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

David K. Yeates

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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.

David K. Yeates, Department of Zoology and Entomology, University of Queensland, Australia.
Present address: CSIRO Division of Entomology, PO Box 1700, Canberra, ACT 2601, Australia.
E-mail: david.yeates@ento.csiro.au

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*

Melander was placed in Hilarimorphidae (Yeates 1994), or given family status *incertae sedis* in Asiloidea (Nagatomi & Liu 1994). Even with the exclusion of Proratinae, one study considered the family paraphyletic with respect to the remaining Asiloidea (Sinclair *et al*. 1994) on the basis of the male genitalia. The poorly known genus *Hilarimorpha* Schiner was raised to family status (Webb 1974) and recent authors place it in or near Bombyliidae (Griffiths 1972; Webb 1981; Woodley 1989; Nagatomi *et al*. 1991b; Yeates 1994) or Therevidae (Sinclair *et al*. 1994). The monophyly of Therevidae is also not well supported (Yeates 1994), raising the possibility that Scenopinidae may have arisen from them (Woodley 1989). *Apsilocephala* Kröber was excluded from Therevidae (Irwin & Lyneborg 1981) and the genus and its relatives were given family status (Nagatomi *et al*. 1991a). The hypothesis that they are close to the stem of Eremoneura (Nagatomi *et al*. 1991b,c; Nagatomi 1992, 1996) has been discounted (Griffiths 1994, 1996; Sinclair *et al*. 1994; Cumming *et al*. 1995; Zatwarnicki 1996). The affinities of this group remain obscure, with some authors placing them inside or near Therevidae (Yeates 1994; Sinclair *et al*. 1994). The monophyly of Asilidae, including the subfamily Leptogastrinae, is not in dispute (Woodley 1989; Yeates 1994). The paraphyly of Apioceridae was suspected based on the male genitalia (Sinclair *et al*. 1994), and, subsequently, the subfamily Megascelinae was transferred to Mydidae (Yeates & Irwin 1996).

Sister group of Eremoneura. Eremoneura is the name given to the muscomorphan lineage containing Empidoidea + Cyclorrhapha. This is one of the best-supported higher-level brachyceran clades (Chvála 1983; Griffiths 1984, 1994; Woodley 1989; Sinclair 1992; Wiegmann *et al*. 1993; Cumming *et al*. 1995), with numerous synapomorphies.

Characters suggesting a sister group relationship between Asiloidea and Empidoidea, such as the presence of three or fewer antennal flagella and the presence of female acanthophorites, are subject to much homoplasy (Hennig 1973; Woodley 1989) — this relationship has been discounted in favour of a sister group relationship between the entire Eremoneura and Asiloidea (Griffiths 1972, 1984; Hennig 1976; Chvála 1983; Sinclair 1992; Cumming *et al*. 1995). Characters supporting the latter are: (1) gonostyli retracted anteriorly to a subapical position on the gonocoxites; and (2) the posterior region of larval cranium subdivided into a hinged metacephalic rod (Sinclair *et al*. 1994).

Uncertainty over the sister group of Eremoneura stems mostly from the poorly supported positions of several genera traditionally placed in or near asiloid families, but whose morphology is difficult to interpret in the context of current higher-level groupings of Asiloidea (Yeates & Irwin 1992; Sinclair *et al*. 1994; Yeates 1994; Cumming *et al*. 1995).

These include *Hilarimorpha*, *Apsilocephala*, *Heterotropus*, *Apystomyia*, and mythicomiine bombyliids. No quantitative phylogenetic study has sampled broadly enough within both Asiloidea and Empidoidea to pinpoint the eremoneuran sister group as either a monophyletic Asiloidea or some asiloid clade. Alternative sister groups have occasionally been proposed, including an assemblage of Asiloidea and Tabanomorpha (Griffiths 1994; Zatwarnicki 1996), and nonmuscomorphans such as Stratiomyiidae (McAlpine 1989) or Bibionomorpha (Disney 1986). These last three suggestions require the paraphyly of Heterodactyla, Muscomorpha and Brachycera, respectively.

Some recent authors have identified synapomorphies for well-established dipteran clades in the nervous system. Support for Eremoneura has been found in the eye photoreceptor synapse architecture (Meinertzhagen 1989) and for Cyclorrhapha in the ventral nerve cord of the larva (Melzer *et al*. 1995). Some characters supporting Brachycera and Eremoneura are reported by Buschbeck (2000) from the second-order visual neuropil associated with innervation of the eye. I include here a character (character 101) found in the adult ventral nerve cord that supports a novel grouping of infraorders (Yeates and Merritt submitted).

Few authors have discussed brachyceran relationships in an explicitly quantitative framework, and most discuss a limited subset of the possible characters. The purpose of this contribution is to synthesize and compile all characters that have been used to describe the relationships between the main brachyceran lineages. These characters have been assembled into a data matrix (Table 1) and analysed quantitatively to produce a hypothesis of relationships. These relationships can be viewed as a summary of current ideas on brachyceran phylogeny. This data set is to be used in forthcoming combined analyses of molecular and morphological data bearing on the lower Brachycera (Wiegmann & Yeates in preparation).

Methods

A number of higher categories in traditional dipteran classifications are paraphyletic. Informal names are used for these groups as follows: lower Diptera for 'Nematocera', lower Brachycera for 'Orthorrhapha', and lower Cyclorrhapha for 'Aschiza'. Wherever possible, the character number or designation in the original reference is quoted.

Ground plan scorings

Family scorings are based on an estimate of the attributes of the most recent common ancestor of the family. Where possible, these estimates are based on a consideration of the cladistic relationships of the subfamilies and genera within the families (Yeates 1995). The cladistic relationships of some families included here are relatively well known, some

Table 1 Data matrix

	10	20	30	40	50
Lower Diptera	0000000000	0000000000	0000000000	0000000000	0000000000
Xylophagidae	1110110010	0000100000	0110001100	0000010010	0000000010
Pantophthalmidae	1000110012	0000200000	0000001100	0000010010	1000000011
Xylomyidae	1000110011	0000200100	0000011100	0000010010	1000000021
Stratiomyidae	1000110011	0000200100	0000011100	0000010010	1100000121
Vermeleontidae	1000110010	0000101000	0010001100	0000010010	0000000010
Rhagionidae	1000110110	0000101000	0000001100	0100010010	0000000010
Pelecorhynchidae	1000111210	0010101000	0000001100	0100010010	0000000010
Athericidae	1000111310	0000101000	1000001110	0100010011	0010000010
Tabanidae	1000111310	0000101000	0000001100	0100010011	0001000010
Nemestrinidae	1000110000	0000100000	0010202100	0000010010	0000001010
Acroceridae	1000110000	0000100000	0000303100	0000010010	0000000010
Hilarimorphidae	??????????	??????????	??????2100	0000010(01)10	0000010010
Asilidae	1000110010	0000110000	0020002100	1011010010	0000000010
Scenopinidae	0000110010	0000110001	0020002100	0000020010	0000010010
Therevidae	0000110010	0000110011	0020002100	0000010010	0000000010
Apsilocephalidae	??????????	??????????	??????2100	0000010010	0000000010
Apioceridae	1000110010	0000110000	0020002100	0000010110	0000100010
Mydidae	1000110010	0000110000	0020002100	0000020110	0000100010
Bombyliidae	1000110010	0000100000	0020(01)02100	0000011110	0000010010
Empidoidea	1000110020	1100110000	0001002101	0000120010	0000010020
Cyclorrhapha	0001110030	1101000000	0001012201	0000020010	0002010020

	60	70	80	90	100	
Lower Diptera	0000000000	0000000000	0000000000	0000000000	0000000000	0
Xylophagidae	0000000001	0000100000	0010000101	0000000000	0000000000	1
Pantophthalmidae	0010000001	0000100000	002001?002	1000000000	0000000001	1
Xylomyidae	0010000001	0100100010	002001?000	2000000111	000011000(01)	1
Stratiomyidae	0011000001	0000100000	002001?000	2000000111	0000000001	1
Vermeleontidae	0000000001	0000100000	0010000(01)01	000???????	?001000000	1
Rhagionidae	0000000001	0000100000	0010000101	0000000000	0001000000	1
Pelecorhynchidae	0000000001	0000100000	0010000101	000???????	?001000010	1
Athericidae	0000000001	0000100120	0010000101	010???????	?001000100	1
Tabanidae	1000000001	0100100120	0010000101	0100100000	0001000100	1
Nemestrinidae	0011000001	0100100000	0020000101	0000000000	0000(01)00100	0
Acroceridae	1011000001	010010010?	1?20000001	0011001000	0000100000	0
Hilarimorphidae	0011100001	0100100001	0120000000	001???????	?000000100	0
Asilidae	0011100001	0100200001	0120001001	0010200000	1010000100	0
Scenopinidae	0011110001	0110100001	0121000002	0010200000	?010100100	0
Therevidae	0111100001	0100100011	0120000002	0010200000	(01)010000100	0
Apsilocephalidae	0111100001	01001(01)1001	0120000002	001???????	?010000100	0
Apioceridae	0011200101	0110100001	0120101002	0010200000	1010000100	0
Mydidae	0011200101	011010000?	1?20001002	0011111101	1010000100	0
Bombyliidae	0011100001	01001000(12)1	0020001001	0010000000	0000001100	0
Empidoidea	0011100001	11011(01)110?	1?20000010	0010000001	0110200100	0
Cyclorrhapha	0011101011	110111111?	1?20000000	3010000001	0100000100	1

others are entirely unknown. Appropriate scorings for the sister group to the Brachycera amongst the lower Diptera were derived from Oosterbroek & Courtney (1995). The within-family cladistic relationships used for ground plan scorings were as follows: Xylophagidae (Palmer & Yeates 2000), Scenopinidae (Yeates 1992a), Bombyliidae (Yeates 1994), Therevidae (Yang *et al.* 1999), Apioceridae (Yeates & Irwin 1996), Mydidae (Yeates & Irwin 1996), Hilarimorphidae (Yeates 1994), Empidoidea (Cumming *et al.* 1995), basal Cyclorrhapha (Cumming *et al.* 1995).

