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# Phylogeny and classification of the Sciaroidea (Diptera: Bibionomorpha): Where do we stand after AMORIM & RINDAL (2007)?

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#### Summary

A paper on the phylogeny of the Sciaroidea by D. AMORIM and E. RINDAL from 2007 is reviewed. The phylogenetic hypothesis derived from morphological quantitative analysis is used by these authors to propose a new classification of the Sciaroidea which differs significantly from previous classifications. In the present review it is shown by way of examples that the data matrix used by AMORIM and RINDAL is fatally flawed in terms of both the employed taxa and characters. As a result, the analysis is not repeatable and the hypothesis resulting from it is neither testable nor rebuttable. It is suggested that the paper in question should not be used as a basis for changes in the traditional classification of the Sciaroidea.

#### Key words

Diptera, Sciaroidea, phylogeny, family classification, review

### Zusammenfassung

Eine Publikation zur Phylogenie der Sciaroidea von D. AMORIM und E. RINDAL aus dem Jahr 2007 wird besprochen. Die phylogenetische Hypothese, die die Autoren aus ihrer quantitativen morphologischen Analyse abgeleitet haben, wird von ihnen benutzt, um eine Neuklassifikation der Sciaroidea vorzuschlagen. Diese unterscheidet sich grundlegend von bisherigen Klassifikationen. In der vorliegenden Besprechung wird an Beispielen aufgezeigt, dass die von AMORIM und RINDAL benutzte Merkmalsmatrix auf verheerende Weise fehlerhaft ist, sowohl was die eingesetzten Taxa als auch die verwendeten Merkmale betrifft. Im Ergebnis muss festgestellt werden, dass diese Verwandtschaftsanalyse nicht wiederholbar und die daraus resultierende Verwandtschaftshypothese weder nachprüfbar noch widerlegbar ist. Deshalb wird nahegelegt, die in Rede stehende Publikation nicht zur Begründung etwaiger Änderungen an der bestehenden Sciaroidea-Klassifikation heranzuziehen.

## Introduction

In 2007 DALTON AMORIM and ERIC RINDAL published a purported new synthesis of the phylogeny of a large group of flies known as the Sciaroidea (their Mycetophiliformia) and which they used as the basis for a new classification of the component families. They stated that their study was "the widest study ever made of the phylogenetic relationships within the higher Bibionomorpha" (p. 41). Their results were based on a numerical analysis of 64 terminal taxa and 137 morphological characters.

The aim of this review is twofold. One is to address the scientific content of that paper and particularly the data matrix. The other is to provide some detail regarding the general circumstances that, in my opinion, have led to its publication. As taxonomists do not work in a social

vacuum, there is a close bond between these two subjects, and neither can be fully understood when examined separately. This review is essentially an Opinion paper, for which this journal does not hold a separate format.

AMORIM & RINDAII (2007) explain and discuss in detail the methods they applied (p. 10 f., 41 f.). Here I refrain from highlighting in detail any theoretical aspects of methodology, which was recently done masterfully by MOOI & GILI (2010) with fish systematics. My approach to illuminate the evolutionary history of a group focuses on individual characters and their homology, function and weight relative to other characters (e.g., JASCHHOF & DIDHAM 2002). This approach, which calls for studying character variation throughout a large number of specimens, species and supraspecific taxa, and thus is slow-going, has proved itself in Cecidomyiidae phylogeny and classification (JASCHHOF & JASCHHOF 2009, GAGNÉ 2010). It differs from AMORIM & RINDAL'S (2007) approach, which tries to impress by the sheer quantity of analyzed characters and taxa (p. 41).

### The taxon in question

Sciaroidea, used here in the sense of WOOD & BORKENT (1989), includes the fungus gnat families (Bolitophilidae, Diadocidiidae, Ditomyiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae), the long-winged fungus gnats (Rangomaramidae, sensu JASCHHOF & DIDHAM 2002), the black fungus gnats (Sciaridae), and the gall midges (Cecidomyiidae). In addition, Sciaroidea contains some 20 genera and 50 species not assigned to any of the traditionally recognized families (JASCHHOF 2009).

