

EVOLUTIONARY ORIGIN OF THE CYCLORRHAPHA (DIPTERA): TESTS OF ALTERNATIVE MORPHOLOGICAL HYPOTHESES

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Abstract—The higher flies, infraorder Cyclorrhapha [=Muscomorpha (McAlpine, 1989)], have undergone enormous radiation since the Cretaceous (~100 Myr). Rapid morphological evolution in cyclorrhaphans has made their phylogenetic placement with respect to more primitive clades a long-standing problem in dipteran systematics. Of the two most plausible hypotheses, one treats the Cyclorrhapha as sister group to the orthorrhaphous superfamily Empidoidea [=Empidiformia (Hennig, 1948), Orthogenya (Brauer, 1883)], while the other places them *within* the empidoids. The debate over cyclorrhaphan origins has heretofore focused on homology interpretations for a few character systems, particularly the male genitalia. We provide the first attempt to assemble and quantify all of the available morphological evidence. By cladistic analysis of these data under alternative codings of genitalic features reflecting opposing homology theories, and then excluding these features altogether, we sought to judge which genitalic theory is better supported by the evidence as a whole, and how much the debate matters to resolving cyclorrhaphan origins. Using the analog of a factorial design, we also measured the effect of alternative transformation series in several other controversial characters, of outgroup choice and of successive weighting. Under all manipulations, including both genitalic codings, the Cyclorrhapha originate within the Empidoidea, near the family Atelestidae. However, trees in which the Empidoidea are constrained to be monophyletic are only 1-6 steps longer (out of ~150), a fit not significantly worse under a permutation test for monophyly. Adult morphological data may not suffice to settle either the placement of Cyclorrhapha or the debate over genitalic homology. Moreover, the issue of genitalic homology does not appear critical to that of cyclorrhaphan origin.

Introduction

A recurrent feature of the history of life is marked non-uniformity of evolutionary rates (Simpson, 1953). Within radiating lineages, rapid proliferation and divergence among early forms can produce higher taxa which are individually distinctive but hard to relate to each other, raising a major problem for systematics. Perhaps the best-known example is the radiation of the mammals, whose origins and relationships remain enigmatic despite intensive morphological and molecular study (Shoshani, 1986; Gauthier et al., 1988; Novacek, 1989; Hedges et al., 1990).

A comparable pattern holds for radiations within the most recently diversified clades of insects, such as in the Diptera, subject of this study. In these insects, the greatest morphological diversity, and hence the clearest evidence for relationships, is found among the relatively species-poor primitive groups, the suborder Nematocera and the "orthorrhaphous" members of the suborder Brachycera. In contrast, the greatest diversity of species is overwhelmingly concentrated in the higher groups—namely the infraorder Cyclorrhapha (=Muscomorpha of McAlpine, 1989). The Cyclorrhapha contain 80 000+ species, a vast majority of the total for Diptera (Bickel, 1982), and they have radiated into an enormous range of both larval and adult niches (Oldroyd, 1964; Ferrar, 1987), a range broader than that of all other flies.

To investigate the possible causes of such radiations (Mitter et al., 1988; Wiegmann et al., in press), we need strong inferences about their phylogenetic origins. However, the origin of the Cyclorrhapha remains one of the most controversial issues in dipteran systematics. Heretofore, the debate has focused primarily on the interpretation of one or a few selected characters, particularly in the male genitalia. Somewhat surprisingly, there has been no attempt to assemble all of the relevant morphological evidence into a comprehensive and quantitative analysis. Extending the results of an initial study (Wiegmann, 1989), we attempt to evaluate the ability of the existing evidence to differentiate among hypotheses of cyclorrhaphan origins, and the sensitivity of any such conclusion to opposing homology interpretations.

HISTORICAL BACKGROUND

There is widespread agreement that the affinities of the Cyclorrhapha lie with some element of the paraphyletic "orthorrhaphous" group in the suborder Brachycera, specifically with either the Asiloidea (~11 000+ spp.) or Empidoidea (9000+ spp.) or both. The monophyly of the group (Asiloidea + Empidoidea + Cyclorrhapha), termed Heterodactyla, seems well supported (Griffiths, 1986; Woodley, 1989). The synapomorphies are: empodium setiform (Griffiths, 1986; Woodley, 1989); antenna with five articles, the terminal two slender (Griffiths, 1986; but see Woodley, 1989); adult mandibles lost; palpus, two articulated; female cerci with single article (Griffiths, 1986). The latter two synapomorphies are questionable, however, as they also appear in some homeodactylan taxa (D. Yeates, pers. comm.).

Debate has centred on where the Cyclorrhapha arise within the Heterodactyla. Cyclorrhapha have most often been placed as sister group to all or some part of the Empidoidea (=Empididae s.l. + Dolichopodidae; Brauer, 1883; Verrall, 1909; Hendel, 1928; Hennig, 1958; Chvála, 1981, 1983), forming the group Eremoneura (Lameere, 1906; Hennig, 1958; Griffiths, 1972, 1990). Griffiths (1984, 1986) listed the following adult synapomorphies for the Eremoneura: (1) male gonocoxae expanded dorsally, with corresponding reduction of the epandrium; (2) the presence of bacilliform sclerites on the inner surfaces of the male gonocoxae; (3) separation of the gonocoxal apodemes from the gonocoxae; (4) hypandrial arms fused above the aedeagus forming an hypandrial bridge; (5) hypandrium with a pair of posterior processes; (6) 10th tergum lost in male; (7) 9th tergum and furca lost in female; (8) media three-branched; (9) and cell (CuP) closed before wing margin; (10) ocellar setae present; and (11) maxillary palpus one-segmented.

