

FRAGMENTA FAUNISTICA

Fragm. faun.

Warszawa, 30.12.2001

44

309–317

R. Henry L. DISNEY

Sciadoceridae (Diptera) reconsidered

Abstract: TONNOIR's (1926) assignment of *Sciadocera rufomaculata* WHITE to the *Phoridae* is supported and SCHMITZ's (1929) transfer of it and *Archiphora patagonica* SCHMITZ to a separate family, *Sciadoceridae*, is rejected. The growing number of fossils bridging the gap between *Sciadoceridae* and *Phoridae* support the view that the sciadocerids are merely an assortment of *Phoridae* that share some plesiomorphic features.

Key words: *Diptera*, *Phoridae*, *Sciadoceridae*, *Aschiza*, systematic position

Author's address: University Department of Zoology, Downing Street, Cambridge CB2 3EJ, U. K.
e-mail: rhld2@hermes.cam.ac.uk

INTRODUCTION

YEATES and WIEGMANN (1999) have provided a useful review of the higher-level phylogeny of *Diptera*. An area of continuing debate relates to the *Aschiza* ("Lower *Cyclorrhapha*" of these authors), especially the families other than the *Syrphoidea*. Perhaps the most intriguing flies in this assemblage are two present-day genera, and several fossil genera, currently assigned to the family *Sciadoceridae*. The present paper reconsiders these genera.

WHITE (1917) described *Sciadocera rufomaculata* (Fig. 1) from Tasmania and assigned it to the *Empidae* (*Empididae*), *Hybotinae* (*Hybotidae*). However, he commented that "the correct position of this curious genus is somewhat doubtful". TONNOIR (1923) agreed and transferred it to the *Platypozidae*, but noting that the wing venation (Fig. 14) is transitional between this family and the *Phoridae*. He subsequently reassigned it to the *Phoridae*, *Sciadocerinae* (TONNOIR 1926). He had shown specimens to Professor Bezzi, who commented that "it is the most wonderful Dipteron he has ever seen". Because it seems to combine features of *Empididae*, *Dolichopodidae*, *Phoridae* and *Platypozidae* it, and

the subsequently described South American *Archiphora patagonica* SCHMITZ (1929b), have intrigued students of *Diptera* phylogeny ever since (e.g. OLDROYD 1964; HENNIG 1966).



Fig. 1. *Sciadocera rufomaculata* male (After OLDROYD 1964).

SCHMITZ (1929b) emphasised the resemblance of these two genera to the *Platyzeziidae*, and then proposed that the subfamily be raised to family rank. However, TONNOIR (in FULLER 1934), when reviewing the details of the larva and puparium of *Sciadocera rufomaculata*, concluded that these indicated a closer affinity with the *Phoridae*. Likewise HENNIG (1964), when commenting on the affinities of *Archiphora robusta* (MEUNIER) from the Baltic amber, agreed with Tonnoir, but supported Schmitz in treating these two genera as belonging to a separate family. Hennig's opinion has since prevailed and nobody now disputes that these two genera belong to the *Platyzezoidea/Phoroidea* section of the *Aschiza*.

