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Pesky gnats: Ridding dipteran classification of the Nematocera

[Lästige Mücken: Befreiung der Dipterenklassifikation von den Nematocera]

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Abstract The classification of the lower Diptera is reviewed. Published papers on the relationships between lower dipteran clades since the 1960's agree that the "Nematocera" is a paraphyletic taxon. A new classification of the Diptera is proposed in which the usual infraorders of Diptera are raised to subordinal rank, and the name Nematocera is abandoned. Possible future changes in Diptera phylogeny are considered and their consequences for Diptera classification are discussed.

Key words Diptera, phylogeny, classification, Nematocera

Zusammenfassung Es wird ein Überblick zur Klassifikation der niederen Dipteren gegeben. Seit den 1960er Jahren gibt es in den Veröffentlichungen, die die Beziehungen zwischen den Zweigen der niederen Dipteren zum Gegenstand haben Übereinstimmung darüber, dass die „Nematocera" als paraphyletisch aufzufassen sind. In der vorliegenden Publikation wird eine neue Klassifikation der Zweiflügler vorgeschlagen in deren Konsequenz die geläufigen Infraordnungen der Diptera auf den Rang von Unterordnungen (suborders) erhoben werden und der Name Nematocera verschwindet. Zukünftig denkbare Änderungen in der Phylogenie der Diptera werden beleuchtet und ihre möglichen Konsequenzen für die Klassifikation der Ordnung diskutiert.

Stichwörter Diptera, Phylogenie, Klassifikation, Nematocera

The phylogeny and classification of lower Diptera

Interest in the phylogeny of the Diptera has long predated the development of a coherent phylogenetic method. EDWARDS' (1925) paper is possibly the most important review of Diptera phylogeny published before Willi HENNIG's "Flügelgeäder", but CRAMPTON (1914, 1918, 1924, 1925, 1926, 1942), SNODGRASS (1935), SHAW (1948), and SHAW & SHAW (1951) also dedicated themselves to this theme. Willi HENNIG produced a series of landmark papers on the phylogeny and classification of Diptera (HENNIG 1954, 1968, 1973) (Fig. 1). There have been a number of more recent contributions towards the classification of Diptera with a more contemporary phylogenetic perspective. These include the works of WOOD & BORKENT (1989) (Fig. 2), GRIFFITHS (1990, 1994), COURTNEY (1990, 1991), OOSTERBROEK & THEOWALD (1991), WOOD (1991), SINCLAIR (1992), KRZEMIŃSKI (1992), AMORIM (1993), BLASCHKE-BERTHOLD (1994), OOSTERBROEK & COURTNEY (1995) (Fig. 3), MICHELSEN (1996), FRIEDRICH & TAUTZ (1997), SAETHER (2000), and KRZEMIŃSKY & KRZEMIŃSKA (2003) (Fig. 4). FRIEDRICH & TAUTZ (1997) published a phylogeny for the basal Diptera using 28S rDNA data, but with few well-supported nodes. YEATES & WIEGMANN (1999) have reviewed most literature and showed that there is still considerable disagreement on the relationships among major clades of Diptera, even though the monophyly of some higher groups, as the Tipulomorpha excluding Trichoceridae, the Culicomorpha, most of the Bibionomorpha, the Brachycera and Muscomorpha, is not under dispute. The monophyly of Ptychopteromorpha is proposed in many papers (e.g. WOOD & BORKENT 1989).