In cases where multiple character states were known in a family and the cladistic relationships within the family were poorly known or unknown, the family was scored with multiple states for the character in question. This is a conservative strategy that allows for both possible state scores for the most recent common ancestor of the family. Once the cladistic relationships of these families are better understood, these ancestral scorings can be estimated with greater accuracy. The three families greatly in need of phylogenetic scrutiny in this data set are the Rhagionidae, Therevidae [but see Yang *et al.* (1999)] and Asilidae.

Two examples of this approach will clarify the scoring method. The scoring of acanthophorites (character 93) in Bombyliidae is instructive. Although acanthophorites (with or without well-developed spines) are found in many members of the Bombyliidae, Yeates' (1994: character 139) cladistic analysis of the family found that the basal subfamilies lack acanthophorites, and the character state optimized at the most recent common ancestor of Bombyliidae is 'acanthophorite spines absent'. Hence, it is appropriate to score the bombyliidae 0 for this present analysis. On the other hand, the cladistic analysis of Apioceridae and Mydidae by Yeates & Irwin (1996) showed that acanthophorites (with spines) were present in the most recent common ancestor of the group and were secondarily lost in some Mydidae. Hence, it is appropriate to score the Apioceridae and Mydidae as 'acanthophorites present' in this analysis.

Groups were scored for multiple states if they possessed more than one state and the most plesiomorphic one could not be reasonably determined. This was usually the case if the phylogenetic relationships of the family were not well understood. For example, some Nemestrinidae have two spermathecae and some have three, so they were scored as multistate (0,1) for this character. Only 10 cells (0.43%) in the matrix were scored as multistate. Multistate scores were treated as uncertainty, not polymorphism.

All terminals in the analysis are extant families. The Mythicomyiinae (Bombyliidae) are the sister group to the remaining Bombyliidae (Yeates 1994) and some recent authors have treated them as a separate family from the remaining bee flies (e.g. Evenhuis & Greathead 1999). Separate family status for Mythicomyiinae has been justified because of the greater geological antiquity of the group. This argument is illogical — if the two groups are sisters then they are the same age by definition.

Immatures of Apsilocephalidae and Hilarimorphidae are unknown, they are scored '?' for all characters of immatures (26% of characters). Male genital musculature of Vermileonidae, Pelecorhynchidae, Athericidae, Hilarimorphidae, Apsilocephalidae and Mythicomyiinae are unknown, they are scored '?' for characters of the male genitalia (8% of characters).

Male genitalic homologies

There are a number of male genitalic characters supporting a sister group relationship between Empidoidea and Cyclorrhapha. Particular views of male genitalic homologies determine the nature of these synapomorphies, and characters have been assembled according to the revised epandrial hypothesis (Cumming *et al.* 1995). Male genitalic synapomorphies for the Eremoneura (Empidoidea + Cyclorrhapha) that are dependent on the periandrial hypothesis Griffiths (1994) are:

1 Hypandrium with a pair of posterior processes.
2 Epandrium much reduced, gonocoxites expanded dorsally.
3 Gonocoxites not closed distally, their inner surfaces bearing separate bacilliform sclerites.
4 Gonocoxal bridge and apodemes separated from inner surface of gonocoxites.

A number of features of the male genital musculature represent synapomorphies of the Eremoneura (Ovtshinnikova 1989, 1994; Griffiths 1996): loss of M32, M28, and gain of M3 and M4.

Results

A total of 101 characters from larvae, pupae and adults have been compiled from the literature. Most are binary, but characters 8, 9 25, 27 and 81 have four states and characters 10, 15, 23, 28, 36, 44, 49, 55, 65, 69, 73, 80 and 85 have three states. Multistate characters were treated as nonadditive. Autapomorphies are retained in the matrix for completeness (Yeates 1992b), as they may define families or other major groups; these are characters 2–4, 13, 14, 19, 21, 22, 29, 31, 33–35, 42, 43, 47, 48, 50, 56, 57, 59, 61, 74, 75, 79, 84, 86, 96 and 99 (28.7% of matrix). The consistency index (CI) of each character on the most parsimonious tree is reported at the end of the character description.

Character analysis
Larva (characters 1–25)
1. *Head capsule:* (0) not extending into thorax; (1) extending posteriorly into thorax. Synapomorphy of the Brachycera (Woodley 1989: 1). Yeates (1994: character 151) found a reversal in Scenopinidae + Therevidae ($ci = 0.33$).
2. *Head capsule shape:* (0) not elongate, cone-shaped and well sclerotized; (1) elongate, cone-shaped and well sclerotized. Synapomorphy of the Xylophagomorpha (Woodley 1989: character 6) ($ci = 1.0$).
3. *Posterior margin of head capsule:* (0) simple; (1) internal portion of cranium forming a pair of metacephalic rods, articulating with the head capsule laterally. Synapomorphy of the Xylophagomorpha (Hennig 1973; Woodley 1989: character 7; Courtney *et al.* 2000). See character 16 ($ci = 1.0$).
4. *Atrium:* (0) not invaginated to form an atrium; (1) invaginated to form an atrium. Synapomorphy of the Cyclorrhapha (Hennig 1973; Cumming *et al.* 1995: character M). The atrium contains the imaginal disks of the adult head (McAlpine 1989: 1403) ($ci = 1.0$).
5. *Labrum:* (0) with toothed premandibles; (1) without premandibles. Synapomorphy of the Brachycera (Sinclair 1992: character 11). Oosterbroek & Courtney (1995) interpreted premandibles as present in the lower dipteran families Anisopodidae, Trichoceridae, Psychodidae, Scatopsidae, Perissomatidae, but lost in Tipulidae and in the Brachycera.

Loss of premandibles may be correlated with predatory habits (Sinclair 1992) (ci = 1.0).

6. *Mandible movement:* (0) moving horizontally or obliquely; (1) moving in a vertical plane. Synapomorphy of the Brachycera (Woodley 1989: character 2; Sinclair 1992: character 9). There is considerable variation in the angle of movement of the larval mandibles of lower Diptera, making outgroup comparisons complex. Wood & Borkent (1989) and Sinclair (1992) found obliquely moving mandibles (not the advanced state here) to unite Ptychopteromorpha + Culicomorpha + Psychodomorpha + Brachycera. 'Near' vertical movement (not the advanced state here) was used to unite Psychodomorpha + Brachycera by Wood & Borkent (1989: character 41) and Sinclair (1992: character 6). Oblique or vertical movement of larval mandibles is distributed so widely in Diptera that it has been considered a ground plan of the order (Oosterbroek & Courtney 1995; Friedrich & Tautz 1997). Oosterbroek & Courtney (1995) reported horizontal movement (their character 18) in Tanyderidae, Bibionomorpha, some Tipulidae, Psychodidae and Chironomidae. Oosterbroek & Theowald (1991) reported that obliquely or vertically moving mandibles are a ground plan for Tipulidae (ci = 1.0).

7. *Mandible:* (0) without poison canal; (1) with poison canal, a groove or canal in the anterodorsal position. Synapomorphy of the Tabanomorpha exclusive of Rhagionidae and Vermileonidae [Woodley 1989: character 2.1; Sinclair 1992: character 14; see also Stuckenberg (1973: 669)]. Nagatomi (1992) misinterpreted the food canal on the adoral surface of the mandible of *Pelecorhynchus* to be the poison canal (Sinclair *et al*. 1994). Mackerras & Fuller (1942) do not report a poison canal in their description of *Pelecorrhynchus* larvae (ci = 1.0).

8. *Mandible:* (0) simple; (1) mandibular brush near base; (2) brush associated with rod held in horizontal position; (3) brush associated with rod held in vertical position. The transformation from 0 to 1 was used by Hennig (1973), Woodley (1989: character 21) and Sinclair (1992: character 12) as a synapomorphy of the Tabanomorpha. The transformation from 1 to 2 is synapomorphic for Pelecorhynchidae + Athericidae + Tabanidae (Sinclair 1992: character 13). The transformation from 2 to 3 was used by Sinclair (1992: character 15) as a synapomorphy of the Athericidae + Tabanidae. Sinclair *et al*. (1994) suggested that the Vermileonidae is the sister to the remaining Tabanomorpha because they possess state 0 of this character (ci = 1.0).

