
Cecidomyia	00011110010000001000010111010201-000101001021202010-000010001
Porricondyla	00011100010000001000010111010201-100101001021202010-000010001
Micromya	0001012001000000100010011010201-100101001021302010-000010001000000-12000000000
Lestremia	0001100000000000001000010111010211-10010100002-2100100000010001
Catotricha ame	1007100001000001700010110000001-0001010000203100100001010000010000-1000000000
Catotricha fra	0007100001000001700010110000001-0001010000203100100001010000010000-1000000000
Starkomyia	10000000000100111000100000100010101010000
Genus 1	0-010020001-0000000001100111101-11020110203000101110001110010000-10000010-01
Genus 2	0-010000001-0000000001100111001-010201102030001000100011100101-?-??000000001

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