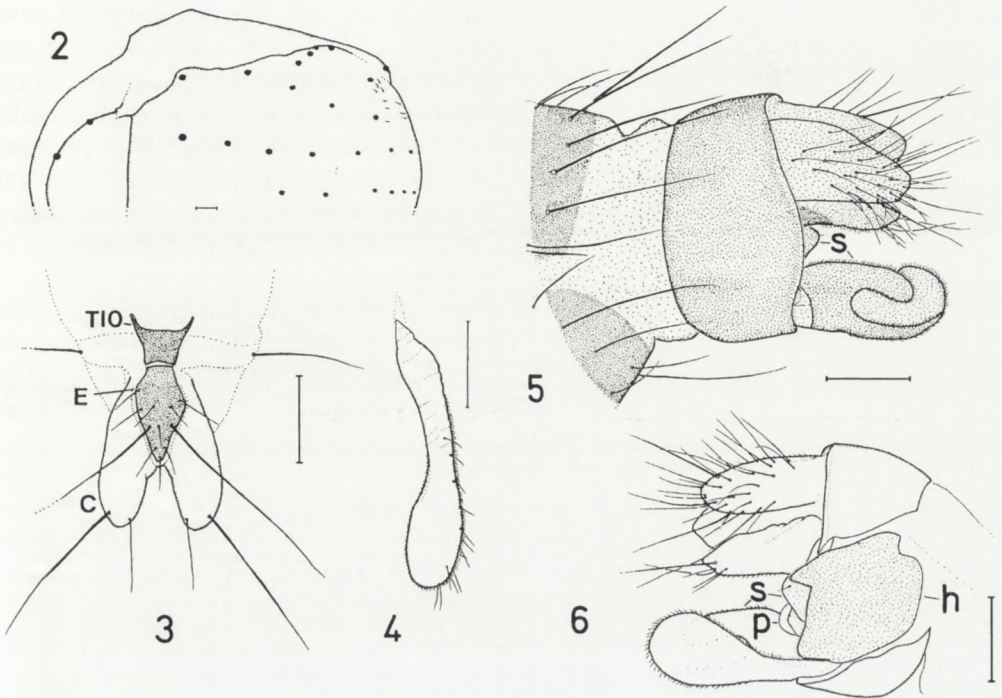
The discovery of fossil *Sciadoceridae* in Tertiary and Cretaceous ambers (HENNIG 1964, MCALPINE & MARTIN 1966) seemed to secure the position of this family as the putative sister group of the *Phoridae*. BROWN (1992)

then used this hypothesis to polarise a number of proposed transformation series relating to the groundplan character states of the *Phoridae*, and then offered some novel hypotheses regarding the supra-generic classification of the *Phoridae*. These in turn engendered a debate (DISNEY 1993; BROWN 1995; DISNEY 1996). The discovery of further Cretaceous fossils (GRIMALDI 1989; BROWN & PIKE 1990; MOSTOVSKI 1996, 1999; ARILLO & MOSTOVSKI 1999; GRIMALDI & CUMMING 1999), belonging to *Sciadoceridae*, *Phoridae*, or of uncertain assignment with respect to these two families, has raised anew the question of the family assignment of the species currently placed in the *Sciadoceridae*. The present paper, therefore, reviews the validity or otherwise of this family.

RELEVANT CHARACTER STATES

The late Colin Patterson is reported to have stated on several occasions that "for a taxonomist it is as important to discover a new character as to discover a new species" (VANE-WRIGHT 2000). The character states that are relevant to the task of phylogenetic systematisation are those considered to be apomorphic. These states, however, may have evolved more than once. Indeed it is now clear that convergent evolution has been widespread and common (e.g. MOORE & WILLMER 1997). Consequently we need to consider how likely it is that a proposed apomorphy has evolved more than once.

The loss of a feature, such as the basal segment of the palp (Fig. 4) or a cross vein in the wing, can be achieved by a single mutation of a critical switching gene. The acquisition of the same feature, however, will require a series of mutations, as we now know that the development of such a cross vein in *Drosophilidae* requires a set of genes. In view of these considerations we can now perceive that the early discussions of the affinities of *Sciadocera* and *Archiphora* have been obscured by paying too much attention to plesiomorphic features, especially those which they share with the *Platypezidae* (e.g. the retention of a series of abdominal sternites), and to the loss of relatively trivial character states, such as details of the wing venation or bristles.