There exists no concise introduction to the natural history of the Sciaroidea as a whole, but family accounts have been published on several occasions (e.g., BROWN et al. 2009). Sciaroidea, which is a superfamily of the infraorder Bibionomorpha (e.g., CHANDLER 2010), comprise more than 13500 named species (PAPE et al. 2009). Among lower dipterans they make up a universe of their own with a tremendous diversity, not only in numbers of species but also in form and function. This is a level of diversity too large to be handled taxonomically by a single expert, a fact that applies also to each of the largest families, such as Mycetophilidae, Sciaridae and Cecidomyiidae. Outside the scope of the Holarctic Region Sciaroidea families are usually listed with the "least known families" category (e.g., PAPE et al. 2009), and up to now the faunas of entire continents have been without a taxonomic Sciaroidea expert over long periods of time. As a result, this superfamily provides an exceedingly large field for research with the potential to keep legions of researchers busy. Unfortunately, owing to the general conditions that affect contemporary taxonomy (e.g., BOERO 2010), world Sciaroidea research is far from thriving. The present author has worked on the taxonomy of various Sciaroidea for the past 20 years. It was particularly the enigmatic group of the Sciaroidea *incertae sedis* that raised the author's interest in Sciaroidea phylogeny, an interest shared with fewer than 10 contemporary dipterists. The following review will be of broader interest for zoosystematists because of broader implications for progress in our collective interest in descriptive taxonomy and phylogenetic analysis (see MOOI & GILL 2010).

### The paper under review – some historical context

AMORIM & RINDAL'S (2007) paper is the last of four papers addressing Sciaroidea phylogeny in the period between 2002–2007. The others are CHANDLER (2002) and HIPPA & VILKAMAA (2005, 2006). This is a remarkable fact, considering that the years before 2002 had generated

fewer. So why did this burst of published phylogenies happen just at that time? AMORIM & RINDAL (2007: 4-7) give a detailed account of the historical development of phylogenetic hypotheses of Sciaroidea, although I disagree with some of their interpretations. The year 2002 saw the release of two papers of special importance for Sciaroidea phylogeny: CHANDLER's (2002) treatment of the *Heterotricha* LOEW group of genera, a taxon approximately identical with the Sciaroidea *incertae sedis* in the present review paper, and the description of a new sciaroid family Rangomaramidae by JASCHHOF & DIDHAM (2002). In retrospect it appears that the introduction of Rangomaramidae in particular had a catalytic effect on the activity that followed as it was the first component of the Sciaroidea incertae sedis that was raised to family rank, leaving the remainder untouched. Introduced as a distinct family to absorb the single genus Rangomarama JASCHHOF & DIDHAM, endemic to New Zealand, the Rangomaramidae were hypothesized to be one of four subfamilies of the family Sciaridae by HIPPA & VILKAMAA (2005, 2006), and, eventually, to form again a distinct family but in the entirely new sense by AMORIM & RINDAL (2007). Rangomaramidae sensu AMORIM & RINDAL (2007) comprise practically all Sciaroidea *incertae sedis*, which apparently is a polyphyletic assemblage as I will discuss below. The phylogenies published by HIPPA & VILKAMAA (2005, 2006) and AMORIM & RINDAL (2007) may be understood as replies to the papers by CHANDLER (2002) and JASCHHOF & DIDHAM (2002). AMORIM & RINDAL (2007) point to the fact that the phylogenies proposed by HIPPA & VILKAMAA (2005, 2006) are "quite different" from each other (p. 7) and (p. 6) from that of Chandler (2002). JASCHHOF & JASCHHOF (2009: 303) underline that HIPPA & VILKAMAA's results from 2005 and 2006 are so contradictory to one another that this alone calls for reservation in accepting their hypotheses. Finally, HIPPA & VILKAMAA's results differ considerably from that of AMORIM & RINDAL (2007).

Recent authors of Sciaroidea phylogenies, AMORIM & RINDAL included, agree that the slightest changes made in the data matrix, such as additional taxa, additional characters, and deleted (problematic) taxa, may have rather dramatic effects on tree topologies (HIPPA & VILKAMAA 2005, 2006; AMORIM & RINDAL 2007). It appears that each new attempt to shed light on Sciaroidea phylogeny leads to a completely new result, which, when it is not adequately discussed, raises the question "What next?". End users of phylogenies, such as ecologists, ethnologists, and catalog authors in need of a classification that lasts longer than just for a few months, may be disconcerted. HIPPA & VILKAMAA's latest phylogeny was published February 20, 2006, that by AMORIM & RINDAL on July 30, 2007. This period of 17 months between the two publication dates is really a short time, considering the complexity of this enormous scientific problem, and that AMORIM & RINDAL endeavoured to include the results of HIPPA & VILKAMAA (2006) in their discussion. When I was given the opportunity to review AMORIM & RINDAL's manuscript, the chapter on Heterotrichinae subfam. n. (a new subfamily announced in their title) was absent.