9. *Mandible components:* (0) solid or weakly articulated into two components; (1) subdivided into two components; (2) subdivided into four components; (3) single component. A weak articulation (part of state 0) is a synapomorphy of Brachycera + Psychodomorpha for Sinclair (1992: character 5), but the full subdivision into two components (transformation from 0 to 1) is apomorphic for the Brachycera (Sinclair 1992: character 8). Sinclair (1992: 242)

noted that nemestrinids and acrocerids have reversed to the plesiomorphic state. The transformation from 1 to 2 was interpreted as a synapomorphy of the Empidoidea (Sinclair 1992: character 21; Cumming *et al*. 1995: character H). The transformation from 1 to 3 was interpreted by Sinclair (1992: character 22) and Cumming *et al*. (1995: character N) as a synapomorphy of the Cyclorrhapha.

Ontological studies suggest that the cyclorrhaphan mouth hook is derived from maxillary material (Jurgens *et al*. 1986; Griffiths 1994), not mandibular (Sinclair 1992; Cumming *et al*. 1995). Griffiths (1994: character 7) considers it likely that larval mandibles were lost in the ground plan of the Brachycera. If this is so, he argues that the development of a slashing distal hook on the maxilla may be a synapomorphy of all Brachycera except Stratiomyomorpha. If the distal hook of noneremoneuran Brachycera is mandibular (and not homologous with the eremoneuran mouth hook), then the loss of the mandible becomes a synapomorphy of Stratiomyomorpha + Eremoneura. The position of a sensory structure and the number of apodemes on the brachyceran mandible argue for a mandibular origin (Courtney *et al*. 2000). Cook (1949), Hennig (1973) and Courtney *et al*. (2000) considered that the brachyceran mouth hooks were composed of mandibular and maxillary components, and this seems to be a useful approach given the complexity of interpreting the ontological evidence, and the progressive fusion of mandible and maxilla found in character 10 (ci = 0.75).

10. *Maxilla:* (0) weakly attached to mandible; (1) weakly fused to basal mandibular sclerite; (2) completely fused. Griffiths (1990) commented that Stratiomyomorpha (including Pantophthalmidae) have state 1, and suggested that mouth hooks are maxillary in origin in this group. Sinclair (1992: character 16) also used the transformation from 0 to 1 as a synapomorphy of the Stratiomyomorpha. Sinclair (1992: character 18) used the transformation from 1 to 2 as a synapomorphy of the Pantophthalmidae (ci = 1.0).

11. *Maxilla:* (0) well-sclerotized lobe articulating with the basal mandibular sclerite; (1) reduced to an elongate, membranous lobe. Sinclair (1992: character 19) used this feature as a synapomorphy of the Eremoneura. Griffiths (1994: 880) suggested revising the description of the advanced state of this character to 'palpiferous lobe of maxilla elongate and primarily membranous, delimited at its base by the antenna'. Cumming *et al*. (1995: character D) rejected this rewording, and considered the character a synapomorphy of the Eremoneura. They also rejected Jürgens *et al*.'s (1986) data for the outgroup comparison of Sinclair (1992), that the cyclorrhaphan mouth hook is mandibular (ci = 1.0).

12. *Labium:* (0) large, rectangular plate; (1) V-shaped. Sinclair (1992: character 20) and Cumming *et al*. (1995: character E) used this character as a synapomorphy of the Eremoneura; also see discussion in Griffiths (1994: 880) (ci = 1.0).

13. *Mouthparts:* (0) without stout spines on labrum and maxilla; (1) with stout spines laterally on labrum and apically on maxilla. Synapomorphy of the Pelecorhynchidae [Woodley 1989: character 2.3; see Courtney *et al.* (2000; fig. 88)] ($c_i = 1.0$).

14. *Internal skeleton of head:* (0) without cephalopharyngeal skeleton; (1) with cephalopharyngeal skeleton. Synapomorphy of the Cyclorrhapha [Hennig 1973; Ferrar 1987; Cumming *et al.* 1995: character L; see McAlpine (1989: 1403)] ($c_i = 1.0$).

15. *Pharynx:* (0) filter device; (1) simple tube; (2) grinding mill. The plesiomorphic state for the Brachycera varies with different rootings in lower Diptera. Oosterbroek & Courtney (1995: character 18) reported a filter (state 0) as part of the dipteran ground plan, and appears to occur in putative sisters of Brachycera such as Tipulidae, Tanyderidae, Trichoceridae Anisopodidae, Scatopsidae, but absent in most Psychodidae. Sinclair (1992: character 2) considered a filter device to be plesiomorphic for the Brachycera, and also considered the transformation from 0 to 1 synapomorphic of the Brachycera (character 10). Sinclair (1992: character 17) used the transformation from 1 to 2 as a synapomorphy of the Stratiomyomorpha (including Pantophthalmidae). Hennig (1973) also considered a specialized pharynx (presumably the transformation from 1 to 2) a synapomorphy of the Stratiomyidae + Xylomyidae. Hennig (1973), Sinclair (1992: character 23) and Cumming *et al.* (1995: character O) considered a reversal from 1 to 0 a synapomorphy of the Cyclorrhapha. See discussion in Griffiths (1994: character 8) ($c_i = 0.66$).

16. *Metacephalic rods:* (0) absent or fixed; (1) hinged. A synapomorphy of all asiloids except Bombyliidae (Woodley 1989: character 3.2). Empidoids have a similar hinged pair of metacephalic rods. Hennig (1976) proposed that this may be a synapomorphy of Asiloidea + Empidoidea. Woodley (1989: character 34) hypothesized that they are independently derived in asiloids and empidoids, Sinclair *et al.* (1994: character C) considered hinged rods synapomorphic for the Asiloidea (excluding Bombyliidae) and Eremoneura. Note that the rods in character 3 (Woodley 1989: character 7) are articulated laterally, and not considered homologous with the rod in asiloids. Yeates (1994: character 152) found a hinged metacephalic rod in nonbombyliid asiloids [see also Yeates & Irwin (1992)]. Andersson (1974) found fixed metacephalic rods in a Mythicomyiinae Bombyliidae. Here, the advanced state has been coded as present in Empidoidea and non-bombyliid asiloids ($c_i = 0.5$).

17. *Head movement:* (0) not retractile; (1) retractile. Synapomorphy of the Tabanomorpha (Woodley 1989: character 22) ($c_i = 1.0$).

18. *Cuticle:* (0) simple; (1) encrusted with warts of calcium carbonate. Synapomorphy of Stratiomyidae + Xylomyidae (Hennig 1973; Woodley 1989: character 10) ($c_i = 1.0$).

19. *Metacephalic rods:* (0) straight; (1) spatulate at tip. Synapomorphy of the Therevidae (Woodley 1989: character 3.4; Yeates 1994: character 153). Sampling of this character within Therevidae is sparse. The absence of tentorial rods may be a synapomorphy of the Scenopinidae (Woodley 1989: 1387). Sinclair *et al.* (1994) added Hilarimorphidae [in Yeates' (1994) sense] to the Therevidae, but their larvae are unknown ($c_i = 1.0$).

20. *Abdominal segments:* (0) normal; (1) secondarily segmented. Synapomorphy of the Therevidae + Scenopinidae (Woodley 1989: character 3.3; Yeates 1994: character 154) ($c_i = 1.0$).

21. *Abdominal segments 1–7:* (0) simple; (1) bearing paired ventral prolegs armed with apical crochets. Synapomorphy of the Athericidae (Stuckenberg 1973; Woodley 1989: character 2.8) ($c_i = 1.0$).

22. *Anal segment:* (0) simple; (1) with sclerotized dorsal plates surrounding the spiracles and ending in a pair of hook-like processes. Synapomorphy of the Xylophagomorpha (Hennig 1973; Woodley 1989: character 8; Palmer & Yeates 2000) ($c_i = 1.0$).

23. *Posterior spiracle position:* (0) at apex of last abdominal segment; (1) anterodorsal on last abdominal segment; (2) anterodorsal on penultimate abdominal segment. The transformation from 0 to 2 is considered synapomorphic for Asiloidea (Hennig 1973; Woodley 1989: character 33). Yeates & Irwin (1992) note that *Heterotropus* (Bombyliidae) and Nemestrinidae have state 1. Sinclair *et al.* (1994) suggested that the transformation from 0 to 1 may be a synapomorphy of the Asiloidea, and this interpretation means that *Heterotropus* would be included in Woodley's Asiloidea and not excluded from the Bombyliidae. Yeates (1994: character 150) found that the character state 1 in *Heterotropus* was a reversal from 2 in Bombyliidae. Note that Xylophagomorpha and Vermileonidae also have state 1 ($c_i = 0.5$).

24. *Number of instars:* (0) more than three (usually four to six); (1) three. Synapomorphy of the Eremoneura (McAlpine 1989: 1402; Cumming & Cooper 1992: 95; Cumming *et al.* 1995: character F; Ferrar 1987: 13–16) ($c_i = 1.0$).

