BOOK REVIEW

MANUAL OF NEARCTIC DIPTERA. Volume 3. J. F. McAlpine and D.M. Wood (editors). 1989. Minister of Supply and Services Canada. vi + pp. 1333-1581. $75.95 (Canada), US $91.15 (outside Canada).

This third (and last) volume of the Manual of Nearctic Diptera contains chapters 114-116 on the phylogeny and classification of subgroups of the Diptera, together with two pages of corrections to volumes 1 and 2 and a very long composite index of the taxonomic names of Diptera and morphological terms used in all three volumes. This third volume is mainly illustrated by phylogeny diagrams (the reader being referred to the previous volumes for morphological illustrations), but a few important new illustrations of larval head structure illustrate chapter 114.

Until publication of this work the most comprehensive modern reviews of the phylogeny of the Diptera were contained in various works of B. B. Rohdendorf and W. Hennig, both of whom died in the seventies. The work of both authors has certain defects. Rohdendorf's system contained much that was arbitrary and not in accordance with cladistic methodology (which he rejected). Hennig pioneered cladistic methods, but in his later years wrote too quickly without sufficient morphological studies; as a result his later works contain much that is superficial or erroneous. The authors of Manual 3 take Hennig's work as the main starting point of their studies, but find much that is in need of revision. I agree that extensive revision of Hennig's system is needed, and welcome the publication of this work which will hopefully stimulate renewed interest in this field of fundamental importance to the whole of dipterology.

Of course this is not to say that I agree with everything proposed, and the authors themselves recognize that there are many areas of the system where only tentative proposals can be offered. In this review I will comment on the validity of new proposals to the extent that this is possible on the basis of existing literature and my previous studies in this field. But there are too many new observations for me to try and check them against insects in the context of writing a review. Evaluation of some new proposals will require a period of years, as the literature develops.

Before discussing each chapter, there are two points of a formal nomenclatural nature and one of a methodological nature which need comment.

Some of the superfamily names used in this work, especially within the Schizophora, are contrary to longstanding usage, e.g. Sciaroidea (for Mycetophiloidea), Ephydroidea (for Drosophiloidea), Carnoidea (for Chloropoidea), Nerioidea (for Micropezoidea) and Oestroidea (for Tachinoidea). It is explained that this is an application of Article 36(a) of the 1985 International Code of Zoological Nomenclature, in which it is stated that "a name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date ... at other ranks in the family group". Thus, the oldest family-group name is used, even if this was previously used only as a family, not as a superfamily, name. It remains to be seen whether other dipterists will accept these changes, or whether reference will be made to the Commission to conserve long-accepted superfamily names. The question of priority of superfamily names was given scant consideration in previous literature, since the dates of first proposal were not known for many of the older family-group names. This situation has changed as a result of bibliographic studies by C. W. Sabrosky, who gave advice to the authors on this matter. If we are to strictly apply the priority principle to superfamily names in the future, it is essential that Sabrosky's work be published.

A second formal question concerns the formation of names for higher taxa (above the family group). Such names are not regulated by the Code. The authors of the Manual have made wide use of the suffix -morpha attached to the root of generic names (following the precedent of Rohdendorf), even in cases where other names are well established and have priority (e.g. Muscomorpha instead of Cyclorrhapha). In my opinion this extension of the principle upon which family-group names are formed to higher levels is misguided, and will cause instability because changes in suffices have to be made whenever new research causes the relative ranking of groups to be revised. Therefore I intend to continue to use names formed upon other principles when these have priority, and to apply names formed by adding suffices to generic roots in their original senses irrespective of ranking changes. In this connection it should be noted that names formed with the suffix -formia have priority over many of those formed with the suffix -morpha.

I have found one difficulty regarding the phylogeny diagrams in this volume. All diagrams are of the type in which characters assumed to be autapomorphies are ascribed to each branch of a dendrogram. This type of illustration is of course widely used and valid. However, there is a difficulty when many of the characters used are subject to homoplasy and the interpretation of their distribution is debatable. In such cases it is necessary to know the complete distribution of the characters in order to be able to judge the validity of proposed groupings. This is especially a problem in the treatment of "Acalyptratae", in which many groupings are based solely on characters known to be subject to homoplasy. I recommend that in future treatments diagrams with bars across showing the total distribution of characters should also be included, so that readers can retrieve this information directly from the illustration without the need to search the text and other literature for information on the wider distribution of characters.

Chapter 114. Phylogeny and Classification of the Nematocera (by D. M. Wood and A. Borkent)

This chapter includes discussion of the origin of the Diptera, as well as the relationships between the groups traditionally included in the "Nematocera" (probably a paraphyletic grouping). A system of seven infraorders is proposed (Tipulomorpha, Blephariceromorpha, Axymyiomorpha, Bibionomorpha, Psychodomorpha, Ptychopteromorpha and Culicomorpha). The major innovation of this system in comparison with Hennig's (1973) treatment is the new concept of Psychodomorpha, containing the Trichoceridae (removed from Tipulomorpha) and four families removed from Bibionomorpha, the Perissommatidae, Anisopodidae, Scatopsidae and Synneuridae (the last should be called Canthyloscelididae on grounds of priority). Groups included in Psychodomorpha by Hennig (1973) but removed by Wood & Borkent are the Blephariceridae, Deuterophlebiidae and Nymphomyiidae (grouped as infraorder Blephariceromorpha) and the Ptychopteridae and Tanyderidae (grouped as infraorder Ptychopteromorpha). The enigmatic family Axymyiidae (formerly in Bibionomorpha) is also segregated as the new infraorder Axymyiomorpha.