I have on various occasions (e.g., JASCHHOF & JASCHHOF 2009: 295ff.) criticized AMORIM & RINDAL's paper as well as the phylogenies proposed by HIPPA & VILKAMAA (2005, 2006). While HIPPA & VILKAMAA'S (l. c.) redefinition and reclassification of the Sciaridae had no echo in subsequent literature, AMORIM & RINDAL'S proposal of a "phylogenetic classification of the Mycetophiliformia" (p. 47 f.) has been accepted by various subsequent authors (e.g., PAPE et al. 2009, HIPPA et al. 2009), in one case even before the official publication date (EVENHUIS 2007, in which the entry "Family Rangomaramidae", with the subfamilies Chiletrichinae, Rangomaraminae and Ohakuneinae, is dated "last revised 24 May 2007"). In *Diptera diversity* – *status, challenges and tools* (PAPE et al. 2009), which, according to WHEELER (2009: XVI), "will stand as an essential reference for dipterists for decades to come", AMORIM & RINDAL'S (2007) concept of Rangomaramidae is applied and accordingly discussed throughout the book. *Systema Dipterorum – The Biosystematic Database of World Diptera* (PAPE & THOMPSON 2010) treats Rangomaramidae in the sense of JASCHHOF & DIDHAM (2002), which may or may not be a result of lack of revision (last revision date: 14 October 2005, remark: "work record").

### The analysis

AMORIM & RINDAL'S (2007) paper has 92 pages, including 38 plates of illustrations which is a large task to read for reviewers and others interested in the subject. To grasp its content and follow the vast quantity of details is really hard work, which lies in the nature of the subject itself. A detailed revision of this paper would result in a large publication of its own. I suggest that AMORIM & RINDAL'S paper should not have been published—a severe judgment calling for an explanation and convincing arguments. My first argument is that the analysis is not repeatable, so the hypotheses resulting from it are neither testable nor rebuttable. My second argument is that the very basis of AMORIM & RINDAL's analysis, i.e. the data matrix, was too poorly conceived to provide convincing results. In the following I base my arguments mainly from the perspective of the groups I know best, the hugely diverse Cecidomyiidae, the limited Rangomaramidae, with five species, and the Sciaroidea *incertae sedis*.

### The treatment of Cecidomyiidae

AMORIM & RINDAL see one of the purposes of their study is "to obtain a phylogeny of the group" including Cecidomyiidae (p. 7). They have indeed obtained a phylogeny of Sciaroidea, and one that places Cecidomyiidae as the sister group to the remainder of the superfamily. As I have stated earlier (JASCHHOF & JASCHHOF 2009: 303) this conclusion from a numerical analysis is not surprising. Cecidomyiidae are segregated from other sciaroids and bibionomorphs by a number of unique characters, including the multiple lack of characters that are unique to the remainder of Sciaroidea. But this is not the problem I am addressing here. AMORIM & RINDAL's proposal of a sister group relationship between Cecidomyiidae and the remainder of their Myctophiliformia, is a result of their data input, which is on an unacceptable low level as will be exemplarily shown below, or has been obtained accidentally rather than through meaningful analysis.

AMORIM & RINDAL (p. 4 f.) refer, in my opinion rightly, to three groups that are exceedingly difficult to position in relation to the other Sciaroidea: Sciaridae, Cecidomyiidae and Sciaroidea *incertae sedis*. The authors realize that in order "to avoid pitfalls", Cecidomyiidae and other large families should be represented in the analysis by a higher number of taxa (p. 7). They state: "The number of species examined in this study is much larger than that listed in Table 1 [list of terminal taxa in the numerical analysis of the Mycetophiliformia and outgroups], which allowed a better understanding of the evolution of characters within each family" (p. 4). However, their table 1 (p. 8) lists *genera*, not species. At the same time their terminal taxa do not correspond with the specimens they examined (p. 51 ff., appendix 1). Students wishing to repeat the analysis, or trying to understand the data matrix, are left with a number of questions. Which specific species do the character states in their data matrix refer? Which concrete sources of information did AMORIM & RINDAL actually use for certain taxa to fill the data matrix: what literature, what advice from colleagues? Among their genera are four genera of Cecidomyiidae: *Catotricha* EDWARDS, *Lestremia* MACQUART, *Porricondyla* RONDANI, and *Asphondylia* LOEW. These represent only four of at least twelve distinct, important family group taxa within the Cecidomyiidae (Catotrichinae,