25. *Biology:* (0) free living; (1) ectoparasitic; (2) endoparasitic on insects; (3) endoparasitic on spiders. The transformation from 0 to 2 or 3 (including hypermetamorphosis) is considered a synapomorphy of the Nemestrinidae + Acroceridae (Hennig 1973; Woodley 1989: character 27). The transformation from 0 to 1 or 2 or 3 in Bombyliidae scored as a synapomorphy of the family (Woodley 1989: character 3.1). Yeates & Irwin (1992) reported that *Heterotropus* larvae are free living (state 0) [see the discussion in Yeates (1994: character 148)]. Yeates & Greathead (1997) found that the basal subfamilies of Bombyliidae are commensal or ectoparasitic and insect endoparasitism (state 2) has only arisen in a few derived

clades. Nemestrinidae (state 2) and Acroceridae (state 3) are entirely endoparasitic ($ci = 1.0$).

Pupa (character 26)

26. *Mode of pupation:* (0) pupa free; (1) pupation within last larval cuticle. Synapomorphy of Stratiomyidae + Xylomyidae (Woodley 1989: character 9) and the Cyclorrhapha (Ferrar 1987: 202; McAlpine 1989: 1409; Cumming *et al*. 1995: character K). The hardened larval cuticle is called the puparium in Cyclorrhapha ($ci = 0.5$).

Adult head (characters 27–38)

27. *Antennal postpedicel segments:* (0) more than eight; (1) eight to five; (2) four to two; (3) one. The transformation from 0 to 1 is a synapomorphy of the Brachycera (Woodley 1989: character 3; Stuckenberg 1999). The transformation from 1 to 2 is a synapomorphy of the Muscomorpha (Woodley 1989: character 24). A reduction to fewer than eight segments in some nonmuscomorphan Brachycera has been noted (Griffiths 1994: character 3). Reduction to a single flagellomere is a synapomorphy of the Acroceridae (Hennig 1973; Woodley 1989: character 29; Yeates 1994: character 5). Scenopinidae have one or two flagellomeres with two flagellomeres being found in the basal subfamilies (Yeates 1992a: character 1). Zaytsev's (1991) report of a six-articled flagellum in Bombyliidae is erroneous (Yeates 1994). Yeates & Irwin (1996: character 1) found that Apioceridae have two flagellomeres and Mydidae have one or two, with two flagellomeres optimized at the base of the Mydidae ($ci = 1.0$).

28. *Modification of antenna:* (0) simple flagella present; (1) modification into a postpedicel and stylus; (2) modification into a postpedicel and arista. Stuckenberg (1999) considered the division of the lower dipteran flagellum into a postpedicel and stylus a synapomorphy of the Brachycera, and modification of the stylus into an arista a synapomorphy of the Cyclorrhapha ($ci = 1.0$).

29. *Antennal flagellum:* (0) simple; (1) stylate. Synapomorphy of the Athericidae, some homoplasy in Rhagionidae has been noted (Stuckenberg 1973; Woodley 1989: character 2.10) ($ci = 1.0$).

30. *Ocellar setae:* (0) absent; (1) present. Synapomorphy of the Eremoneura (Griffiths 1994) ($ci = 1.0$).

31. *Adult face:* (0) simple; (1) vesture of strong bristles. Synapomorphy of the Asilidae (Woodley 1989: character 3.9; Yeates 1994: character 17) ($ci = 1.0$).

32. *Adult clypeus:* (0) flattened; (1) bulbous. Synapomorphy of the Tabanomorpha (Nagatomi 1981; Woodley 1989: character 23); the only exception noted was *Austroleptis* (Rhagionidae). Sinclair *et al*. (1994) noted state 0 in Vermileonidae, suggesting a sister group relationship to the remaining Tabanomorpha ($ci = 1.0$).

33. *Adult labellae:* (0) simple; (1) strongly reduced, fused with prementum. Synapomorphy of the Asilidae (Hennig 1973; Woodley 1989: character 3.7; Yeates 1994: character 25) ($ci = 1.0$).

34. *Adult hypopharynx:* (0) simple; (1) sclerotized, hypodermic, needle-like. Synapomorphy of the Asilidae (Woodley 1989: character 3.8; Yeates 1994: character 23) ($ci = 1.0$).

35. *Adult mouthparts:* (0) simple; (1) modified for piercing, with a pair of apical epipharyngeal blades. Many empidoids have piercing mouthparts and are predatory as adults. Daugeron (1997) optimized predation in flight at the basal node of the Empidoidea, therefore it is an additional synapomorphy of the superfamily. The form of predatory mouthparts in empidoids is different from those found in Asilidae ($ci = 1.0$).

36. *Maxillary palpus:* (0) more than two segments; (1) two segments; (2) one segment. The transformation from 0 to 1 is a synapomorphy of the Brachycera (Hennig 1973; Woodley 1989: character 4). The transformation from 1 to 2 is a synapomorphy of the Mydidae [family concept of Yeates & Irwin (1996)] (Woodley 1989: character 3.13; Yeates 1994: character 26; Sinclair *et al*. 1994: character D; Yeates & Irwin 1996: character 16). The transformation from 1 to 2 is a synapomorphy of the Scenopinidae (Yeates 1992a). The transformation from 1 to 2 is a synapomorphy of the Eremoneura (Griffiths 1994; Cumming *et al*. 1995: character A) ($ci = 0.5$).

37. *Occipital apodemes:* (0) absent; (1) present. Synapomorphy of the Bombyliidae (Yeates 1994: character 42) ($ci = 1.0$).

38. *Occipital pockets:* (0) absent; (1) present, partial or complete. Synapomorphy of the Hilarimorphidae and Bombyliidae (Yeates 1994: character 41). Also found in *Prorates*, Mydidae and Apioceridae, absent in *Apystomyia*. Hilarimorphidae were coded polymorphic (0,1) for this character ($ci = 0.66$).

Adult thorax (characters 39–55)

39. *Mesothorax:* (0) pleural suture straight or slightly sinuous; (1) pleural suture between episternum and epimeron is bent twice at almost a right angle. Synapomorphy of the Brachycera (Hennig 1973). It occurs occasionally in some lower Diptera such as Psychodidae and Scatopsidae ($ci = 1.0$).

40. *Metathorax:* (0) without postspiracular plate; (1) with postspiracular plate. Synapomorphy of the Athericidae and Tabanidae (Stuckenberg 1973; Woodley 1989: character 2.7) ($ci = 1.0$).

41. *Costal vein:* (0) circumambient; (1) ending at or before M_2. Synapomorphy of the Stratiomyidae + Xylomyidae (Hennig 1973, 1976; Woodley 1989: character 12). Woodley (1989: character 3.6) considered this character a synapomorphy of the Scenopinidae but Yeates (1992a: character 8) relegated this character to a synapomorphy of the Scenopininae and

Proratinae. The costal vein narrows slowly in *Hilarimorpha* and it does not possess the advanced state ($ci = 1.0$).

42. *Radial veins:* (0) evenly distributed; (1) crowded towards costal margin, R_5 ending before wing apex. Synapomorphy of the Stratiomyidae (Woodley 1989: character 19) ($ci = 1.0$).

43. *Wing vein R_{2+3}:* (0) long, ending near wing apex; (1) shortened, ending near R_1. Synapomorphy of the Athericidae (Stuckenberg 1973; Woodley 1989: character 2.9), homoplasy in some species of *Chrysopilus* (Rhagionidae) has been noted ($ci = 1.0$).

44. *Wing vein R_{4+5}:* (0) forks ending either above or below wing tip; (1) forks encompassing wing tip; (2) unbranched. The transformation from 0 to 1 is a synapomorphy of the Tabanidae (Nagatomi 1981; Woodley 1989: character 2.11). Homoplasy in *Pelecorhynchus* has been noted. The transformation from 0 to 2 is a synapomorphy of the Cyclorrhapha (Cumming *et al.* 1995: character J). See also Griffiths (1972: 60) and Chvála (1983: 27–29) ($ci = 1.0$).

45. *R_5 and M_1:* (0) simple; (1) strongly curved at tip of wing, ending anterior to wing apex. Synapomorphy of the Mydidae + Apioceridae (Woodley 1989: character 3.10; Yeates 1994: character 58; Yeates & Irwin 1996: character 39). Scenopininae also have R_5 and M_1 weakly curved forward to be level with or just anterior to the wing tip ($ci = 1.0$).

46. *Wing vein M_3:* (0) present; (1) absent. Synapomorphy of the Hilarimorphidae and Bombyliidae (Yeates 1994: character 59). Scenopinidae and Eremoneura have also lost M_3 (Hennig 1973; Yeates 1992a: character 10) ($ci = 0.33$).

47. *Wing venation:* (0) diagonal vein absent; (1) diagonal vein present. Synapomorphy of the Nemestrinidae (Woodley 1989: character 28; Yeates 1994: character 61). Superficial resemblance in *Exeretonevra* (Xylophagidae) noted (Palmer & Yeates 2000) ($ci = 1.0$).