In the discussion of the origin of the Diptera, Wood and Borkent advance the hypothesis that the Nannochoristidae are the sister-group of the Diptera + Siphonaptera despite certain contrary evidence. I do not find the evidence they offer for regarding the Siphonaptera as the sister-group of the Diptera (larval thoracic legs absent, pupal mandibles immovable) convincing, as these characters are subject to homoplasy. There is a series of characters which suggests that the

Siphonaptera are more closely related to the Mecoptera, especially the structure of the spermatozoa (see Christensen 1975, 1981). The question of the relationships of the Nannochoristidae is addressed in greater detail in a new work by Willmann (1989), which also redescribes and reinterprets Mesozoic fossils relevant to the origin of the Diptera. Willmann's outstanding work will obviously provide the main starting point for future investigations of the origin and relationships of the Diptera as well as Mecoptera. Willmann treats the Nannochoristidae as the sister-group of all other Mecoptera in the recent fauna, while leaving open the question of the position of the Siphonaptera within the Antliophora (= Diptera + Mecoptera + Siphonaptera).

Although Wood & Borkent's opinion that the Nannochoristidae should be removed from the Mecoptera because they are more closely related to the Siphonaptera + Diptera seems unlikely, it should be noted that use of the Nannochoristidae as an outgroup for assessing character polarity in the Diptera is not in contention. The Nannochoristidae are recognized by Willmann and other mecopterists as the relatively plesiomorphous subgroup of the Mecoptera in most respects. They remain an important basis of outgroup comparison in studies of relationships within the Diptera and Siphonaptera, irrespective of what view is taken of their position within the Antliophora.

The changes in the content of the infraorders of "Nematocera" proposed by Wood & Borkent in my opinion represent a considerable advance over the systems proposed by Hennig and Rohdendorf. Their work should provide one of the main starting points for further investigations in this field. My main criticism is that the changes do not go far enough.

The new concept of Psychodomorpha is justified by Wood & Borkent on the basis of a complex of characters (nos. 38-42) of the larval head (labrum with posteriorly pointed hairs, "premandibles" dentate or pectinate, torma articulating with dorsal labral sclerite, mandible moving in nearly vertical plane and striking hypostoma, mandible chela-shaped). I support the view that this character complex is apomorphous and characterizes the groundplan of a major subgroup of the Diptera. However, I think that the group to whose groundplan these characters belong may be more extensive than Wood & Borkent's Psychodomorpha. There are grounds for suggesting that the larval head structures of the groups called Tipulomorpha, Ptychopteromorpha and Culicomorpha by Wood & Borkent represent further modifications of the same groundplan condition.

Wood & Borkent show the Tipulomorpha (Tipulidae *s.l.*) as the sister-group of all other "Nematocera" on their phylogeny diagram, the grouping of all other Nematocera being supported by the apomorphous state of character 1 (prostheca arising directly from median surface of larval mandible). The opposing state (mandible with prostheca on articulated lobe) is assumed to belong to the groundplan of the Tipulomorpha (and of the Diptera as a whole) on the basis of outgroup comparison with Nannochoristidae. I am sceptical whether the presence of an articulated prosthecal lobe in *Tipula* is a genuinely plesiomorphous character. The larval head capsule of *Tipula* is of a highly modified type with the posterior margins of the capsule strongly indented. The interpretation that an articulated prosthecal lobe belongs to the groundplan of the Tipulomorpha will only be convincing, if it is also shown to be present in other groups of Tipulomorpha with less modified head capsule. I favour a quite different interpretation of the relationships of the Tipulidae *s.l.*

It appears to me that the apparent synapomorphies between Tipulidae (*s.l.*) and Trichoceridae (especially reduction of the male cerci, development of gonopods from posterolateral zones of proliferation, female cerci with single article, only 3 branches of radial sector reaching wing margin, forwards displacement of distal section of m_{1+2}) cannot be dismissed as due to homoplasy. The view that the Trichoceridae and Tipulidae *s.l.* are sister-groups is reconcilable with Wood & Borkent's justified emphasis on the synapomorphies between the larval head structure of Trichoceridae and that of other Psychodomorpha, if we assume that the considerable diversity of head structure shown by the larvae of Tipulidae *s.l.* represents a transformation series from a groundplan structure similar to that of *Trichocera*. On this interpretation the horizontal plane of movement of the mandibles of some Tipulidae *s.l.* is assumed to be secondary. Final resolution of how the polarity of characters of the larval head structure in Tipulidae *s.l.* should be interpreted must obviously await more detailed comparative morphological studies than we presently have available. Meanwhile, readers should note that Wood & Borkent's interpretation of the position of the Tipulidae *s.l.* as the sister-group of all other "Nematocera" is poorly supported, and other interpretations are possible. I would place the Tipulidae *s.l.* within their Psychodomorpha as the sister-group of the Trichoceridae.