Lestremiinae, Micromyinae, Asynaptini, Dicerurini, Heteropezini, Porricondylini, Winnertziini, Brachineuridi, Cecidomyiidi, Lasiopteridi, and Stomatosematidi; GAGNÉ 2010). How did AMORIM & RINDAL manage to understand the character evolution within Cecidomyiidae on the basis of the few taxa they studied? It may be that they studied intensively cecidomyiid literature, as opposed to examining specimens. Descriptive literature is not always meant to support phylogenetic considerations, however, and most of us know from personal experience that the comparative re-study of specimens is an inevitable routine in the course of phylogentic analyses, often resulting in the correction or re-evaluation of character states. Some readers may object that the purpose of AMORIM & RINDAL'S analysis was not to study the phylogeny of Cecidomyiidae but its position within Sciaroidea, so studying representatives of one or two basal groups should be sufficient. Why then, I have to respond, did AMORIM & RINDAL aim to analyse "a larger number of species of more diverse families: Mycetophilidae with 14 species, Keroplatidae with 6 species and Ditomyiidae with 5 species" (p. 41)? Are Keroplatidae and Ditomyiidae larger or more complex families than both Cecidomyiidae and Sciaridae? Of course they are not. Sciaridae is represented in AMORIM & RINDAL'S study by only three taxa (p. 8) and all of these are badly chosen (MENZEL, pers. comm.). Both Apelmocreagris ENDERLEIN (type species: Lycoria bibionea SPEISER from the Afrotropical Region) and Trichomegalosphys ENDERLEIN (type species: T. funesta ENDERLEIN from the Oriental Region) are small genera of which it is doubtful whether or not they are distinct from Sciara MEIGEN and, respectively, Pseudosciara SCHINER, and whether or not they occur in the Neotropical Region (all Sciaridae specimens studied by AMORIM & RINDAL are from Brazil, p. 52). The genus Bradysia WINNERTZ is a polyphyletic, extremely complex grouping of several hundred species worldwide (MENZEL & MOHRIG 2000). As AMORIM & RINDAL in their "Appendix 1. List of examined specimens" (p. 51 f.) do not refer to concrete species of these three genera, one cannot know what Sciaridae they actually studied for their analysis.

Under the headline of Cecidomyiidae AMORIM & RINDAL's Appendix 1 lists the following material (p. 51 ff.): "Porricondylinae sp. - 4 spp., CHILE ...; Porricondylinae sp. - 2 spp., BRAZIL ...; Lestremid sp. - 7 females, BRAZIL ...; Lestremid sp. - 7 females, BRAZIL ...". Porricondylinae is a "diverse subfamily of 131 genera and 731 species", "especially poorly known outside the Palaearctic Region" and "paraphyletic with regard to the subfamily Cecidomyiinae" (GAGNÉ 2010). Consequently, the "Porricondylinae spp." studied by AMORIM & RINDAL remain entirely dubious; if the authors really have seen authoritatively identified Porricondylinae specimens, which may or may not be the case, these belong to a taxon (most likely an unnamed one) of completely unknown identity. We cannot even know whether they studied males or females. This, however, is essential to know, as cecidomyiids including porricondylines show considerable sexual dimorphism. What effects have these shortcomings on the analysis? Just one example: AMORIM & RINDAL's character 8 refers to the number of flagellomeres, for which they differentiate among 5 character states (p. 23). One may debate on whether these states reflect any meaningful patterns, or are just randomly chosen as a result of poor taxon sampling. More important is that AMORIM & RINDAL do not differentiate between male and female antennae. For instance, Lestremid males have 14 flagellomeres (their state 1 in the analysis), whereas females have 9 or 10 flagellomeres (states 4 and 3 respectively) (JASCHHOF & JASCHHOF 2009). According to AMORIM & RINDAL's matrix (table 3, p. 21 f.), their "Lestremia" match state 5, which means 6 flagellomeres. If 6 flagellomeres is correctly observed, this means almost certainly that AMORIM & RINDAL have studied a male Anareted sp., not a female Lestremid sp. (see JASCHHOF & JASCHHOF 2009: 62 f.). Anarete are known to occur in the Neotropics (AMORIM & RINDAL'S "Lestremia" are from Brazil, as mentioned above). Adults of those flies are usually found swarming in the open landscape (GAGNÉ & JASCHHOF 2009), which would make them likely catches for museum collections. I checked for coding errors among AMORIM & RINDAL's characters 1 to 15, and then only for some of the Cecidomyiidae and Sciaroidea *incertae sedis*, and found erroneous codings for 12 characters, including an unnecessary high number of question marks (unknown character state). For *Catotricha*, a taxon reflecting the ground-plan of Cecidomyiidae morphology and thus being of major importance for phylogenetic considerations, 56 of 137 characters are question-marked. That practice stands in strong contrast to the facts that modern reviews of *Catotricha* morphology exist (JASCHHOF 1998, 2001) and specimens of both sexes and larvae are available for study from museum collections. AMORIM & RINDAL's procedure (p. 9) that "immature characters (when available) were generalized at the family level, except for the Rangomaramidae" challenge the rhetorical question: Is it a surprise, then, that the four Cecidomyiidae taxa anaylized were gathered in one and the same clade when their character states had been "generalized at family level" without checking these characters with specimens? Of course there was no other way for the authors than to generalize taxa of unknown identity.