48. *Discal cell:* (0) large; (1) small, short and broad. Synapomorphy of the Stratiomyidae (Woodley 1989: character 20) ($ci = 1.0$).

49. *Veins CuA_2 and A_1:* (0) apices far apart; (1) apices close together; (2) apices fused. The transformation from 0 to 1 is a synapomorphy of the Brachycera (Woodley 1989: character 5). The transformation from 1 to 2 is synapomorphy of the Eremoneura (Hennig 1973; Cumming *et al.* 1995: character C; Griffiths 1994). Hennig (1973) reported state 2 in Stratiomyidae and Xylomyidae ($ci = 0.66$).

The distal widening of wing cell m1 was used as a synapomorphy of the Scenopinidae (Woodley 1989: character 3.5; Yeates 1994: character 63). Yeates (1992a: character 12) relegated this character to a synapomorphy of the Scenopininae. Hence, it was not coded here.

50. *Wing cell m3:* (0) open; (1) closed before wing margin. Synapomorphy of the Xylomyidae and Pantophthalmidae, some homoplasy reported in Xylophagomorpha (Woodley 1989: character 16) ($ci = 0.5$).

51. *Lower calypter:* (0) simple; (1) much enlarged. Independent derivation of the advanced state used as a synapomorphy of the Tabanidae and Acroceridae (Hennig 1973; Woodley 1989: characters 2.12, 30; Yeates 1994: character 67). Hennig (1973) considered the development of a lower calypter ('squamula thoracalis') a synapomorphy of the Brachycera, but it is not coded as such here ($ci = 0.5$).

52. *Hind coxa:* (0) simple; (1) well-developed rounded projection on anterior face. Yeates (1994: character 92) found that this feature was a synapomorphy of the Therevidae (including *Apsilocephala*). More rounded, nonhomologous projections are found in some nonmuscomorphan Brachycera and in *Hilarimorpha* and some Bombyliidae (Yeates 1994; D. Webb, personal communication) ($ci = 1.0$).

Thickened spine-like bristles on the hind femora have been interpreted as a synapomorphy of the Mydidae (Woodley 1989: character 3.12; Yeates 1994: character 95). Yeates & Irwin (1996: character 33) redefined the Mydidae and relegated this character to a synapomorphy of the apomorphic Mydidae.

53. *Fore tibial spurs:* (0) present; (1) absent. Tibial spurs emerge from the membrane between the tibia and the first tarsomere and usually have a vestiture of microtrichia (Hennig 1973; Woodley 1989). Loss of fore tibial spurs was considered a synapomorphy of the Stratiomyidae, Xylomyidae and Pantophthalmidae (Woodley 1989: character 11). Loss of all tibial spurs (including those on the forelegs) was considered a synapomorphy of the Muscomorpha (Woodley 1989: character 25). Yeates (1994: character 90) found true mid-tibial spurs in a number of Bombyliidae. Independent losses have been noted in some nonmuscomorphan infraorders of Brachycera (Griffiths 1994: character 2) ($ci = 0.5$).

54. *Hind tibial spurs:* (0) present; (1) absent. The loss of all tibial spurs was considered a synapomorphy of the Muscomorpha (Woodley 1989: character 25; Yeates 1994: character 89) and the loss of hind tibial spurs was also recorded as a synapomorphy of the Stratiomyidae (Woodley 1989: character 17). Independent losses have been noted in some nonmuscomorphan infraorders of Brachycera (Griffiths 1994: character 2) ($ci = 0.5$).

55. *Empodium:* (0) pad-like; (1) bristleform; (2) absent. Synapomorphy of the Heterodactyla (Woodley 1989: character 32; Griffiths 1994: character 1; Yeates 1994: character 97). Bequaert (1961) and Yeates & Irwin (1996: character 37) found that the empodium is absent (the transformation from 1 to 2) in Apioceridae and Mydidae ($ci = 1.0$).

Adult abdomen, nongenitalic (characters 56–58)

56. *Abdominal tergite 2:* (0) simple; (1) with an area of modified setae. Synapomorphy of the Scenopinidae (Yeates 1992a: character 15, 1994: character 100) ($ci = 1.0$).

57. *Abdominal plaques:* (0) present; (1) absent. Synapomorphy of the Cyclorrhapha (Stoffolano *et al.* 1988; Wiegmann *et al.* 1993; Cumming *et al.* 1995: character I) ($ci = 1.0$).

58. *Rectal papillae:* (0) four; (1) supernumerary (12–80). Synapomorphy of the Apioceridae + Mydidae (Woodley 1989: character 3.11). Yeates & Irwin (1996) reported that *Neorhaphiomydas* had only four rectal papillae ($ci = 1.0$).

Adult male genitalia (characters 59–91)

59. *Hypopygium:* (0) not permanently rotated 360°; (1) rotated permanently through 360°. Synapomorphy of the Cyclorrhapha (Hennig 1973; Cumming *et al.* 1995: character 7). Facultative circumversion or rotation less than 360° sometime after eclosion may occur in empidoids and asiloids (McAlpine 1989; Yeates 1994: 83–88; Cumming *et al.* 1995) ($ci = 1.0$).

60. *Segment 9:* (0) ring-like; (1) tergite and sternite separate. Synapomorphy of the Brachycera (Sinclair *et al.* 1994: character 3) ($ci = 1.0$).

61. *Postgonites:* (0) absent; (1) present. At one time interpreted as gonostyli (Cumming *et al.* 1995), the postgonites are a synapomorphy of the Eremoneura (Sinclair 2000). See character 71 ($ci = 1.0$).

62. *Epandrium articulation:* (0) free; (1) articulated on gonocoxites. Sinclair *et al.* (1994: character 12) found that a synapomorphy of the Muscomorpha is the epandrium (with anterolateral extensions) articulated on the gonocoxites. Found also in Tabanidae and Xylomyidae ($ci = 0.33$).

63. *Epandrium:* (0) single sclerite; (1) divided into two pieces. Yeates (1992a) considered this character a synapomorphy of the Scenopinidae (including Proratinae and Caenotinae). Also occurs in Mydidae and Apioceridae (Yeates 1994: character 105; Yeates & Irwin 1996: character 52), and some derived Asilidae (Sinclair *et al.* 1994) ($ci = 0.5$).

64. *Epandrium:* (0) simple posterior margin; (1) posterior margin deeply emarginate. Synapomorphy of the Eremoneura (Cumming *et al.* 1995: character 4). Note that the epandrium is entirely divided into two pieces in the Scenopinidae, Apioceridae and Mydidae (character 66) ($ci = 1.0$).

65. *Epandrium and hypandrium:* (0) fused ring; (1) separate; (2) articulate on one another. The transformation from 0 to 1 is a synapomorphy of the Brachycera (Sinclair *et al.* 1994: character 3; Griffiths 1996). The transformation from 1 to 2 is a synapomorphy of the Asilidae (Sinclair *et al.* 1994: character 19; Yeates 1994: character 107; Yeates & Irwin 1996: character 55) ($ci = 1.0$).

66. *Surstyli:* (0) absent; (1) present, composed of epandrium dorsally and bacilliform sclerites ventrally. Cumming *et al.* (1995: character 9) made this strict definition of surstyli to exclude similar but nonhomologous features in some asiloids (however, *Apsilocephala* is included; cf. Nagatomi *et al.* 1991c). Synapomorphy of the Cyclorrhapha, but also independently

derived in some lineages of Empidoidea (coded 0 and 1) (Cumming *et al.* 1995). Absent in Lonchopteridae (Cumming *et al.* 1995: character 21). The revised epandrial hypothesis (Cumming *et al.* 1995) considers that the surstyli are derivatives of tergite 9 dorsally and subepandrial membrane ventrally (between the aedeagus and sternite 10). See character 67 ($ci = 1.0$).

67. *Subepandrial membrane:* (0) membranous; (1) sclerotized along its length, forming bacilliform sclerites (processus longi) laterally. Synapomorphy of the Eremoneura (Cumming *et al.* 1995: characters 1, 2). Note that the character state is also present in *Apsilocephala*, and some sclerotization is found in many other asiloids ($ci = 0.5$).

68. *Hypandrium and gonocoxites:* (0) separate; (1) fused. Synapomorphy of the Athericidae + Tabanidae (Woodley 1989: character 2.4; Sinclair *et al.* 1994: character 6). Synapomorphy of the Eremoneura (Cumming *et al.* 1995: character 5). The hypandrium has been lost or fused with the gonocoxites in Acroceridae, various asiloids (Yeates 1994: character 110). Yeates (1994) noted cases where the hypandrium appeared to be in the process of loss and others where it appeared to be becoming fused to the gonocoxites ($ci = 0.33$).