The grouping of Ptychopteridae and Tanyderidae (as Ptychopteromorpha) following Hennig (1973) is supported only by character 52 (male tarsal claws folding against basal swelling on tarsomere 4), a character found in the Tanyderidae and *Ptychoptera* (but not in other Ptychopteridae). Whether this feature belongs to the groundplan of the Ptychopteridae is doubtful, since it has not been found in any of the Mesozoic Ptychopteroidea (information from N. S. Kalugina). In my opinion the relationships of the Ptychopteroidea (Ptychopteridae and related fossil groups) and Tanyderidae should be considered separately. Both groups are archaic, represented in the earliest Mesozoic fossil assemblages. In their discussion Wood & Borkent present new evidence that the Ptychopteridae alone may be the sister-group of the Culicomorpha based on the structure of the larval labrum and mandibles. This seems to me more convincing evidence of the relationships of the Ptychopteridae than the dubious tarsal character. At the same time we must not lose sight of the fact that the larval head structures of the Tanyderidae, Ptychopteridae and Culicomorpha may be derived from the same groundplan structure as that postulated for the groundplan of the Psychodomorpha. Wood & Borkent do in fact unite these groups at a higher level on their phylogeny diagram, but do not name the more inclusive group.

The inclusion of the Scatopsoidea (Scatopsidae + Canthyloscelididae) in the Psychodomorpha on the basis of larval head structure seems to me fully justified. Wood & Borkent place this group as the sister-group of the Anisopodidae. However, I am aware of one unique character which suggests that they may be the sister-group of the Psychodidae. This is that the 8th pair of abdominal (the larval hind) spiracles lacking in most adult Diptera persist in the adult male but are displaced to a dorsal position within the 9th tergite (epandrium). Further investigation of the position of the Scatopsoidea within the Psychodomorpha is needed. The transference of the Perissommatidae to the Psychodomorpha based on new observations of the larval head structure also appears fully justified. Krivosheina (1988) has also recently examined the larvae of Perissommatidae, and concludes that they "have characters relating them variously with the Scatopsidae, Trichoceridae, and to a considerable degree with the Psychodidae" (*i.e.* with families included by Wood & Borkent in the Psychodomorpha). It seems that there was no contact between Krivosheina and Wood & Borkent, but both reached similar conclusions independently.

Wood & Borkent expand the concept of Blephariceromorpha (Blephariceridae + Deuterophlebiidae) to include also the Nymphomyiidae. This is controversial, and rests on interpreting the abdominal prolegs of larval Deuterophlebiidae and Nymphomyiidae as of common origin and belonging to the groundplan of the Blephariceromorpha. Unfortunately, the development of prolegs is subject to much homoplasy in Diptera, so I do not have confidence in this character in isolation. In Rohdendorf's (1964) system the Nymphomyiidae (as Archidiptera) were considered the sister-group of all other recent Diptera, a view which is best justified by the primitive structure of the adult nervous system (retaining 8 separate ganglia, as in larvae). Wood & Borkent argue that this character may be neotenous, a possibility which certainly cannot be excluded. The position of the Nymphomyiidae remains in doubt. The two interpretations currently held are both essentially based on the distribution of single characters. Further morphological studies are needed, so that additional evidence can be brought to bear on the problem.

The treatment of the Bibionomorpha is a weak part of Wood & Borkent's work, and no constitutive (autapomorphous) characters of this group are suggested. After removal of the heterogenous elements included by previous authors, the Bibionomorpha in Wood & Borkent's sense consists of two certainly monophyletic groups: the Pachyneuroidea + Bibionoidea (which I would amalgamate) and the Sciaroidea. These groups have been closely associated in all recent systems and may well be monophyletic, but a critical assessment is still impeded by lack of sufficiently detailed studies of primitive Sciaroidea (especially Ditomyiidae). The monophyly of the Pachyneuroidea + Bibionoidea is demonstrated by the synapomorphous structure of the larval labium and hypopharynx, which Wood & Borkent do not discuss.

The recognition of Axymyiidae as a group of high rank (Axymyiomorpha) is probably the best treatment on present information, since there are no convincing grounds for including the group within any other infraorder. Krivosheina (1989), who has made special studies of this group, has also accepted the concept of Axymyiomorpha.

The strongest part of Wood & Borkent's work is no doubt the treatment of the Culicomorpha, a group on which both authors have worked for many years. I agree with them that the content of this group is no longer contentious. Their discussion is authoritative and will provide a sound basis for future studies.

Chapter 115. Phylogeny and classification of the "Orthorrhaphous" Brachycera (By N.E. Woodley)

This chapter treats all Brachycera except the Cyclorrhapha (= Muscoidea in the sense of this chapter, Muscomorpha in the sense of chapter 116). Four infraorders are recognized, the Xylophagomorpha, Stratiomyomorpha, Tabanomorpha and Muscomorpha (in a new wide sense, different from the usage in chapter 116). The different usages of the same names in the two chapters is confusing, and well illustrates how the use of suffices to denote relative ranking causes instability.

