Relationships of extant lower Brachycera (Diptera): a quantitative synthesis of morphological characters

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With over 80 000 described species, Brachycera represent one of the most diverse clades of organisms with a Mesozoic origin. Larvae of the majority of early lineages are detritivores or carnivores. However, Brachycera are ecologically innovative and they now employ a diverse range of feeding strategies. Brachyceran relationships have been the subject of numerous qualitative analyses using morphological characters. These analyses are often based on characters from one or a few character systems and general agreement on relationships has been elusive. In order to understand the evolution of basal brachyceran lineages, 101 discrete morphological characters were scored and compiled into a single data set. Terminals were scored at the family level, and the data set includes characters from larvae, pupae and adults, internal and external morphology, and male and female terminalia. The results show that all infraorders of Brachycera are monophyletic, but there is little evidence for relationships between the infraorders. Stratiomyomorpha, Tabanomorpha, and Xylophagomorpha together form the sister group to Muscomorpha. Xylophagomorpha and Tabanomorpha are sister groups. Within Muscomorpha, the paraphyletic Nemestrinoidea form the two most basal lineages. There is weak evidence for the monophyly of Asiloidea, and Hilarimorphidae appear to be more closely related to Eremoneura than other muscomorphs. Apsilocephalidae, Scenopinidae and Therevidae form a clade of Asiloidea. This phylogenetic evidence is consistent with the contemporaneous differentiation of the main brachyceran lineages in the early Jurassic. The first major radiation of Muscomorpha were asiloids and they may have diversified in response to the radiation of angiosperms in the early Cretaceous.

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Introduction

The dipteran suborder Brachycera is a monophyletic group, with a large number of undisputed synapomorphies from the larva and adult (Hennig 1973; Woodley 1989; Sinclair 1992; Sinclair *et al*. 1994; Griffiths 1996; Stuckenberg 1999). The first brachyceran fossils are known from the Lower Jurassic, and the group probably arose in the Triassic (208–245 mya) (Kovalev 1979; Woodley 1989). With over 80 000 described species, Brachycera represent one of the most diverse clades of organisms with a Mesozoic origin. Well-preserved tabanids, nemestrinids, bombyliids and mydids have just been recovered from the Upper Jurassic of China (Ren 1998). A number of species-rich families of the lower Brachycera diversified in the mid-Cretaceous, coincident with the radiation of angiosperms (Grimaldi 1999). Most brachyceran larvae inhabit moist terrestrial habitats, and their adults are more stout bodied and compact than those of the lower Diptera. While the monophyly of the four infraorders of Brachycera (Xylophagomorpha, Stratiomyomorpha, Tabanomorpha, Muscomorpha) are well established, relationships between them are not (Yeates & Wiegmann 1999).

Synapomorphies for the Xylophagomorpha include some extremely distinctive features of the larvae: the elongate, conical, strongly sclerotized head capsule, the development of a pair of metacephalic rods from the posterior portion of the cranium, and the apex of the abdomen with a sclerotized dorsal plate surrounding the spiracles and ending in a pair of hook-like processes (Hennig 1973; Woodley 1989). Xylophagid larvae are predators of other soft-bodied invertebrates in wood or soil and adults feed on nectar and pollen.

Synapomorphies of the Tabanomorpha include the apomorphic presence of a brush on the larval mandible, larval head retractile, and adult with convex, bulbous clypeus

(Hennig 1973; Woodley 1989; Sinclair 1992). The expanded first article of the female cercus was also proposed as a synapomorphy of the group (Sinclair *et al.* 1994) but is not accepted by all (Stuckenberg 1995; Griffiths 1996). Larval Tabanomorpha are predators in soil or in aquatic and semi-aquatic habitats and their adults feed on nectar and pollen, except for female Tabanidae and a few Rhagionidae that feed on vertebrate blood.

Synapomorphies for Stratiomyomorpha are the larval maxilla and basal mandibular sclerite weakly fused to form a mandibular–maxillary complex, larval pharyngeal filter and grinding apparatus, loss of tibial spurs on prothoracic legs, costal vein terminating at M_2 (Woodley 1989; Sinclair 1992; Courtney *et al.* 2000), and two features of the male sperm pump (Sinclair *et al.* 1994). Larval Stratiomyomorpha feed on decaying organic matter or wood and the adults feed on nectar and pollen.