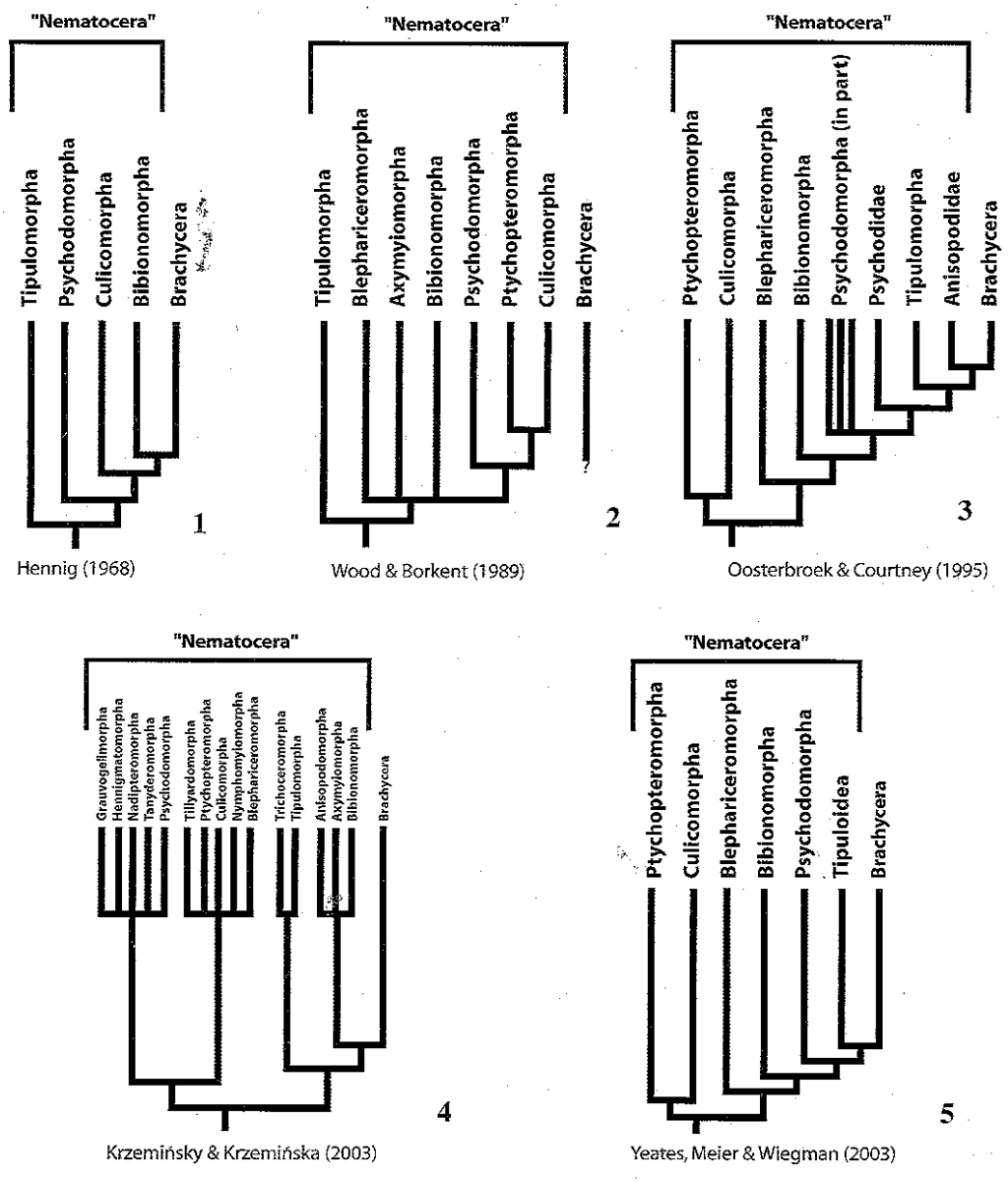

Fig. 1–5: Different systems proposed for basal Diptera phylogenetic relationships since Hennig (1968). "Nematocera" is paraphyletic in all schemes.