Woodley's discussion is generally sound, and I do not find much to disagree with. But I think that his Xylophagomorpha and Tabanomorpha can be combined at infraordinal level, thus reducing the number of infraorders to three. I base this suggestion on the structure of the male genitalia in the Coenomyiinae (Xylophagidae), which agrees substantially with that of Rhagionidae (Tabanomorpha). I infer from the work of Nagatomi (1984) that there is a major subgroup of the Brachycera corresponding to the Xylophagomorpha + Tabanomorpha *sensu* Woodley characterized by fusion of the ejaculatory apodeme with the base of the aedeagus and sheathing of the aedeagus and gonites ("tines") by a dorsal and pair of lateral/ventral processes.

The Stratiomyomorpha should probably also include the Pantophthalmidae, listed by Woodley as *incertae sedis*. The distal parts of the powerful mouthhooks of pantophthalmid larvae bear palpi, indicating that they are of maxillary origin as in the Stratiomyidae and Xylomyidae. Also the structure of the male genitalia described by Nagatomi (1984) is incompatible with inclusion of this family in the Xylophagomorpha + Tabanomorpha.

Regarding the genera *Exeretoneura* and *Heterostomus*, also listed as *incertae sedis* by Woodley, Nagatomi's descriptions of the male genitalia suggest that both belong somewhere in the Xylophagomorpha + Tabanomorpha. Woodley's placement in the vicinity of Xylophagidae seems appropriate pending further studies.

More enigmatic is the position of the Vermileonidae, listed by Woodley as a family *incertae sedis* within the Tabanomorpha. I agree with Woodley that this family cannot belong in the Asiloidea, where it was placed by Teskey in Volume 1 of this Manual. If Kovalev (unpublished MSS) is correct in referring the lower Jurassic *Protobrachyceron* (the earliest described fossil brachyceron) to this family, then it is possible that it merits higher rank in the system. Woodley's proposal to place the Vermileonidae provisionally in the Tabanomorpha seems reasonable pending further studies.

The infraorder Muscomorpha is proposed by Woodley in a new sense, inclusive of the Nemestrinoidea, Asiloidea, Empidoidea and Muscoidea. The concept seems to me well justified, but not the nomenclature. The numerous different senses in which the name Muscomorpha has been used cause confusion. A new name would have been preferable. The superfamilies Asiloidea, Empidoidea and Muscoidea are ranked more highly by most other authors (including McAlpine in chapter 116), who hence use other suffices if they believe in forming names of higher taxa in this way. I recommend forgetting about rank and suffices and using the earliest appropriate names (Pleroneura, Orthogenya and Cyclorrhapha). These names can remain applied to the same groups, irrespective of different relative ranking by different authors.

Woodley (correctly in my opinion) restricts the concept of Nemestrinoidea to the Nemestrinidae + Acroceridae, referring the Bombyliidae to the Pleroneura ("Asiloidea"). Some previous authors, including Hennig (1973), placed the latter family in the Nemestrinoidea on account of the hypermetamorphic larval development, but subsequent morphological studies leave no doubt that it belongs to the Pleroneura. Woodley considers that all Muscomorpha except Nemestrinoidea form a monophyletic group characterized by a setiform empodium. I agree with this view, and suggest that we follow the precedent of Lameere (1906) in applying the name Heterodactyla to this group.

In his phylogeny diagram Woodley shows a trichotomous subdivision of the Heterodactyla into Asiloidea (Pleroneura), Empidoidea (Orthogenya) and Muscoidea (Cyclorrhapha). This fence-sitting on the issue of the validity of the concept Eremoneura (Orthogenya + Cyclorrhapha) presumably reflects the fact that he has not worked personally on these groups and does not wish to involve himself in controversy. At the end of the chapter he quotes verbatim the characterization of the Eremoneura which I gave in 1984, with the disclaimer that "I cannot personally evaluate these characters and their distributions within the Brachycera". I suggest that these characters and their distributions have already been evaluated, and that the grounds for grouping the Orthogenya with the Cyclorrhapha are in fact overwhelming. This grouping is indicated by numerous autapomorphies involving the structure of the male and female terminalia, the wing venation and the chaetotaxy, probably also by the larval head structure (but interpretation of the character sequence in larvae remains problematical due to inadequate information on the larvae of Orthogenya). Woodley offers two characters in support of the traditional grouping of the Orthogenya with the Pleroneura; presence of three antennal flagellomeres, and presence of acanthophorites (spinous halves of 10th tergite) in the female. In my opinion neither of these characters provides reliable evidence for such a relationship. Presence of three (as in most Orthogenya) or four (as in most Cyclorrhapha) flagellomeres does not indicate that the aristate antennae in these groups originated independently. Several cases are now known in which the change from a 3- to 4-articled flagellum or vice versa must have occurred. Within the Orthogenya, 4-articled flagella are certainly known in *Dryodromia* and *Meghyperus*; within the Cyclorrhapha 3-articled flagella are known in *Opetia* (the probable sister-group of all other Cyclorrhapha) and in one subgroup of Diopsidae. Thus there is no fundamental difference between the aristate antennae of Orthogenya and Cyclorrhapha. Development of spines on the female 10th tergite is also a character prone to homoplasy. For instance, my studies indicate that such spines have evolved several times within the family Anthomyiidae alone. So even if more complete information causes us to revise the prevailing opinion that acanthophorites do not belong to the groundplan of the Orthogenya, I fail to see how this could cast doubt on the validity of the concept of Eremoneura. In this connection I draw attention to the recent thesis by Wiegmann (1989), who sees the problem not as determining whether the Eremoneura are monophyletic but whether the Orthogenya are monophyletic or paraphyletic with respect to the Cyclorrhapha.