The infraorder Muscomorpha contains all brachyceran families except those belonging to Stratiomyomorpha, Xylophagomorpha and Tabanomorpha (Woodley 1989). Synapomorphies include loss of tibial spurs, antennal flagellum with one to four flagellomeres, a single article in the female cercus (Woodley 1989) and the base of epandrium articulated on the gonocoxites (Sinclair *et al.* 1994).

Relationships of infraorders

Relationships among the four infraorders of Brachycera remain unresolved (Hennig 1973; Krivosheina 1989, 1991; Woodley 1989; Sinclair *et al.* 1994; Griffiths 1994; Nagatomi 1996). Certain larval and adult features support a basal clade of Brachycera that excludes Stratiomyomorpha alone (Griffiths 1994; Nagatomi 1996). The remaining groups of Brachycera may be united by the loss of a pharyngeal filtering apparatus, the presence of a slashing distal hook in the mouthparts, a primary predatory larval lifestyle with either an external channel or an internal duct for delivery of saliva to prey, the presence of lateral ejaculatory sclerites in the male genitalia. This interpretation requires that the formation of a fused phallus is not homologous in Stratiomyomorpha and Muscomorpha or was secondarily lost in Tabanomorpha and Xylophagomorpha. Xylophagomorpha and Tabanomorpha have been united based on synapomorphies of the male genitalia, a membranous outer wall of the aedeagus and the development of an endophallic guide inside the sperm pump (Griffiths 1994). The distribution and homology of these features requires further documentation before this clade can be considered well established. The distribution and development of a complex parameral sheath over the aedeagus of basal brachycerans has been used as evidence of synapomorphy among the infraorders in a number of different combinations (Sinclair *et al.* 1994; Griffiths 1996; Zatwarnicki 1996).

Clades of Muscomorpha

Nemestrinoidea. Nemestrinidae and Acroceridae have been united by their parasitic larval lifestyle (Hennig 1973; Woodley 1989), but authors have found the superfamily paraphyletic (Yeates 1994) or suggest the group may be better placed in Tabanomorpha (Nagatomi 1992; Griffiths 1994). Hennig (1973) placed Bombyliidae in a group with Nemestrinoidea because of their parasitic larvae, but recent treatments have placed Bombyliidae in Heterodactyla (Woodley 1989; Nagatomi 1992, 1996; Yeates 1994). This interpretation suggests that the parasitic lifestyle of the three families arose independently. Indeed, Bombyliidae are primitively ectoparasitic, whereas Nemestrinidae and Acroceridae are exclusively endoparasitic; hosts of the former are insects, the latter only spiders (Araneae) (Yeates & Greathead 1997).

Heterodactyla. Muscomorpha excluding Nemestrinoidea were united in a clade called Heterodactyla (Woodley 1989). All Heterodactyla have a synapomorphic setiform empodium. However, the homology of the empodium in Asiloidea and Eremoneura is questioned (Röder 1984; Griffiths 1994). The presence of spine-bearing acanthophorites in the female was also interpreted as a synapomorphy of this group (Sinclair *et al.* 1994), but the homology of these structures in Empidoidea is also questioned (Griffiths 1994). The absence of male tergite 10 has also been suggested as a synapomorphy of Heterodactyla (Sinclair *et al.* 1994), but this interpretation is hampered by its absence also in Acroceridae (Yeates 1994).

Asiloidea. The families Asilidae, Apioceridae, Mydidae, Scenopinidae, Therevidae and Bombyliidae have been united in Asiloidea on the basis of the apomorphic position of the larval posterior spiracles in the penultimate abdominal segment (Woodley 1989; Yeates 1994). This feature does not occur in the bombyliid *Heterotropus* Loew (Yeates & Irwin 1992) and the character description has been modified to deal with them (Sinclair *et al.* 1994). Bombyliidae alone (Woodley 1989), or with Hilarimorphidae (Yeates 1994), have been considered the sister group to the remaining Asiloidea. Most asiloid larvae are soil-dwelling predators and their adults feed on nectar and pollen. Notable exceptions are Bombyliidae with primarily parasitoid larvae and adult Asilidae (robber flies), that are aerial predators of other adult insects. A number of asiloid families have received critical phylogenetic scrutiny in recent years, partly because of their proximity to Eremoneura.

The monophyly of Bombyliidae is not well supported morphologically (Yeates 1994), and Zaytsev (1991) proposed raising four subfamilies to family status. Most genera of the subfamily Proratinae were removed to Scenopinidae (Yeates 1992a; Nagatomi *et al.* 1994) but the genus *Apystomyia*