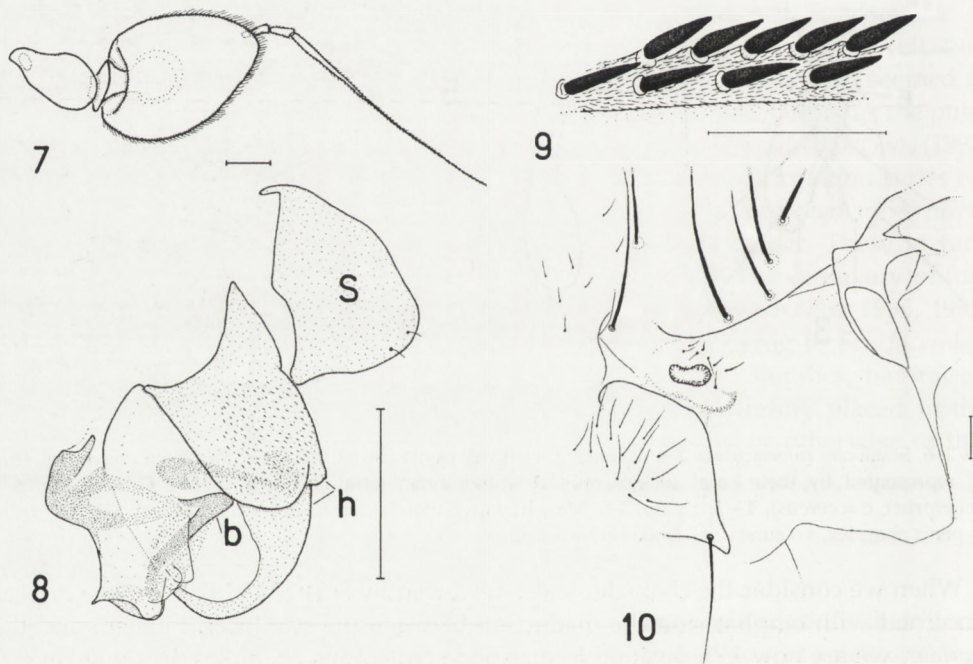


Figs 2–6. *Sciadocera rufomaculata*. 2–4. Female: 2 – left halves of scutum and scutellum from above, with bristles represented by their basal sockets only, 3 – abdominal terminalia from above (T10 = tergite 10, E = epiproct, c = cercus), 4 – left palp. 5–6. Male hypopygium: 5 – left face, 6 – right face (h = hypandrium, p = penis complex, s = surstylus). Scale bars = 0.1 mm.

When we consider the character states reviewed by SCHMITZ (1929b), when he was concerned with emphasising the distinction between the sciadocerid genera and the *Phoridae*, we are now in a position to question some of his examples. In some genera, e.g. *Pseudacteon* COQUILLET females, abdominal sternite 6 is present. The reduction and loss of small hairs on the thoracic scutum (Figs 2 & 10) is also a feature of some *Termitoxeniinae* (DISNEY & KISTNER 1995, 1997). Furthermore, before the discovery of the flying-stage females of these peculiar flies, which he erroneously assigned to a

new subfamily linking the *Termitoxeniinae* to the *Phoridae* (SCHMITZ 1951), he had strongly defended the separate family status of these flies. The recognition of the males of the *Termitoxeniinae* finally resolved these confusions (DISNEY & CUMMING 1992). By contrast the possession of numerous bristles on the scutum (Figs 1 & 2) is not only found in some *Termitoxeniinae* but is now considered to be a plesiomorphic feature of the *Cyclorrhapha* (SIMPSON *et al.* 1999).

The female abdominal terminalia (Fig. 3) are essentially of the phorid type, but with the apomorphy of the cerci not being demarcated at the base (as is the case in some *Phoridae*). GRIMALDI & CUMMING (1999) cite the asymmetry of the male hypopygium as an autapomorphy of the *Sciadoceridae*. However, several phorid genera possess markedly asymmetric hypopygia. The hypopygium of *Sciadocera* (Figs 5, 6 & 8), which has been discussed recently (DISNEY 1999), is now perceived to be more phorid like than platypezid. Indeed some subsequently described phorids have parts of the hypopygia that more closely resemble those of *Platypezidae*, such as *Chonocephalus blackithorum* DISNEY (1986), which has platypezid-like gonopods (Fig. 11), and *Xenotriphleba dentistylata* BUCK (1997), which has platypezid-like surstyli (Fig. 12). Likewise the anterior thoracic spiracle of *Sciadocera* is indeed unusual in not being circular (Fig. 10), but it is also not circular in several unrelated genera of *Phoridae*.



Figs 7–10. *Sciadocera rufomaculata*. 7 – female, left antenna. 8 – male, penis complex still attached to hypandrium (h), viewed from above and from right (b = paraphysis, s = surstylus); 9 – female, dorsal face of part of costa, 10 – female, anterior spiracle and adjacent regions of thorax. Scale bars = 0.1 mm.