Chapter 116. Phylogeny and Classification of the Muscomorpha

(by J. F. McAlpine)

The Muscomorpha in the sense of this chapter is the group normally called Cyclorrhapha, here ranked as an infraorder (both naming and ranking being inconsistent with the previous chapter). In order to avoid confusion I shall refer to this group as the Cyclorrhapha. This chapter is the longest of the three, and sets out J. F. McAlpine's views on the origins of the Cyclorrhapha and the relationships between included families in far more detail than previously available. I welcome its publication as a major contribution to this field, although I do not accept the author's views regarding the origin of the Cyclorrhapha and homologization of the male genitalia and proctiger. McAlpine's system of superfamilies and families contains a variety of differences from previous treatments by me (Griffiths [1972]) and by Hennig (1973, with modifications in subsequent papers). Some of the changes are clearly justified, a few seem to me retrograde.

I included extensive comments on McAlpine's interpretation of the homologies of the male genitalia and proctiger in my review of Volume 1 of this Manual (Griffiths 1981). His views seem little changed, so the criticisms remain. But it does not seem necessary to occupy space in this review by repeating them. Readers who want a summary of my views may refer to that review and also to my characterization of the Eremoneura (Griffiths [1984]) quoted at the end of Chapter 115. Of course the description of some of the characters used by McAlpine to characterize the groundplan of the Cyclorrhapha is affected by how homologies are interpreted, and I would describe some of the genitalia characters quite differently. Despite disagreements over the interpretation of certain characters, I recognize McAlpine's long and detailed review of the groundplan characters of the Cyclorrhapha as an important contribution and certainly justifying his conclusion that the monophyly of this group is "one of the best substantiated and most universally accepted assumptions in the phylogeny of the Diptera".

McAlpine goes on to present an interesting argument that the Cyclorrhapha are more closely related to Stratiomyoidea (= Stratiomyomorpha in the sense of chapter 115) than to the Orthogenya or Pleroneura. In my opinion this cannot be correct in view of the overwhelming evidence for the monophyly of the Eremoneura (Orthogenya + Cyclorrhapha). I offer the following comments on the list of 12 suggested synapomorphies: The first five characters involve alleged synapomorphies in the larval head structure and feeding mechanism. However, Schremmer (1951) established that the mouthparts of larval Stratiomyoidea are of a fundamentally different type from those of all other Brachycera (including Cyclorrhapha) with the palpus-bearing part of the maxilla involved in the formation of the mouthhooks. Characters 8 and 9 can be dismissed also. The presence of a cone-shaped condyle inserted into the base of the first flagellomere is not a groundplan character of the Cyclorrhapha. Nor is the first flagellomere of Cyclorrhapha of composite origin as in some Stratiomyoidea. Characters 7, 10 and 11 are inconclusive, since not confined to the Stratiomyoidea and Cyclorrhapha. There remain only two characters (6 and 12): formation of a puparium, and male with ejaculatory apodeme free from aedeagus and body wall. The first feature is found only in Stratiomyidae among the Stratiomyoidea, where it is normally assumed to have evolved independently of the Cyclorrhapha. The ejaculatory apodeme character requires clarification. The ejaculatory apodeme is primitively a separate sclerite in Diptera, but connected by muscles to some part of the outer body wall around the base of the aedeagus. The apomorphous modification in Cyclorrhapha is that the muscles on this apodeme connect only to the walls of the ejaculatory bulb, which has allowed the apodeme to become withdrawn from the base of the aedeagus. A similar modification is reported to have occurred in Stratiomyidae, but no detailed morphological description is available. Nor is it known whether a free ejaculatory apodeme belongs to the groundplan of the Stratiomyoidea. Even if the condition in Stratiomyidae proves to be the same as in Cyclorrhapha, I think that homoplastic modification will have to be assumed in view of the extensive evidence for the monophyly of the Eremoneura. A free ejaculatory apodeme also has evolved independently in some Scatopsidae.

McAlpine accepts the traditional division between Aschiza and Schizophora as the primary subdivision of the Cyclorrhapha. The recent suggestion that *Opetia* (Opetiidae) may be the sister-group of all other Cyclorrhapha unfortunately is not discussed. Although the larvae of *Opetia* are unknown, Wiegmann (1989) points out that the lack of pupal muscle plaques on the adult abdomen indicates that the pupa is contained within a puparium. Thus there seems no possibility that *Opetia* is misplaced in the Cyclorrhapha. Either it is the sister-group of all other Cyclorrhapha, or its lack of hypopygial rotation is secondary. Presumably McAlpine holds the latter opinion, since he lists Opetiidae as a synonym of Platypezidae.