69. *Gonocoxal apodemes:* (0) moderate length, extending to anterior margin of hypandrium; (1) reduced or absent; (2) elongate, extending well beyond hypandrium. The transformation from 0 to 1 is a synapomorphy of the Xylomyidae (Woodley 1989: character 14). Yeates (1992a) found long gonocoxal apodemes in *Bonjeania* Irwin and Lyneborg (Therevidae), which is a highly autapomorphic genus (Yang *et al.* 1999; Winterton *et al.* 2000). Hence, Therevidae are coded 1. Yeates (1994: character 113) found that gonocoxal apodemes were reduced or lost in most Bombyliidae and very small in Therevidae. Sinclair *et al.* (1994: character 5) found long gonocoxal apodemes (0 to 2) to be a synapomorphy of the Athericidae + Tabanidae within Tabanomorpha. Sinclair *et al.* (1994: character 16) found short gonocoxal apodemes to be a synapomorphy of the Bombyliidae except Mythicomyiinae. Yeates (1994: character 113) considered that the long posterior processes in Mythicomyiinae were part of the aedeagal sheath, not gonocoxal apodemes. However, Bombyliidae are coded (1,2) here. Cumming *et al.* (1995: character 8) used the transformation from 0 to 1 as a synapomorphy of the Cyclorrhapha, but with considerable homoplasy in Empidoidea (coded 0 and 1 here). Gonocoxal apodemes are generally short in Empidoidea, but in Atelestinae the apodemes are very long (Cumming *et al.* 1995: character 13; Sinclair 2000) ($ci = 0.5$).

70. *Gonostyli articulation:* (0) transverse or oblique; (1) dorso-ventral. Lower Diptera, Xylophagomorpha, Stratiomyomorpha, Tabanomorpha and Nemestrinidae have (0), the remainder have (1) (Yeates 1994: character 122; Griffiths 1996). Sinclair *et al.* (1994: character 13) incorrectly considered

this a synapomorphy of the Muscomorpha. Coded as unknown in Acroceridae, Mydidae and Eremoneura which lack gonostyli (see character 71) (ci = 1.0).

71. *Gonostyli:* (0) present; (1) absent. The apomorphic state is an independent synapomorphy for each of the Acroceridae and Mydidae (Yeates 1994: character 122; Sinclair *et al.* 1994: character 14; Yeates & Irwin 1996: character 61). Sinclair *et al.* (1994) considered gonostyli lost in all Eremoneura (character 17). However, Cumming *et al.* (1995: character 10) considered the postgonites to be homologous with the gonostyli under the revised hypandrial hypothesis. After re-evaluating the gonostyli in Eremoneura, Cumming & Sinclair (1996) and Sinclair (2000) considered them absent, and they are coded as absent here. There is considerable variation in this character in lower Cyclorrhapha — postgonites are absent in Ironomyiidae, Sciadoceridae, Phoridae, some Platypezidae and most Pipunculidae (Cumming *et al.* 1995). Gonostyli are homologous with parameres under the periandrial theory (Griffiths 1996). The postgonites have a single abductor muscle (M39) in Calliphoridae, unlike the abductor and adductor muscles (M27, M28) found in lower Brachycera (Griffiths 1996) (ci = 0.3).

72. *Gonostyli:* (0) apical; (1) subapical. Synapomorphy of the Asiloidea + Eremoneura (Sinclair *et al.* 1994: character 17). Hilarimorphidae have the apomorphic state and Bombyliidae (including Mythicomyiinae) have the plesiomorphic state. Acroceridae, Mydidae and Eremoneura, with gonostyli absent, were coded '?' for this character (ci = 0.5).

73. *Aedeagus:* (0) free; (1) surrounded by parameral sheath; (2) fused to parameral sheath at apex, forming phallus. Wood (1991) proposed that the aedeagus covered by a sheath of parameral origin be termed the phallus, and Griffiths (1994) agreed with this terminology. Sinclair *et al.* (1994) used the transformation from 0 to >1 as a synapomorphy of the Brachycera and from 1 to >2 as a synapomorphy of the Brachycera except for the Xylophagomorpha and Tabanomorpha (character 8). Note that Tabanomorpha and Xylophagomorpha have the sheath (state 1), it is just not fused to the aedeagus at the tip (state 2). Griffiths (1996: characters 4, 5) believes that some Tabanomorpha may not have apomorphic state 1, so doubts 1 is a ground plan for the Brachycera. Note that some lower Diptera have fused parameres (Blephariceromorpha, Psychodomorpha and Bibionomorpha), but this fusion is not the same as state 1 here. Griffiths (1996: character 5) appears to have confused Sinclair *et al.*'s (1994) conception of the transformation from 1 to >2 in Stratiomyomorpha and Muscomorpha (p. 110), but nevertheless doubts the validity of the transformation from 1 to >2 (p. 111). Griffiths (1990) found a sheathed aedeagus in Xylophagomorpha, Tabanomorpha Nemestrinoidea and Asiloidea (Pleroneura) and found a free aedeagus in Stratiomyidae, Xylomyidae and Eremoneura (ci = 1.0).

74. *Aedeagus:* (0) single tube apically; (1) bifid or trifid at the apex. Synapomorphy of the Scenopinidae (including Proratinae and Scenopininae) (Yeates 1992a: character 20, 1994: character 117) (ci = 1.0).

75. *Phallus:* (0) undivided; (1) subdivided into a dorsal guide and a ventral needle-like component. Synapomorphy of the Apioceridae (Sinclair *et al.* 1994: character 20; Yeates & Irwin 1996: character 68) (ci = 1.0).

76. *Ejaculatory apodeme:* (0) present, rod-like; (1) concave plate. Synapomorphy of the Stratiomyomorpha including Pantophthalmidae (Ovtshinnikova 1994; Sinclair *et al.* 1994; red-coloured sclerite). Griffiths (1990) used this character as a synapomorphy of the Xylophagomorpha + Tabanomorpha (ci = 1.0).

77. *Ejaculatory apodeme:* (0) not laterally compressed; (1) laterally compressed. The advanced state is found in Bombyliidae and a number of other asiloids; the plesiomorphic state is found in Scenopinidae + Therevidae, Hilarimorphidae and *Apsilocephala* (Yeates 1994: character 120) (ci = 0.5).

78. *Ejaculatory apodeme:* (0) simple, without posterior projection; (1) with a posterior extension into the sperm sac (endoaedeagal guide). Synapomorphy of the Brachycera (Sinclair *et al.* 1994: character 2), secondarily lost in some Xylophagomorpha, Stratiomyomorpha and most Muscomorpha (the latter coded 0 here). Griffiths (1994) considered this feature a synapomorphy of the Tabanomorpha (as the endophallic guide). I have coded the advanced state in Xylophagomorpha, Tabanomorpha and Nemestrinidae (Richter & Ovtshinnikova 1996), and taking into account homoplasy discussed by Sinclair *et al.* (1994), have coded Vermileonidae as polymorphic (0,1) for this character (ci = 0.66).

79. *Ejaculatory apodeme:* (0) operating in horizontal plane as a piston; (1) operating in dorsoventral plane as a lever. Synapomorphy of the Empidoidea (Cumming *et al.* 1995: character 11) (ci = 1.0).

80. *Lateral aedeagal apodemes:* (0) absent; (1) large, external; (2) small, retracted within base of phallus. Yeates (1994: character 119), found state 1 in Bombyliidae, Asilidae, Nemestrinidae and Acroceridae, but state 0 in Hilarimorphidae. Ovtshinnikova & Yeates (1998) noted state 2 in Scenopinidae. Griffiths found lateral aedeagal apodemes (as external ejaculatory sclerites) present as an apomorphy of Tabanomorpha, Nemestrinoidea + Asiloidea. Sinclair *et al.* (1994: character 1, as lateral ejaculatory processes) used the transformation from 0 to >1 as a synapomorphy of the Brachycera, but lost or modified in some Xylophagomorpha, Tabanomorpha, all Stratiomyomorpha (their character 9), some asiloids and all Eremoneura. Sinclair *et al.* (1994: character 18) considered the transformation from 1 to >2 a synapomorphy of the Therevidae and Scenopinidae (including Hilarimorphidae). Ovtshinnikova (1994) reported small lateral aedeagal apodemes (as ejaculatory sclerites) in Pantophthalmidae.

Yeates & Irwin (1992) reported state 1 in *Bonjeania* (Therevidae), thus adding homoplasy to Sinclair *et al.*'s (1994) conception that the transformation from 1 to 2 is a synapomorphy of the Therevidae. Ovtshinnikova & Yeates (1998) also found modified lateral aedeagal apodemes (state 2) in an *Anabarhynchus* Macquart species (Therevidae). Yeates & Irwin (1996: character 66) and Sinclair *et al.* (1994: character 21) found reduced lateral aedeagal apodemes in Apioceridae and Mydidae (state 2). Griffiths (1996: character 1) doubts that lateral aedeagal apodemes are plesiomorphic in Brachycera because of their loss in Stratiomyomorpha, and doubts Ovtshinnikova's (1994) finding that they are present in Pantophthalmidae. Cumming *et al.* (1995: character 3) used the transformation from 1 to 0 as a synapomorphy of the Eremoneura (ci = 0.4).