The emergence during evolution of the *Sciadoceridae* and *Phoridae* was marked by changes in the geometry of the wing veins. These are fundamentally related to vein R4+5 no longer reaching, or over-reaching, the wing tip (MCALPINE & MARTIN 1966).

The *Ironomyiidae* retain the plesiomorphic state, along with a stigma (bounded by the costa and the tips of the Sc and R1 veins). *Sciadoceridae* and *Phoridae*, however, both possess a shortened R4+5, a loss of the stigma and of the ending of the Sc in the costa. A similar change has occurred in some *Empidoidea* (e.g. Fig. 13), but in these cases the costa still extends to the tip of the M1+2. MCALPINE (1989) proposed the loss of the discal (discal medial) cell of the wing as the principal apomorphy distinguishing *Phoridae* from *Sciadoceridae*. He also proposed a reduced dm cell as an autapomorphy of the *Sciadoceridae*. Nobody doubts that the progressive simplification of the wing venation has been a major feature of the process leading to the evolutionary emergence of the *Phoridae*. Not surprisingly, therefore, the interpretation of the homologies of the very simplified phorid wing venation has been at the centre of the debates relating to the classification of the *Sciadoceridae*. A pivotal question

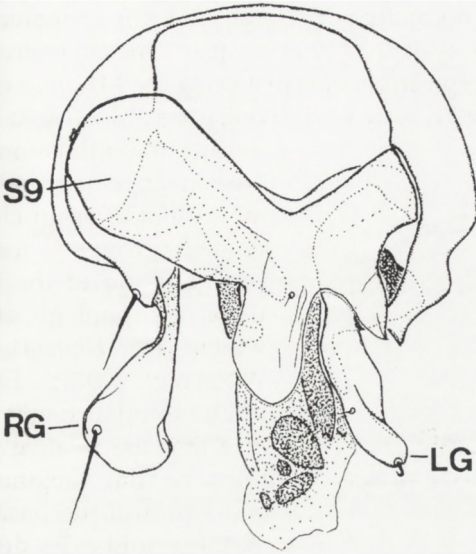


Fig. 11. *Chonocephalus blackithorum* male, hypopygium from below (S9 = sternite 9, LG, RG = left and right gonopods). Scale bar = 0.1 mm.

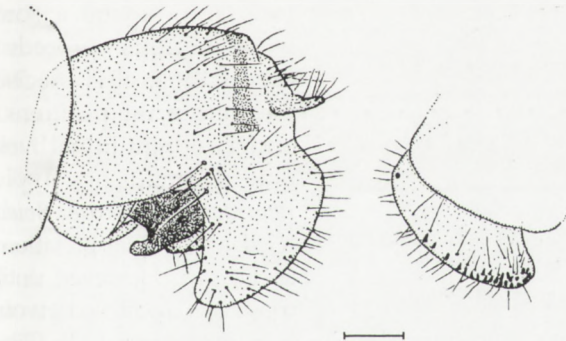
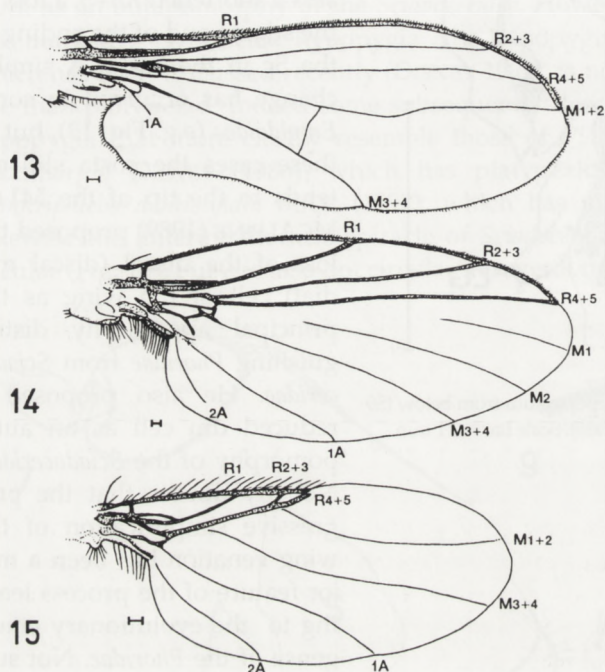