Yeates et al. (2003, and »http://www.inhs.uiuc.edu/cee/FLYTREE/supertree.html«) (Fig. 5) produced a supertree of dipteran relationships at family level. This method produced a highly resolved tree that is similar in many respects to that of Oosterbroek & Courtney (1995) (Fig. 4) in the lower Diptera. This result can be interpreted as a quantitative consensus of current opinion on dipteran relationships. However this method does not take into account the strength of support for nodes in the input phylogenies, and it is particularly weak between the lower

dipteran suborders. In addition, this method will decisively choose a topology found in the majority of input trees, even though there may be alternative arrangements in other input trees.

We are now entering a new era in development of studies of Diptera phylogeny (e.g., the FLYTREE project, »www.inhs.uiuc.edu/cee/FLYTREE/«) and large sources of information are now available on the Internet (e.g. »http://www.sel.barc.usda.gov/Diptera/diptera.htm«). These studies will soon lead to a new classification of Diptera that reflects our deeper understanding of their relationships. We are particularly eager for the results of a comprehensive analysis of lower dipteran relationships using molecular data.

Willi HENNIG (1966) not only proposed Diptera phylogenies, but also a method of phylogenetic reconstruction, and a scheme of classification that would unequivocally reflect the accepted phylogenetic relationships among the groups classified. Only monophyletic groups should receive formal names in a phylogenetic classification. Because of these innovations, names for paraphyletic groups, such as Pisces and Reptilia in the vertebrates, were abandoned in classification. In recent years the paraphyletic dipteran groups Orthorrhapha and Aschiza of the Brachycera have been abandoned as paraphyletic. These groupings can be referred to as Lower Brachycera and Lower Cyclorrhapha respectively (YEATES & WIEGMANN 1999, 2005). However, as we show, Dipterists themselves have been slow to abandon some other papraphyletic group names used in dipteran classification.

Most accepted higher-level classifications of Diptera differ only slightly from the one below (e.g., »http://www.sel.barc.usda.gov/Diptera/names/famlistt.htm«):

Order Diptera
- Suborder Nematocera
  - Infraorder Tipulomorpha
  - Infraorder Psychomorpha
  - Infraorder Ptychopteromorpha
  - Infraorder Culicomorpha
  - Infraorder Blephariceromorpha
  - Infraorder Bibionomorpha
  - Infraorder Axymyiomorpha
- Suborder Brachycera

Despite some disagreements about the details, there is at least one point upon which there has been no dispute in the literature over the past 40 years: "Nematocera" is paraphyletic, and the sister-group of Brachycera is a subordinate group of "Nematocera" (Fig. 1). HENNIG (1968) proposed that Bibionomorpha is the sister group of Brachycera, in which he was followed by AMORIM (1993) and MICHELSEN (1996). WOOD & BORKENT (1989) did not specifically identify the sister-group of the Brachycera (see AMORIM & CARVALHO 1992), but WOODLEY (1989) proposed the Anisopodidae as the sister-group of the Brachycera, as did OOSTERBROEK & COURTNEY (1995). The paraphyly of the Nematocera is also implicit in the phylogeny of KRZEMIŃSKI (1992) and KRZEMIŃSKY & KRZEMIŃSKA (2003) based on dipteran fossils.

In short, the literature has not supported a monophyletic Nematocera since HENNIG (1968). It seems, hence, that time has come to abandon such a basal, paraphyletic taxon in the classification of the Diptera. It is likely that difficulties in reconstructing the relationships among the "Nematocera" have hindered the appearance of a robust alternative. However, there are solutions available giving higher ranks to the well accepted higher monophyletic clades without

major changes in the classification. This paper introduces the first phylogenetic classification of Diptera that recognizes the paraphyly of the lower Diptera.

A new higher classification for the Diptera

We propose here that the name "Nematocera" be abandoned and the included infraorders raised to subordinal rank, coordinate with Brachycera. This classification does not adhere to the phyletic sequencing convention (NELSON 1972, WILEY 1981), and the sequence of taxa has no meaning. This reflects the lack of consensus on lower dipteran relationships. Once the order of branching is known with more certainty, the phyletic sequencing convention could be used to reflect this arrangement. We have included a classification of the Suborder Brachycera into Infraorders and Sections.