81. *Sperm pump:* (0) inside parameral sheath; (1) lying exposed on a concave aedeagal sclerite; (2) separated from ventral sclerite, lying free in base of phallus; (3) free from base of phallus. The transformation from 0 to 1 is used as a synapomorphy of the Stratiomyomorpha (Sinclair *et al.* 1994: character 10). The transformation from 1 to 2 is used as a synapomorphy of the Xylomyidae + Stratiomyidae (Sinclair *et al.* 1994: character 11). Cumming *et al.* (1995: character 6) used the transformation from 0 to 3 as a synapomorphy of the Cyclorrhapha (ci = 1.0).

82. *Sperm pump:* (0) without strongly developed tines; (1) with strongly developed tines. Synapomorphy of the Athericidae and Tabanidae (Stuckenberg 1973; Woodley 1989: character 2.5). Sinclair *et al.* (1994) found the advanced state also in the rhagionid *Bolbomyia Loew* (ci = 1.0).

83. *Male tergite 10:* (0) present; (1) absent. Used as a synapomorphy of the Heterodactyla (Sinclair *et al.* 1994: character 15), but Acroceridae have the advanced state (Yeates 1994: character 124). Griffiths (1994) incorrectly considered this a synapomorphy of the Eremoneura. Hennig (1973) reported the advanced state in Tabanidae (not coded as such here) (ci = 1.0).

84. *Muscle M1, protractor of aedeagal sheath:* (0) present; (1) absent. This muscle is present in Brachycera but absent in Mydidae and Acroceridae (Ovtshinnikova 1989; Yeates 1994: Appendix 2, character 1) (ci = 0.5).

85. *Muscle M5:* (0) divided into two; (1) single muscle; (2) divided into three. M5 is divided into three bundles in Asilidae, Apioceridae, Therevidae and Scenopinidae. Mydidae and Tabanidae have a single M5 bundle, and Bombyliidae and the other Brachycera have two (Ovtshinnikova 1989; Yeates 1994: Appendix 2, character 10; Ovtshinnikova & Yeates 1998) (ci = 0.66).

86. *Muscle M27, adductor of gonostylus:* (0) present; (1) absent. Synapomorphy of the Mydidae (Ovtshinnikova 1989; Yeates 1994: Appendix 2, character 8; Ovtshinnikova & Yeates 1998). Also lacking in Cyclorrhapha (Ovtshinnikova 1994) (ci = 0.5).

87. *Muscle M28, abductor of gonostylus:* (0) present; (1) absent. The advanced state is found in Acroceridae and Mydidae (Ovtshinnikova 1989; Yeates 1994: Appendix 2, character 9; Ovtshinnikova & Yeates 1998). Sinclair *et al.* (1994: character 14) noted its absence in Acroceridae (ci = 0.5).

88. *Muscle M3(0), retractor of ejaculatory apodeme:* (0) present; (1) absent. This muscle is generally present in Brachycera but absent in Mydidae and Stratiomyomorpha (except Pantophthalmidae) (Ovtshinnikova 1989, 1994; Yeates 1994: Appendix 2, character 3) (ci = 0.5).

89. *Muscle M31, protractor of the ejaculatory apodeme:* (0) present; (1) absent. This muscle is generally present in Brachycera but absent in Stratiomyidae and Xylomyidae (Ovtshinnikova 1989, 1994) (ci = 1.0).

90. *Muscle M32, protractor of ejaculatory apodeme:* (0) present; (1) absent. These muscles are generally present in Brachycera, and even in some lower Diptera such as Trichoceridae. They are associated with the lateral aedeagal apodemes (Griffiths 1994; Sinclair *et al.* 1994). Apomorphically the muscles are absent in the Mydidae and Stratiomyomorpha (except Pantophthalmidae) (Ovtshinnikova 1989, 1994; Yeates 1994: Appendix 2, character 4). Sinclair *et al.* (1994) used this as a synapomorphy of the Eremoneura (ci = 0.33).

91. *Muscle M38, adductor of lateral process of gonocoxite:* (0) absent; (1) present. M38 is present in the asiloid families Asilidae, Apioceridae and Mydidae, and one of two therevids studied [Therevidae are coded (0,1)] (Ovtshinnikova 1989; Yeates 1994: Appendix 2, character 7; Ovtshinnikova & Yeates 1998) (ci = 1.0).

Adult female genitalia (characters 92–100)

92. *Female abdominal tergite 9:* (0) present; (1) absent. Synapomorphy of the Eremoneura (Griffiths 1983: 484; Cumming & Cooper 1992: 954; Cumming *et al.* 1995: character B) (ci = 1.0).

93. *Acanthophorites:* (0) absent; (1) present. Woodley (1989) mentioned this character as a possible synapomorphy uniting the Asiloidea and Empidoidea. Acanthophorites (and their associated spines) occur in all asiloid families (Yeates 1994: character 139; Yeates & Irwin 1996: character 69) and appear to have been lost numerous times in the superfamily. Within Bombyliidae, all basal subfamilies lack acanthophorites (Yeates 1994), so this family was coded 0. The homology of the acanthophorites and spines in Empidoidea with those in Asiloidea is the subject of debate. Griffiths (1990, 1994) discounted their homology, but Sinclair *et al.* (1994: character B) considered them homologous and considered this character a synapomorphy of the Heterodactyla. Sinclair *et al.* (1994) considered the presence of acanthophorites to be plesiomorphic within Empidoidea. Hence, the empidoids were coded 1 for this character (ci = 0.5).

94. *Female cercus:* (0) first segment normal; (1) first segment expanded ventrolaterally. Synapomorphy of the Tabanomorpha (including Vermileonidae; Sinclair *et al.* 1994: character A). Griffiths (1996) doubted this synapomorphy as the shape of the cerci is quite different in the Vermileonidae and other Tabanomorpha (ci = 1.0).

95. *Number of spermathecae:* (0) three; (1) two; (2) one. Three spermathecae is the plesiomorphic condition in Diptera and Brachycera [see Nagatomi & Liu (1995) for the spermathecal number in basal Brachycera]. The transformation from 0 to 1 has been used as a synapomorphy of the Xylomyidae and the transformation from 0 to 2 is a synapomorphy of the Empidoidea (Hennig 1973; Woodley 1989: characters 13, 35; Cumming *et al.* 1995: character G). Yeates (1992a: character 18) used the transformation from 0 to 1 as a synapomorphy of the Scenopinidae. Yeates (1994: character 142) noted that Acroceridae also have only two spermathecae, and Nemestrinidae have two to three spermathecae (coded 0 and 1 here). The number of spermathecae in *Opetia* Meigen was not determined because they are difficult to observe (Chandler 1981). Cumming *et al.* (1995: character Q) interpreted *Opetia* as having no spermathecae. If this scoring is correct the female reproductive system of this fly is different from all other Diptera (ci = 0.6).

96. *Spermathecal ducts:* (0) of moderate length, at most less than the length of the abdomen; (1) very long, at least much longer than the abdomen. Synapomorphy of the Xylomyidae (Woodley 1989: character 15), and homoplasy reported in *Xylophagus* (Xylophagidae) (ci = 1.0).

97. *Complex sperm pump:* (0) absent; (1) present, well-developed musculature and sclerotized collars at each end. Synapomorphy of the Bombyliidae (Yeates 1994: character 145) (ci = 1.0).

98. *Female cerci:* (0) two-segmented; (1) one-segmented. Synapomorphy of the Muscomorpha (Hennig 1973; Woodley 1989: character 26; Yeates 1994: character 140). Independent derivations in nonmuscomorphan infraorders of Brachycera have been noted (Griffiths 1994: character 6). Synapomorphy of the Athericidae + Tabanidae, an exception is the *Austroleptis* (Rhagionidae) with a single-segmented cercus (Woodley 1989: character 2.6) (ci = 0.5).

99. *Female cerci:* (0) simple; (1) with strong lateral process. Synapomorphy of the Pelecorhynchidae (Woodley 1989: character 2.2). Illustrated in Nagatomi & Iwata (1978). Woodley (1989) noted some homoplasy in a few rhagionid genera (ci = 1.0).

100. *Female cerci:* (0) simple; (1) separated by abdominal tergite 10. Synapomorphy of the Stratiomyidae (Woodley 1989: character 18). Illustrated in Nagatomi & Iwata (1978). Woodley (1989) reported this feature to be present in Pantophthalmidae as well (coded as such here). Griffiths (1994) found the apomorphic state in Stratiomyidae and some Xylomyidae (coded 0 and 1 here) (ci = 1.0).

Table 2 Synaptomorphies of infraorders and other major groups

Clade	Synapomorphies (ACCTRAN)
Stratiomyomorpha	10, 15, 41, 50, 53, 76, 81, 100
Xylophagomorpha	2, 3, 22
Tabanomorpha	17, 94
Muscomorpha	27, 53, 54, 62, 80, 98
Heterodactyla	70, 72, 83
Asiloidea	23, 77
Eremoneura	30, 36, 49, 61, 64, 66, 67, 68, 71, 92

Nervous system (character 101)

101. *Adult ventral nerve cord:* (0) neuromeres T1 + T2 and T3 + A1 separate; (1) neuromeres T1 + T2 and T3 + A1 fused. Yeates & Merritt (2001) found that Stratiomyomorpha, Tabanomorpha and Xylophagomorpha had fused neuromeres T1, T2, T3 and A1 (ci = 0.5).