Fig. 12. *Xenotriphleba dentistylata* male, left face of hypopygium, with inner face of left surstylus to right. Scale bar = 0.1 mm.

is the homologies of the fourth and fifth longitudinal veins, the first two thin veins. TONNOIR (1926) regarded these as being the M1 and M2 in both *Phoridae* and *Sciadocera*. However, SCHMITZ (1929a) interpreted them as being the M1+2 and M3 in the *Phoridae*. By contrast he considered those of the *Sciadoceridae* to be the M1 and M2 (SCHMITZ 1929b). However, he subsequently reinterpreted those of the *Phoridae* as also being the M1 and M2 (SCHMITZ 1938). This interpretation prevailed until consideration of some mutants in *Phoridae* challenged it (DISNEY 1985, 1991; REEVES &

DISNEY 1999; DISNEY & MICHAILOVSKAYA 2000). These mutants include a forked vein 4, a cross vein linking veins 4 and 5 and the latter plus a complete discal cell. The interpretation that involves the fewest assumptions is that the genes required to allow the development of these states are ancestral genes that are normally not expressed because an upstream switching gene is normally not activated. When a mutation reverses this then the ancestral states may be expressed once again. The alternative line of evidence employed to support the interpretation of vein 4 being the M1 alone comes from consideration of the positions of the folds between the wing veins (MOSTOVSKI 1996),

despite the admission that "the arrangement of folds may differ even in closely related groups". Indeed, consideration of the functional morphology of the wings in *Diptera* (e.g. WOOTTON 1981; ENNOS 1989) would strongly indicate that the relative positions of the longitudinal veins control the positions of these folds. To deduce the homologies of the veins from the relative positions of the folds would, therefore, seem to be a somewhat curious procedure; especially as it is precisely the shift in the positions of critical longitudinal veins that distinguishes typical *Phoridae* from the *Sciadoceridae*. My interpretation is as Fig. 15. However, until a consensus is achieved it would



Figs 13–15. Proposed homologies of wing veins. 13 – *Dolichopus pennatus* MEIGEN (*Dolichopodidae*). 14 – *Sciadocera rufomaculata*. 15 – *Megaselia rufipes* (MEIGEN) (*Phoridae*). Scale bars = 0.1 mm.

seem best to concentrate on other putative apomorphies. The short robust costal cilia (Fig. 9) are probably a plesiomorphic feature.

McALPINE (1989) proposed the loss of the empodium as an autapomorphy of the *Sciadoceridae*. However, such losses are liable to occur independently in related taxa. Indeed McAlpine noted that this loss had also occurred in the *Lonchopteridae*. It has also occurred in some *Phoridae*. McAlpine also refers to the lack of a sperm pump and ejaculatory apodeme in the males and the unsclerotised spermathecae in the females in the *Phoridae*. However, BROWN (1992) pointed out that these two features are also characteristic of the *Sciadoceridae*. Furthermore, the single spermatheca in the phorid genus *Chonocephalus* is sclerotised (DISNEY 1986). Likewise McAlpine's reference to the

form of the antennal pedicel in *Sciadoceridae* (Fig. 7) as being unique, is contradicted by several genera of *Phoridae*. Also GRIMALDI and CUMMING (1999) proposed a dorsal arista of the third antennal segment (a composite segment termed the postpedicel by STUCKENBERG, 1999) as an autapomorphy of *Sciadoceridae* plus *Phoridae*. However, this apomorphy is not shared by many genera of *Phoridae*, which retain an apical arista. Apart from the reductions in the wing venation, BROWN (1992) cites the loss of the 'proscutellum' (in the sense of MCALPINE & MARTIN 1966; not the scutellum of the pronotum of most authors) as an autapomorphy of the *Phoridae*. This feature is a more or less well defined region at the rear of the scutum in some fossils assigned to the *Sciadoceridae*. It is certainly not readily apparent in *Sciadocera* (Fig. 2). I therefore endorse BROWN's (1992) comment on this character state, that "its usefulness is questionable". Despite this MOSTOVSKI (1999) uses this same feature in both his cladograms for various fossils. His defining autapomorphy for the *Phoridae* is the short fork of the wing vein Rs. However, some *Phoridae* have