Order Diptera
- Suborder Tipulomorpha
- Suborder Psychomorpha
- Suborder Ptychopteromorpha
- Suborder Culicomorpha
- Suborder Blephariceromorpha
- Suborder Bibionomorpha
- Suborder Axymyiomorpha
- Suborder Brachycera
  - Infraorder Tabanomorpha
  - Infraorder Xylophagomorpha
  - Infraorder Stratiomyomorpha
  - Infraorder Muscomorpha
    - Section Nemestrinoidea
    - Section Asiloidea
    - Section Empidoidea
    - Section Cyclorrhapha

If a collective noun for non-brachyceran dipterans is needed, they can be referred to as **lower dipterans** (for example YEATES & WIEGMANN 1999, 2005).

Future changes in Diptera phylogeny and their impact on the classification

The arrangement we have proposed should be robust to most advances in our knowledge of lower dipteran relationships. Most disagreements among authors concern the relationships between lower dipteran clades, with few disagreements about the monophyly of the major clades at suborder rank in our new classification. Because we avoided a classification reflecting the relationships among the suborders, this system can easily incorporate such information in the future. The classification represents a polytomy at the base of the Diptera, which is a conservative approach given the lack of a well-supported lower dipteran phylogeny (YEATES & WIEGMANN 1999).

Some families have been attributed to different suborders in our system. For example, the Trichoceridae belong to the Tipulomorpha in HENNIG (1973) and OOSTERBROEK & COURTNEY (1995), and to the Psychodomorpha by WOOD & BORKENT (1989). The Scatopsoidea belong to the Bibionomorpha in HENNIG (1973), but WOOD & BORKENT (1989), AMORIM (1994) and Oos-

TERBROEK & COURTNEY (1995) place them in the Psychodomorpha. These differences in the composition of the suborders do not affect the higher classification we have proposed.

More radical changes to the classification are implied if one or more suborders are found to be included within other suborders. For example, Ptychopteromorpha, Blephariceromorpha and Axymyiomorpha are very small clades (in terms of number of species and families) and increased phylogenetic resolution could show that they belong inside other clades (for example the Blephariceromorpha inside the Psychodomorpha). This would demand a change in the classification, but would be nothing more than the synonymy of one suborder with another.

A more delicate point concerns the Psychodomorpha. Some authors see them as a grade basal to Brachycera (e.g., OOSTERBROEK & COURTNEY 1995). If this comes to be confirmed, it would have to be subdivided in such a way that smaller psychodomorphan clades would be raised to Suborder rank. However, this does not affect any other suborders, and there will always be a Psychodomorpha, however its composition might change.

If future research finds support for clades grouping lower dipteran Suborders, there are already some names available. HENNIG (1954) used "Oligoneura" for all Diptera except the Tipulomorpha, and "Polyneura" for Tipulomorpha including Trichoceridae. MICHELSEN (1996) proposed the "Neodiptera" for the clade including the Bibionomorpha and the Brachycera. KRZEMINSKY & KRZEMINSKA (2003) also proposed a number of names for clades here ranked as suborders. Their "Anisoneura" includes Anisopodomorpha (= Anisopodidae), Axymyiomorpha, and Bibionomorpha; "Neoneura" includes the Culicomorpha, Blephariceromorpha, Ptychopteromorpha and Nymphomyiomorpha (= Nymphomyiidae); and their "Diarchineura" includes Tanyderomorpha (= Tanyderidae), Psychodomorpha and a number of extinct families. Some of these names may come to be accepted when relationships between the dipteran Suborders are supported more robustly.