If we accept that *Opetia* is probably the sister-group of all other Cyclorrhapha, the question arises whether the Aschiza exclusive of *Opetia* form a monophyletic group. The evidence in favour of this interpretation according to McAlpine's extensive tabulation of the "character states in ground plans of Aschiza and Schizophora" is fusion of the larval hypopharyngeal and tentopharyngeal sclerites and enlargement of the pupal respiratory horns. On the other hand it may be pointed out that the immature stages of some families of Aschiza (especially Platypezidae) are poorly studied, so the existence of these synapomorphies needs confirmation. An equally plausible hypothesis is that the Platypezidae are the sister-group of all other Cyclorrhapha (exclusive of *Opetia*), since only in platypezids is hypopygial rotation partly reversible. Pending further studies I think we should keep an open mind.

It is interesting that McAlpine regards the Lonchopteridae as the sister-group of the group usually called Hypocera or Phoridea (Ironomyiidae + Sciadoceridae/Phoridae). Formerly (Griffiths 1972) I followed the opinion that the Lonchopteridae (= Acroptera, Anatriata) are the sister-group of all other Cyclorrhapha (Atriata), but now regard this as improbable. The sole apomorphous character upon which McAlpine bases his grouping of the Lonchopteridae with the Phoridea is the dichoptic condition in males. However, the apparently synapomorphous structure of the male postabdomen (loss of 7th tergite, 7th sternite and inverted 8th tergite) also supports this grouping. These sclerites are present in the groundplan of all other subgroups of Cyclorrhapha except *Opetia* . The position of the cleavage lines on the puparium may also represent a synapomorphy of the Lonchopteridae and Phoridea. McAlpine interprets the pattern in Lonchopteridae as closest to the groundplan of the Cyclorrhapha, but it is more parsimonious in terms of his phylogeny diagram to interpret is as apomorphous. In all other Cyclorrhapha the operculum which is broken off when the adult emerges includes the dorsal half of the thoracic segments of the puparium. McAlpine places the Platypezidae as the sister-group of the Lonchopteridae + Phoridea (forming the superfamily Platypezoidea), but I regard this with scepticism. He justifies this concept of Platypezoidea mainly on the basis of chaetotaxy. However, the chaetotactic characters may not be apomorphous, since the reduced chaetotaxy of the Syrphoidea is surely secondary. Some of the setae in question (such as ocellar setae) belong to the groundplan of the Cyclorrhapha, if not of the Eremoneura as a whole. The relationships between the Platypezidae and other Cyclorrhapha remain controversial and in need of further study.

The treatment of the families of Schizophora is long and detailed. McAlpine follows the traditional subdivision of this group into the Acalyptratae and Calyptratae, rejecting my criticism of the former as a residual paraphyletic group (Griffiths 1972). I have checked the apomorphous character states listed in the extensive table of "character states in ground plans of Acalyptratae and Calyptratae" and do not find the suggested apomorphies of the former convincing. There is no groundplan difference in the development of the pupal respiratory horn, which pierces the wall of the puparium in Heleomyzidae as well as in many Calyptratae. Since there are several groups with holoptic male eyes also in the Acalyptratae, it cannot be assumed that dichopticism belongs to the groundplan of this group; and in any case the change from a holoptic to dichoptic condition is very prone to homoplasy. Presutural dorsocentral and postsutural acrostichal setae are both present in some Acalyptratae (e.g. Agromyzidae), so I am sceptical whether the absence of these setae can be ascribed to the groundplan. Some other chaetotactic characters suggested (lower surface of scutellum bare, latepimeron bare, meron bare, laterotergite bare) seem to me trivial, and I cannot accept them as significant without more information on their distribution. The relative size of the lower calypter is prone to variation both in Acalyptratae and Calyptratae, and I know of no basis in terms of outgroup comparison for inferring that possession of a relatively large lower calypter is the groundplan condition of the Schizophora. Only the two characters of the female reproductive system listed at the end of McAlpine's table represent major structural differences. But I doubt that their distribution validates the concept of Acalyptratae. Possession of a common duct by 2 of the 3 spermathecae is in my opinion an autapomorphy of the Cyclorrhapha exclusive of *Opetia*, not of the Acalyptratae alone, and certainly belongs to the groundplan of the Calyptratae also (possession of 3 spermathecae with 3 separate ducts in part of the Oestroidea being secondary). Information on the arrangement of spermathecae in the families of "Aschiza" is meagre, but at least in some Phoridae there are 3 spermathecae of which 2 share a common duct (information from B. V. Brown). The question of the ventral receptacle requires further study. Such a structure is certainly widespread in the "Acalyptratae", but the information on non-sclerotized parts of the female reproductive system in other Cyclorrhapha seems to me too meagre for us to determine whether or not homologous structures occur.

The basic subdivision of the Schizophora remains controversial. In my 1972 book I subdivided this group into 5 superfamilies (Lonchaeoidea, Lauxanioidea, Drosophiloidea, Nothyboidea and Muscoidea) mainly on the basis of the structure of the male postabdomen. Subsequently the description of *Morgea* (McAlpine 1981) has satisfied me that the Lonchaeoidea belong within what I called the "Tephritidae family-group" (Tephritoidea in McAlpine's sense) within the Muscoidea in my sense. McAlpine's remarks on the Lauxanioidea and the families I included in the Nothyboidea indicate that he believes that the male postabdominal structure of these groups too is derived from the muscoid type. I have not seen some of the insects upon which his remarks are based, so refrain from agreeing or disagreeing with him at this time. However, if it is confirmed that what I called the muscoid type of postabdominal structure (with asymmetrically reduced 7th tergite) is also basic to the Lauxanioidea and Nothyboidea, this would leave the Ephydroidea (Drosophiloidea) as the sister-group of all other Schizophora. For further discussion of the fundamental differences between the male postabdominal structure and development in the Ephydroidea and Muscoidea (in my sense) see pages 81-83 of that book (Griffiths 1972).