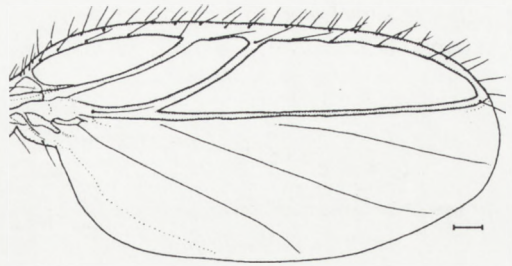


Fig. 16. *Dicranopteron palmasetorum* female, right wing. Scale bar = 0.1 mm.

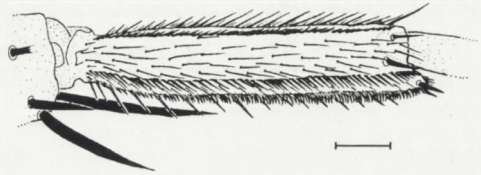


Fig. 17. *Triphleba collini* SCHMITZ male, anterior face of hind basitarsus. Scale bar = 0.1 mm.

an enormous fork, for example *Dicranopteron palmasetorum* DISNEY (DISNEY & KISTNER 1994) (Fig. 16). I suggest that the essential perception that emerges from the papers of MOSTOVSKI (1999) and GRIMALDI & CUMMING (1999) is that a number of fossil genera span the supposed gap between the *Sciadoceridae* and *Phoridae*.

By contrast with the wing characters, most of which amount to varying degrees of reduction and loss, and the even more dubious 'proscutellum' character, both *Sciadoceridae* and *Phoridae* possess longitudinal hair palisades on the hind basitarsus (Fig. 17). A few *Platypezidae* possess this feature. However, this family and the *Opetiidae* lack the enlarged conus of the antennal pedicel that characterises the rest of the *Aschiza* (DISNEY 1988, 1996). In practice *Phoridae*, including all the genera with flightless females, plus *Sciadoceridae* can be recognised by the combination of these two features (DISNEY 1994). If we allow for the convergent evolution of similar basitarsal hair palisades in a few *Platypezidae*, then this character constitutes a positive, neomorphic, autapomorphy of the *Sciadoceridae* plus *Phoridae* as a single monophylum.

CONCLUSION

No convincing synapomorphy characterises the *Sciadoceridae*. I therefore suggest that these genera comprise an assemblage of *Phoridae* that possess a mosaic of plesiomorphic

and apomorphic character states. This assemblage is probably paraphyletic or polyphyletic. I therefore formally propose the return of *Sciadocera* and *Archiphora* to the *Phoridae*, as originally proposed by TONNOIR (1926, 1934 – in FULLER 1934). In assigning fossils to the *Phoridae*, two critical autapomorphies are the possession of longitudinal hair palisades on the hind basitarsus and vein R4+5 ending before the wing tip.

ACKNOWLEDGEMENTS

My studies of *Phoridae* are funded by the Isaac Newton Trust (Trinity College, Cambridge).