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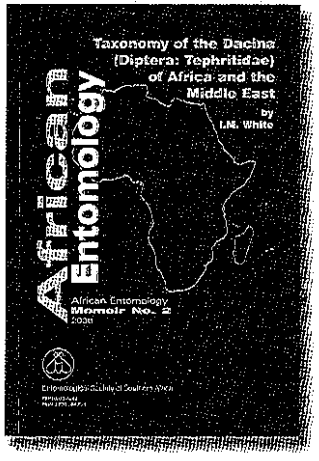

Neue Bücher – New books

Ian M. WHITE (2006): **Taxonomy of the Dacina (Diptera: Tephritidae) of Africa and the Middle East.** – African Entomology, Memoir **2**: 156 pp. & CD-ROM, published by the Entomological Society of Southern Africa. ISSN 0373-4242; ISBN 0-620-36425-4. Prize unknown.

Within the large family Tephritidae (over 4400 species described worldwide) one group is of particular economic interest, the Dacina. This subtribe includes only 3 genera: *Bactrocera* (some 500 species, mainly known from the Oriental and Australasian Regions), *Dacus* (about 250 species, predominantly Afrotropical with some Oriental and Australasian species), and *Monacrostichus* with 2 Oriental species. All species with known biology attack fleshy fruit and the Cucurbitaceae and Asclepiadaceae are the most important plant families for Dacina. Thus it is not surprising that some Dacina include notorious agricultural pests, like *Bactrocera tryoni* (Queensland fruit fly), *B. dorsalis* (Oriental fruit fly) *B. cucurbitae* (Melon fruit fly), *B. zonata* (Peach fruit fly), *B. oleae* (Olive fly), *Dacus bivittatus* (Pumpkin Fly), *D. ciliatus* (Cucurbit fly), or *D. vertebratus* (Jointed Pumpkin Fly). Whereas the genus *Bactrocera* was extensively studied by R. A. I. DREW and D. L. HANCOCK for the Australasian and partly the Oriental Regions there is an important gap in knowledge of the genus *Dacus*, also because the monograph of H. K. MUNRO (1984) about the African Dacidae is partly outdated and almost impossible to use for a non-expert.

It is therefore very welcome to see the new masterpiece of I. M. WHITE about the Dacina of Africa and the Middle East. This monograph summarizes our present knowledge of the group, with an extensive

treatment of 15 species of *Bactrocera* and 177 species of *Dacus* occuring in this area. In total, 25 species are described as new and 26 species are synonymized. A new classification is proposed based on a cladistic analysis, changing radically the concept of MUNRO (1984).

The book starts with a comparatively short introduction: a review of existing classifications, the evaluation of the characters used in the cladistic analysis, the analysis itself and its conclusions, terminology, biogeography, host-plant associations, and response to male lures. The main part is the taxonomic treatment with a key to the species (320 couplets) and to the subgenera (17 couplets). A computerised system was used to construct them. The species are thereafter treated always in the same way: Synonymy, description, material and distribution, lures, and remarks. The material section, however, only lists the type material and country records. In order to limit costs and size of the printed book all illustrations and a full database of the 6000 specimens studied are exclusively found on the CD. The latter contains other important files (acronyms of studied collections, etc.), and another version of the key. The two items, book and CD, must therefore be used together.

The quality of the book, and in particular of the illustrations (over 1000 photos of 190 of the 192 treated species) is simply excellent. I have tested the key and it is working perfectly for the 20 or so species that I have tried to identify using both keys, the book and the CD version. The key length (35 pages) may induce some hesitations to a beginner of Dacina. However, I. M. WHITE has developed a key beginning with characters easy to evaluate, and with large jumps between couplets, so that identifications can be done in reasonable time with a good percentage of correctness.

This book is a real milestone in Tephritidae research. It is an excellent example of a user-friendly, modern revision. It treats a Diptera group of very high interest to all students of applied entomology, especially in agriculture, ecology, pest species research and related topics, but also taxonomy. Such a modern, attractive book will hopefully help to stop the steady decline of fundings for taxonomic research. It is therefore my big hope that it will find its way in all entomological libraries of museums, universities, and research stations with biology departments.

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