I could go on with this but the general problem should have become obvious here. What was discussed here concerning Cecidomyiidae, could be substantiated with similar reviews of the Sciaroidea *incertae sedis* and Sciaridae (F. MENZEL, pers. comm.).

#### The Rangomaramidae problem

Another purpose of the study under review was "to solve the problem of the genera of uncertain position" (p. 7). What has been achieved by AMORIM & RINDAL's analysis, despite my opinion that any results are highly dubious if obtained on the basis of the crude data matrix reviewed above. The way AMORIM & RINDAL themselves see it (p. 44) "there is considerable advance" regarding "the question of the relationships of the genera around *Heterotrichal* and *Ohakunea*". I strongly disagree. The Rangomaramidae sensu AMORIM & RINDAL "include most of these genera of uncertain position" (p. 44), and this is exactly the problem. Latest CHANDLER (2002) made quite clear that the Sciaroidea incertae sedis are not a monophyletic group, and I do not know of any sciaroidologist, with the exception of AMORIM & RINDAL, who would not agree with CHANDLER on this point. Even HIPPA & VILKAMAA'S (2005, 2006) results suggest the Sciaroidea incertae sedis are a polyphyletic grouping. So, to lump the Sciaroidea incertae sedis together again under the name of a previously monophyletic family, Rangomaramidae, is clearly a setback (see also AMORIM & FALASCHI 2010). There are, in fact, no synapomorphies to provide any evidence of these taxa as a monophyletic group (their Rangomaramidae). There are other setbacks. Within the "Mycetophiliformial incertae sedis" sensu AMORIM & RINDAL (p. 48) one finds genera that have never before been questioned as belonging to the Mycetophilidae, such as Taxicnemis TONNOIR & EDWARDS and Loicia VOCKEROTH, side by side with true incertae sedis, such as Freemanomyia JASCHHOF and Starkomyia JASCHHOF. AMORIM & RINDAL have not seen specimens of any of these genera. A closer look at their preferred topology (p. 69, fig. 68) reveals the absence from that topology of these four genera and of the unplaced genera Afrotricha CHANDLER, Anisotricha CHANDLER, Nepaletricha CHANDLER, Sciarosoma CHANDLER and Sciaropota CHANDLER. In other words, a considerable number of the unplaced genera which the study was initially attempting to reinterpret were excluded from the most critical analysis.

I leave it to future workers of Sciaroidea phylogeny to deal with the details of AMORIM & RINDAL's concept of Rangomaramidae (p. 11 f.). I cannot see any purpose in a family description which employs words such as "usually" and "with exception of" when trying to find common characters of the taxa included, and that does not refer to any synapomorphies. What is their concept of the family? In their discussion of Rangomaramidae AMORIM & RINDAL state (p. 12): "Even though there is still some instability, there is phylogenetic signal that allows familial assignment

to all these genera that were orphans within the system. A number of other genera might fit in the clade, but because of missing data, we preferred to keep their inclusion in the family still pending." This is one of many text passages in which the authors admit "instabilities" in their tree topologies, even "the position of the genus [*Rangomarama*] in the system should still be taken carefully" (p. 45). Nevertheless, on pages 47–48 readers of AMORIM & RINDAL's paper find what is titled "A phylogenetic classification of the Mycetophiliformia". These two pages are in my opinion a great disservice to the science, because they present a concise and ready-made account for all those who need a handy classification, no matter how this classification was generated.