REFERENCES

- ARILLO M. & MOSTOVSKI M. B. 1999. A new genus of *Prioriphorinae* (Diptera, *Phoridae*) from lower Cretaceous amber of Alava (Spain). *Studia dipt.* 6: 251–255.
- BROWN B. V. 1992. Generic revision of *Phoridae* of the Nearctic Region and phylogenetic classification of *Phoridae*, *Sciadoceridae* and *Ironomyiidae* (Diptera: *Phoridae*). *Mem. ent. Soc. Can.* 164: 1–144.
- BROWN B. V. 1995. Response to Disney. *J. nat. Hist.* 29: 259–264.
- BROWN B. V. & PIKE E. M. 1990. Three new fossil phorid flies (*Diptera: Phoridae*) from Canadian late Cretaceous amber. *Can. J. Sci.* 27: 845–848.
- BUCK M. 1997. A new genus and species of *Phoridae* (Diptera) from Central Europe with remarkably primitive male genitalia. *Ent. scand.* 28: 351–359.
- DISNEY R. H. L. 1985. Re-interpretation of the wing veins in the *Phoridae* (Diptera). *Entomologist's mon. Mag.* 121: 55–58.
- DISNEY R. H. L. 1986. Morphological and other observations on *Chonocephalus* (*Phoridae*) and phylogenetic implications for the *Cyclorrhapha* (Diptera). *J. Zool., Lond. (A)* 210: 77–87.
- DISNEY R. H. L. 1988. The form of articulation between the pedicel and first flagellar segment of the antenna in flies (Diptera). *Entomologist* 107: 99–103.
- DISNEY R. H. L. 1991. Support for the revised interpretation of the wing veins of *Phoridae* (Diptera). *Entomologist's mon. Mag.* 127: 73–76.
- DISNEY R. H. L. 1993. Mosaic evolution and outgroup comparisons. *J. nat. Hist.* 27: 1219–1221.
- DISNEY R. H. L. 1994. Scuttle Flies: The *Phoridae*. Chapman and Hall, London, xii + 467 pp.
- DISNEY R. H. L. 1996. Continuing the debate relating to the phylogenetic reconstruction of the *Phoridae* (Diptera). *G. it. Ent.* 7: 103–117 (1994). + (1997). *Note. G. it. Ent.* 7: 338 (1995).
- DISNEY R. H. L. 1999. A troublesome sibling species complex of scuttle flies (*Diptera: Phoridae*) revisited. *J. nat. Hist.* 33: 1159–1216.
- DISNEY R. H. L. & CUMMING M. S. 1992. Abolition of the *Alamirinae* and ultimate rejection of Wasmann's theory of hermaphroditism in *Termitoxeniinae* (Diptera, *Phoridae*). *Bonn. zool. Beitr.* 43: 145–154.
- DISNEY R. H. L. & KISTNER D. H. 1994. A new species of *Dicranopteron* (Diptera: *Phoridae*) associated with a termite (*Isoptera: Termitidae*) in Malaysia. *Sociobiology* 23: 315–320.
- DISNEY R. H. L. & KISTNER D. H. 1995. Revision of the Afrotropical *Termitoxeniinae* (Diptera: *Phoridae*). *Sociobiology* 26: 117–225.
- DISNEY R. H. L. & KISTNER D. H. 1997. Revision of the Oriental *Termitoxeniinae* (Diptera: *Phoridae*). *Sociobiology* 29: 1–118.
- DISNEY R. H. L. & MICHAILOVSKAYA M. V. 2000. New species of *Pseudacteon* COQUILLET (Diptera: *Phoridae*) from the Far East of Russia. *Fragm. faun.* 43: 35–45.
- ENNOS R. A. 1989. Comparative functional morphology of the wings of *Diptera*. *Zool. J. Linn. Soc.* 96: 27–47.
- FULLER M. E. 1934. The early stages of *Sciadocera rufomaculata* White (Dipt. *Phoridae*). *Proc. Linn. Soc. N. S. Wales* 59: 9–15.
- GRIMALDI D. 1989. The genus *Metopina* (Diptera: *Phoridae*) from Cretaceous and Tertiary ambers. *J. N. Y. ent. Soc.* 97: 65–72.