Phylogenetic analysis

The matrix (Table 1) was analysed heuristically using PAUP 4.0 (Swofford 1999) with the following settings: multistate taxa = uncertainty (not polymorphism), tree bisection reconnection branch swapping and 10 random addition sequences. A single most parsimonious tree resulted (Fig. 1), with length 178 steps [ci = 0.74; retention index (RI) = 0.78; CI, excluding uninformative characters = 0.66]. Support for nodes on Fig. 1 is indicated by their Bremer support (decay index) values (Bremer 1988). The higher the value for Bremer support, the greater the support. These values represent the number of synapomorphies supporting any alternative resolution that would be needed to break the clade. Synapomorphies (under ACCTRAN optimization) for named nodes in Fig. 1 are given in Table 2.

Discussion

These results represent a synthesis of morphological research to uncover the relationships of basal brachyceran flies over the past 200 years. An important conclusion is that there is very little morphological evidence available on the relationships between the infraorders of Brachycera. This may indicate that these lineages differentiated contemporaneously. The first molecular data set addressing these relationships also indicates little differentiation between the infraorders (Wiegmann pers. comm.), lending further credence to this notion. The tree produced here suggests a phylogeny that is in agreement with recent classifications of the group to a large extent, summarized by Yeates & Wiegmann (1999). I will concentrate on the few novel groupings here.

Xylophagomorpha + Tabanomorpha + Stratiomyomorpha

This was a surprising clade that emerged from the analysis, and is weakly supported, mainly by character 101, the apomorphic
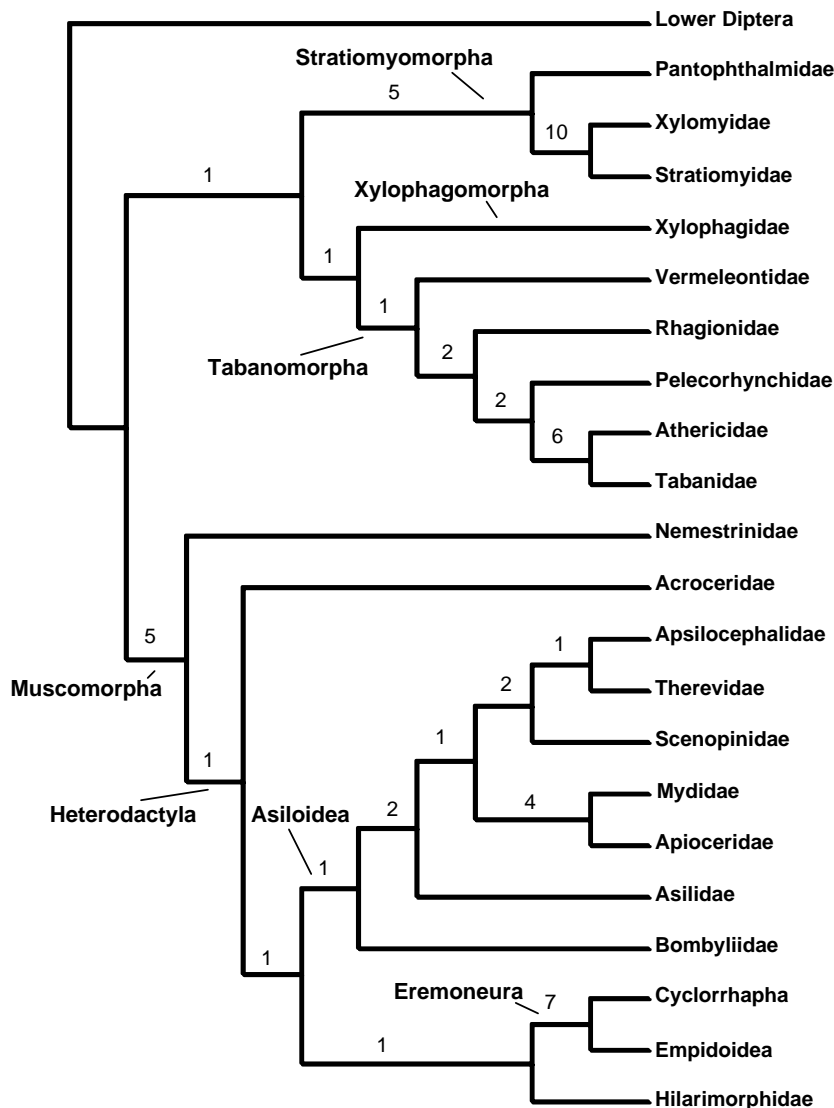
Fig. 1 Most parsimonious tree from PAUP analysis, with Bremer support (decay indices) mapped on to nodes. Length = 178; consistency index (CI) = 0.74; retention index (RI) = 0.78.

fusion of thoracic ganglia. This is an intriguing hypothesis that is worth further scrutiny. The clade of Tabanomorpha + Xylophagomorpha is supported by character 73 (aedeagus fused to parameral sheath) and character 78 (ejaculatory apodeme with posterior projection into the sperm sac). Both these features require further scrutiny before they can be considered robust evidence of relationships. The Xylophagomorpha and Tabanomorpha have predatory larvae, and further evidence of relationships may be found in the larval mouthpart structure. For example, the distribution of a poison canal or duct on the mandibles in these infraorders may be informative at this level. The relationships between the families of Tabanomorpha found in this study are exactly the same as those found by Wiegmann *et al*. (2000) using 28S ribosomal gene sequences. The congruence discovered using two independent data sources gives us encouragement that the phylogeny represents the true relationships for this group.

Hilarimorphidae and the Eremoneura
Another surprising result was the grouping of the enigmatic family Hilarimorphidae with the Eremoneura. On examination of the data, the only character supporting this position is the loss of wing vein M_3 (character 46). This is a phylogenetically labile character that appears in asiloids and other groups. However, this result indicates that there is little morphological data unequivocally placing the hilarimorphids in the Asiloidea, where they are traditionally placed. Tree length increases by only two steps (161) when the hilarimorphids are placed in the Asiloidea as sister to the Bombyliidae.

The therevoid group of families

The scenopinids, apsilocephalids and therevids are united by the secondary segmentation of the larvae (character 20). However, the distribution of this character requires clarification because the apsilocephalids are unknown as larvae. Apsilocephalidae was recently removed from the Therevidae (Nagatomi *et al.* 1991) and these two families are united by the presence of a distinct knob (character 52) on the anterior surface of the hind coax that is not found in scenopinids. A similar but nonhomologous knob is found in a more ventral position in some tabanomorphs and a bombyliid (Yeates 1994).

The early evolution of the Brachycera

Fossil evidence indicates that the Brachycera probably arose in the early Jurassic (Woodley 1989; Yeates 1994; Grimaldi 1999), and I have suggested here that the infraorders may have diverged relatively quickly at this time due to the lack of support in both morphological and molecular data sets for particular sister group relationships between them. A diverse assemblage of rhagionids and their relatives are the commonest brachyceran fossils from the Jurassic (Evenhuis 1994). This was a warm, wet period of Earth history when all continents were united in the supercontinent Pangea. Not surprisingly, all infraorders are widely distributed around the globe. Identifying the geographical origin of Brachycera is quite a challenge as many of the most basal extant groups of the brachyceran infraorders have widespread distributions in both Gondwanan and Laurasian sectors of Pangea. More detailed phylogenetic information on families such as the Xylophagidae, Rhagionidae and Stratiomyidae may shed light on this issue. The oldest fossils attributable to the Brachycera are Laurasian.

The early brachyceran lineages have larvae that are either predatory or saprophytic in soil or decaying organic matter with adults that feed on nectar and pollen (if at all). The larvae of these groups no doubt lived in the extensive gymnosperm forests of the Jurassic period (White 1986), either feeding on decaying plant material or preying on larvae that did. Adult flies belonging to the Jurassic brachyceran lineages possessed two important morphological head modifications: a shortened, brachyceran antenna and the development of pseudotracheae on the labellar lobes (Stuckenberg 1999). These lapping and sponging mouthpart modifications allowed flies to exploit plant and hemipteroid exudates (Labandeira 1997) and the antennal modifications may have facilitated the exploration of diverse plant surfaces for olfactory cues using antennal and mouthpart chemoreceptors (Stuckenberg 1999).

The earliest lineages of Muscomorpha (the Nemestrinidae and Acroceridae) have endoparasitic larvae and adults that feed on nectar and pollen. Upper Jurassic nemestrinids (Ren 1998) with elongate mouthparts may have fed on nonangiospermous anthophytes such as Bennettitales and Gnetales (Grimaldi 1999). The first major radiation of muscomorphan flies belonged to the Asiloidea. Grimaldi (1999) used palaeontological and phylogenetic evidence to link much of the early diversification of these flies to the diversification of angiosperms in the early Cretaceous. Evidence for the monophyly of the Asiloidea is weak, and the Eremoneura either form the sister group to part or all of this assemblage. The Eremoneura probably evolved from asiloid-like ancestors in the early Cretaceous and their adults fed on nectar and pollen from the first evolving angiosperms.

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