### Where do we stand after AMORIM & RINDAL (2007)?

I admit I was lost for words more than once when I read completely AMORIM & RINDAL's paper during a dipterological field trip in May–July 2010. The implications resulting from it were disturbing. How could it happen that this paper became a milestone in the literature on Diptera? The conclusions are based on a matrix which includes numerous questionable character states, missing data (when these are actually available) and the weak use of exemplars for very diverse groups. In many cases it is unknown to which species and genera these exemplars actually belong. The resulting cladogram, which differs so significantly from previous results, is therefore fatally flawed. To use this paper as a basis for further changes in the classification of the Sciaroidea is premature and unwise.

In regards to the phylogeny and classification of Sciaroidea, I propose to follow the family classification of the Sciaroidea used by CHANDLER (2010), which is based to a large extent on the works of MATILE, particularly his monograph on Keroplatidae (MATILE 1990). CHANDLER's proposal refers to the British fauna for which no Sciaroidea *incertae sedis* are known. When the family Rangomaramidae sensu JASCHHOF & DIDHAM (2002) and the Sciaroidea *incertae sedis* are added, the classification alternative to that by AMORIM & RINDAL (2007) reads as follows:

#### Infraorder Bibionomorpha

Superfamily Sciaroidea (= Mycetophiloidea)

Bolitophilidae (fungus gnats)

Diadocidiidae (fungus gnats)

Ditomyiidae (fungus gnats)

Keroplatidae (fungus gnats)

Lygistorrhinidae (fungus gnats)

Mycetophilidae (fungus gnats)

Rangomaramidae (long-wing fungus gnats)

Sciaridae (black fungus gnats)

Cecidomyiidae (gall midges)

Sciaroidea incertae sedis (Afrotricha Chandler, Anisotricha Chandler, Cabamofa Jaschhof, Chiletricha Chandler, Colonomyia Colless, Eratomyia Amorim & Rindal, Freemanomyia Jaschhof, Heterotricha Loew, Insulatricha Jaschhof, Kenyatricha Chandler, Madagotricha Jaschhof & Jaschhof, Nepaletricha Chandler, Ohakunea Tonnoir & Edwards, Rhynchoheterotricha Freeman, Rogambara Jaschhof, Sciaropota Chandler, Sciarosoma Chandler, Starkomyia Jaschhof) Readers of the present paper may ask why I am making a counterproposal that is not backed by another analysis of Sciaroidea phylogeny. The answer is that I cannot present a new phylogeny at this time. The reality is that we need more careful morphological study of further characters, broader comparisons of homologous character states, and more extensive outgroup comparisons, before a more stable and reliable interpretation of the phylogeny of the Sciaroidea is possible. In my opinion, the phylogeny of Sciaroidea can be illuminated only through the combined expertise of specialist-taxonomists of all the taxa concerned, and must be regarded as a major enterprise that will need years of dedicated work to accomplish. Methods to address the problem must be chosen carefully to avoid going down the same blind alleys of the past. The future will show whether or not sciaroidologist are prepared for such a combined effort. Difficulties in shedding light on the phylogeny of Sciaroidea, whatever methodological approach, lie in the peculiar character distribution of this ancient and diverse group. It appears that we are still lacking the right approach to master this situation and to reach significantly beyond the state of knowledge of early Sciaroidea authorities, such as Edwards. Numerical analysis, as it has been applied hitherto, has failed to contribute to the progress made in parts of the field, despite the fact that it has become the method of choice in recent years. As far as I can see a two-fold strategy will lead out of the blind alley: (1) use a broad range of methods, and (2) make new data available for analysis through search for, and description of missing links. To escape the blind alley will be extremely difficult, if not impossible in an intellectual environment that is more and more limiting itself to quantitative analysis. I am convinced that there would not have been a need for the present review were there a healthier environment for all of us for practising taxonomy, with less pressure to publish high impact results in a rapid sequence and with more intellectual freedom.

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