- GRIMALDI D. A. & CUMMING, J. M. 1999. Brachyceran *Diptera* in Cretaceous ambers and Mesozoic diversification in *Eremoneura*. *Bull. Am. Mus. Nat. Hist.*, N. Y. 239: 1–124.
- HENNIG W. 1964. Die Dipteren – Familie *Sciadoceridae* im Baltischen Bernstein (*Diptera: Cyclorhapha Aschiza*). *Stuttg. Beitr. Naturk.* 127: 1–10.
- HENNIG W. 1966. *Phylogenetic Systematics*. University of Illinois Press: London. xiii + 263 pp.
- MCALPINE J. F. 1989. Phylogeny and classification of *Muscomorpha*. In: MCALPINE J. F. and WOOD D. M. (eds), *Manual of Nearctic Diptera* Volume 3. Canada: Agriculture Canada Research Branch. 116: 1397–1518.
- MCALPINE J. F. & MARTIN J. E. H. 1966. Systematics of *Sciadoceridae* and relatives with descriptions of two new genera and species from Canadian amber and erection of family *Ironomyiidae* (*Diptera: Phoroidea*). *Can. Entomologist* 98: 527–544.
- MOORE J. & WILLMER P. 1997. Convergent evolution in invertebrates. *Biol. Rev.* 72: 1–60.
- MOSTOVSKI M. B. 1996. A new species of phoromorph Dipteran (*Diptera, Phoromorpha*) from the Upper Cretaceous of Eastern Siberia. *Palaeont. J.* 30: 436–439 (*Paleont. Zh.* 3: 69–72).
- MOSTOVSKI M. B. 1999. Curious *Phoridae* (*Insecta, Diptera*) found mainly in Cretaceous ambers. *Estudios Mus. Ciencias nat. Alava* 14 (Núm. esp. 2): 231–243.
- OLDROYD H. 1964. *The Natural History of Flies*. Wiedenfeld & Nicolson: London, xiv + 324 pp.
- REEVES W. K., DISNEY R. H. L. 1999. Taxonomy and biology of two Nearctic species of cavernicolous scuttle flies (*Diptera: Phoridae*). *Studia dipt.* 6: 207–218.
- SCHMITZ H. 1929a. *Revision der Phoriden*. Ferd. Dummlers: Berlin, 211 pp.
- SCHMITZ H. 1929b. *Diptera of Patagonia and South Chile*, based mainly on material in the British Museum (Nat. Hist.). Part VI. fasc. 1. *Sciadoceridae* and *Phoridae*. British Museum (Natural History): London, 42 pp.
- SCHMITZ H. 1938. *Phoridae*. In: LINDNER E. (ed.), *Die Fliegen der palaearktischen Region* 4 (33) (Lieferung 123): 1–64.
- SCHMITZ H. 1951. Myrmekophile und termitophile *Phoriden* (*Diptera*), von S. Patrizi und F. Meneghetti in Africa gesammelt. *Boll. Ist. Ent. Univ. Bologna* 18: 128–166.
- SIMPSON P., WOEHL R. & USUI K. 1999. The development and evolution of bristle patterns in *Diptera*. *Development* 126: 1349–1364.
- STUCKENBERG B. R. 1999. Antennal evolution in *Brachycera* (*Diptera*), with a reassessment of terminology relating to the flagellum. *Studia dipt.* 6: 33–48.
- TONNOIR A. L. 1923. Aperçu sur la Faune diptérienne de la Nouvelle Zelande. *Bull. Soc. ent. Belg.* 5: 91–100.
- TONNOIR A. L. 1926. A new and primitive sub-family of the *Phoridae* (*Dipt.*). *Rec. Canterbury Mus., Christchurch, N. Z.* 3: 31–38.
- VANE-WRIGHT R. I. 2000. On influence. In: FOREY P. L., GARDINER B. G. & HUMPHRIES C. J. (eds), *Colin Patterson (1933–1998) a celebration of his life*. *Linnean Special Issue* 2: 64–6.
- WHITE A. 1917. The *Diptera-Brachycera* of Tasmania, Part III. Families *Asilidae, Bombyliidae, Empididae, Dolichopodidae*, and *Phoridae*. *Pap. Proc. R.Soc. (Tasmania)* 1916: 148–266.
- WOOTTON R. J. 1981. Support and deformability in insect wings. *J. Zool., Lond.* 193: 447–468.
- YEATES D. K. & WIEGMANN B. M. 1999. Congruence and controversy: toward a higher-level phylogeny of *Diptera*. *Ann. Rev. Ent.* 44: 397–428.

STRESZCZENIE

[Tytuł: Rewizja rodziny *Sciadoceridae* (*Diptera*)]

Sciadoceidae to rodzina o dyskutowanej pozycji taksonomicznej. Zaliczane do niej gatunki: tasmański *Sciadocera rufomaculata* WHITE i południowoamerykański *Archiphora patagonica* SCHMITZ włączano do *Empididae*, *Platypezidae*, *Phoridae* oraz wydzielano w odrębną rodzinę. W obecnej pracy rodzinę tę poddano powtórnej analizie, w wyniku której traci dotychczasowy status, a tworzące ją gatunki ponownie zostały włączone do rodziny *Phoridae*.