I have the following comments on the treatment of particular superfamilies of "Acalyptratae". They have to be brief in order to contain the length of this review.

The treatment of the first superfamily, Nerioidea (= Micropezoidea) has my support. This grouping has been accepted by all recent authors.

The "Diopsoidea" appear to me to be an assemblage of heterogenous long-bodied forms. For the Diopsidae and its close relatives Syringogastridae and Centrioncidae, the new work of Feijen (1989) gives a more detailed and up-to-date treatment. Feijen treats these families as monophyletic (grouped as the prefamily Diopsioinea). The Megamerinidae are a possible sister-group of the Diopsioinea, but the family is too poorly studied for a firm opinion to be given. Whether the further relationships of the Megamerinidae and Diopsioinea are with the Nothybidae, as McAlpine suggests, or with the Sciomyzoidea (as suggested in my 1972 book) should be addressed in future studies. Two other families included by McAlpine in the "Diopsoidea", the Tanypezidae (including Strongylophthalmyiidae) and Psilidae, have elongate ovipositors with partially fused cerci and may belong to or be closely related to the Tephritoidea (see below).

McAlpine recognizes the Conopoidea (Conopidae *s.l.*) as closely related to the Tephritoidea, in agreement with my opinion (Griffiths 1972).

The concept of Tephritoidea proposed by McAlpine is equivalent to the Tephritidae family-group of my 1972 book with the addition of the Lonchaeidae. This inclusion is justified, but I think that the Cryptochetidae should also be included. McAlpine places the Cryptochetidae as the sister-group of the Chloropidae, *i.e.* within the group Milichiidae + Chloropidae characterized by reduced spermathecae with long fine ducts. This is wrong, because the female reproductive system in Cryptochetidae is not of that type. On present information I continue to regard the Cryptochetidae as probably derived from a lonchaeid-like ancestor and would include them in Tephritoidea. But I agree with the exclusion of *Librella* from the Cryptochetidae for the reasons given by McAlpine.

In connection with the Cryptochetidae, I was astonished to read on page 1406 that I mistook the female for the male terminalia of *Cryptochetum nipponense* Tokunaga in my 1972 book. Evidently this is a reference to the unfounded claim by D. K. McAlpine (1976) that both I and Okada (1956) had mistaken the sexes of this species. For the record, the mistake was D. K. McAlpine's, as anyone can confirm by reviewing other literature on this group. For instance, Hennig's (1937) figures of the male terminalia of *C. buccatum* Hendel are quite similar to my figures of *C. nipponense* Tokunaga.

While McAlpine's concept of Tephritoidea is clearly an advance, I suggest that there may be additional families which belong in this group: for instance, the Carnidae. The structure of *Neomeoneurites* Hennig (1972) casts doubt on the traditional grouping of this family with the Milichiidae + Chloropidae. The structure of both the male and female terminalia in *Neomeoneurites* (long coiled aedeagus, extremely long ovipositor bearing fused cerci) indicate that the Carnidae belong to the Tephritoidea. Other groups which should be reviewed for possible inclusion in the Tephritoidea on the basis of the structure of the male and female terminalia are the Tanypezidae (including Strongylophthalmyiidae) and the Psilidae.

McAlpine accepts the concept of Lauxanioidea introduced by Hennig (1958) and followed by me (Griffiths 1972). His interpretation differs from mine at that time in that he regards the male postabdominal structure of this group as derived from what I called the muscoid type. This allows him to consider *Cremifania* (a genus of typical muscoid structure which I removed to the Sciomyzoinea as family Cremifaniidae) as a primitive chamaemyiid. He also claims to have evidence that the postabdominal structure of Lauxaniidae is similarly derived.

As far as *Cremifania* is concerned, its position remains disputed. Tanasiychuk (1986) did not accept it as a chamaemyiid. The undoubted chamaemyiids with somewhat asymmetrical postabdomen (*Acrometopia* and *Parochthiphila*) do not show the typical muscoid pattern of sclerites (asymmetrical reduction of 7th tergite not demonstrable). I am not aware of any lauxaniid with an asymmetrical postabdominal structure. If such exist, it would be helpful if the species were stated so that McAlpine's arguments can be checked.

McAlpine's concept of Sciomyzoidea is close to that in other recent treatments by Hennig and me. All recent authors include here the families included by McAlpine. There is disagreement only regarding whether additional families, such as Cremifaniidae and Megamerinidae, should also be included. As noted above, if the Megamerinidae belong to the Sciomyzoidea, probably the Diopsioinea should also be included here as a subordinate group. Since the Megamerinidae are poorly studied, I note this possibility as one to be considered in future studies, not as a firm opinion.

The concept of Opomyzoidea is new and unsatisfactory. That should not be taken as a criticism, since the relationships of most of the included families have been poorly studied and any superfamily arrangement at this time must be arbitrary and tentative. The apomorphous characters given for the groundplan of the Opomyzoidea all have wider distributions and may be subject to homoplasy. Regarding the subgroups (suprafamilies sensu McAlpine) of Opomyzoidea, it appears to me that the Opomyzoinea and Asteioinea are defensible groupings which will serve as a good basis for further studies. But his Clusioinea and Agromyzoinea seem to me most improbable groupings. The structure of the male genitalia suggests that the Acartophthalmidae and Odiniidae belong in the vicinity of the Tethinidae and other families included by McAlpine in the "Carnoidea", as they were treated in my 1972 book. I find McAlpine's argument that the characters of the fossil *Acartophthalmites* demonstrate a relationship between Acartophthalmidae and Clusiidae unconvincing, since the only synapomorphies suggested between these families are in characters subject to homoplasy.

In connection with the comments on Agromyzidae, it should be noted that the old report of sclerotized strips on the left side of the male abdomen was checked many years ago and found to be erroneous. I am not aware of any members of this family with any asymmetry in the structure of the male postabdomen. If McAlpine has observed anything different, he should state what species he examined so that specialists can check the observation.

McAlpine's concept of "Carnoidea" mainly includes families treated in my 1972 book as belonging to the Tephritoinea but not to the Tephritidae family-group, that is families in which the aedeagus is long and flexible (or assumed to be derived from such a type) and in which a retractile ovipositor is developed but not showing the full suite of apomorphies (such as fused cerci) shown by females of the Tephritidae family-group (Tephritoidea in McAlpine's sense). This concept of relationship remains valid, but there remain problems regarding which families belong in the Tephritoinea *sensu lato.* McAlpine's proposal to recognize a separate superfamily for the Tephritoidea exclusive of the Tephritidae family-group seems reasonable pending further investigations. But the superfamily cannot be called Carnoidea, because (as noted above) the Carnidae belong to the Tephritidae family-group (Tephritoidea sensu McAlpine). I think the name Chloropoidea is the appropriate one.

There are some other misplacements in McAlpine's treatment of the "Carnoidea". The Cryptochetidae do not belong in the subgroup Milichiidae + Chloropidae, as discussed above. More probably they are close to the Lonchaeidae (Tephritoidea). The Risidae belong to the Ephydroidea (see Chandler 1987), and in my opinion represent an aberrant subgroup of the Ephydridae not a separate family. On the other hand, two families placed in Opomyzoidea by McAlpine, Acartophthalmidae and Odiniidae, should be included here according to the structure of their male and female terminalia.

The relationships of the two families separated by McAlpine at the base of the "Carnoidea", Australimyzidae and Braulidae, are unclarified. The case for including them here (or in any other superfamily of "Acalyptratae") is quite weak, since based only on characters subject to homoplasy. The Australimyzidae show some highly plesiomorphous features, and may represent a group of higher rank (as treated in my 1972 book).

The superfamily Sphaeroceroidea is proposed by McAlpine for part of the Anthomyzoinea in the sense of my 1972 book. The concept is reasonable pending further investigations. While most of the Heleomyzidae of the Northern Hemisphere probably represent a monophyletic group, the same cannot be said for the Southern Hemisphere forms. D. K. McAlpine (1985), the lone current worker on these southern groups, was unable to justify his suprageneric concepts in terms of cladistic analysis, so we may well be dealing with an assemblage of diverse origins. It is obvious that progress in clarifying the limits of and relationships within the Sphaeroceroidea will be slow, so long as additional dipterists do not take up the study of the "Heleomyzidae" of the Southern Hemisphere.

McAlpine's treatment of the Ephydroidea (= Drosophiloidea) generally has my support, except that he tries to reverse the separation of the Campichoetidae from *Diastata* proposed in my 1972 book. This seems to me retrograde. That these groups are not monophyletic is confirmed in the important paper by Chandler

(1987), which contains a review of the relationships between the families of Ephydroidea (in which Risidae must also be included, as noted above). Presumably McAlpine's manuscript was finalized before Chandler's work was received, since he does not mention it. Future studies should take account of Chandler's, as well as McAlpine's, treatment.

The treatment of the Calyptratae contains much less that is controversial than the treatment of the "Acalyptratae". Numerous autapomorphies justify the concept of Calyptratae, as shown in McAlpine's table of "character states in groundplans of Acalyptratae and Calyptratae". Three subgroups are recognized (ranked as superfamilies), the Hippoboscoidea, Muscoidea and Oestroidea. The first and last are groups recognized (under a diversity of names) in all recent treatments. But whether the Muscoidea (sensu McAlpine) is a monophyletic group requires further study. The three characters of this group shown on his phylogeny diagram in my opinion all belong to the groundplan of more inclusive groups.

CONCLUSION

The publication of this volume represents an important advance in our understanding of the phylogeny of the Diptera. In writing this critical review I have tried to distinguish what seems to me well established from what is controversial or in certain cases demonstrably erroneous. I hope my remarks will assist future workers in this most interesting field. J. Frank McAlpine is to be congratulated for his persistence and hard work over many years in bringing the Manual project to completion. This phylogeny volume will prove seminal, but should not be regarded as the source of all truth on this subject. We are still at a stage where considerably divergent opinions can reasonably be held concerning many areas of the system, and many changes may be expected as a result of future research.

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