Alternatives to an empidoid origin of the Cyclorrhapha have been suggested most recently by Disney [1986a,b, 1987, 1988a, 1988b, fig. 1(D)], McAlpine [1989, fig. 1(E)] and Nagatomi et al. (1991). All these proposals, however, fail to take into account the strong evidence for eremoneuran monophyly, focusing instead on characters which are likely convergent (Griffiths, 1990). Each hypothesis also requires reversals in many characters usually ascribed to the Cyclorrhaphan groundplan (Griffiths, 1990; B. Brown pers. comm.). For a time, Hennig also questioned eremoneuran monophyly based on the possibly plesiomorphic three-articulated antennal style of Cyclorrhapha, proposing instead a sister group relationship for Asiloidea and Cyclorrhapha [Hennig, 1972, fig. 1(B)]. Hennig (1976) reverted to his former view when the primitive cyclorrhaphan *Opetia* was discovered to have a two-articulated arista.

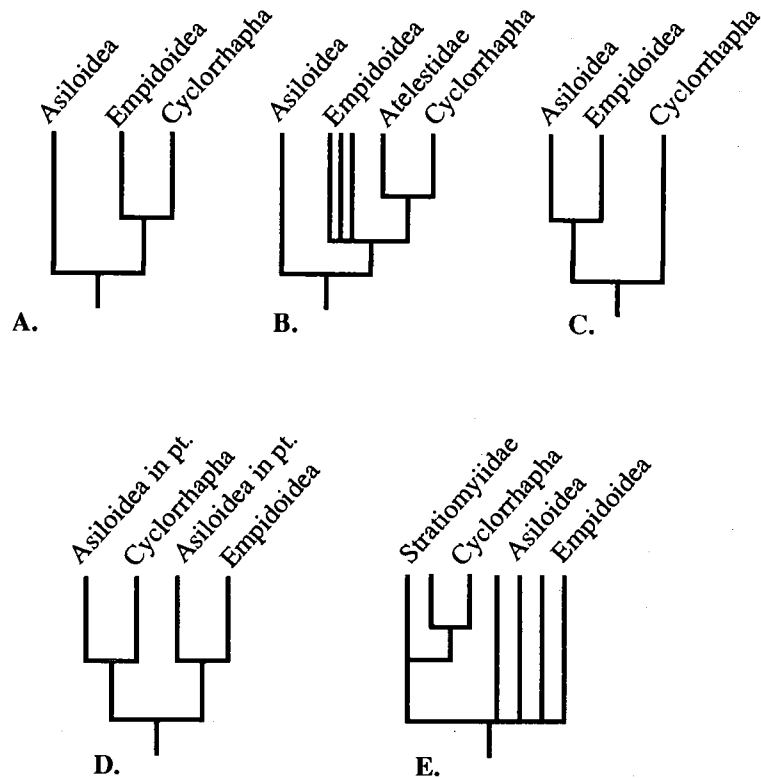


Fig. 1. Competing hypotheses for the origin of the Cyclorrhapha. Hypotheses shown are those of: (A) Hennig (1958), Griffiths (1972, 1984); (B) Chvála (1983); (C) Hennig (1972); (D) Disney (1986); (E) McAlpine (1989).

Although two of the synapomorphies (1 and 6) are dependent on acceptance of Griffiths' (1972) "periandrial" theory of male genitalic homologies (see below), the evidence for eremoneuran monophyly is convincing, and in this study we restrict our attention to hypotheses incorporating eremoneuran monophyly. The sister group of the Eremoneura would seem to be Asiloidea. Woodley (1989), Yeates and Irwin (1992) and Griffiths (1986) have defended the monophyly of the Asiloidea based on the following synapomorphies: larval spiracle situated in apparent penultimate segment (Woodley, 1989), aedeagal sheath formed by fusion of the gonites, pair of transverse sclerites at the base of the phallic complex and female 10th tergum divided into a pair of spine-bearing tergites (Griffiths, 1986).

Hypotheses on the position of Cyclorrhapha within the Eremoneura have been advanced by Hennig (1958, 1976), Griffiths (1986) and Chvála (1983) [Fig. 1(a)-(c)]. Monophyly for the Empidoidea and a sister-group relationship of these to the Cyclorrhapha is favored by Hennig (1958, 1976) and Griffiths (1986). The most convincing character for empidoid monophyly has been the single sclerotized spermatheca in females of primitive empidoids, although sclerotization of this structure is absent in more advanced groups (Chandler, 1981; Griffiths, 1986; Woodley, 1989). The recurved vein Cu1 (Griffiths, 1986), and, in larvae, fragmented mouthhooks (Griffiths, 1986; Sinclair, 1992) and the presence of two slender meta-cephalic rods (Woodley, 1989), have been cited as additional evidence of empidoid

monophyly, though vein Cu1 is variable within the empidoidea and the latter two characters are taken from a limited sample of known empidoid larvae.

In contrast, Chvála (1983) considered the Empidoidea to be paraphyletic, and proposed the small empidoid family Atelestidae as sister group to the Cyclorrhapha [Fig. 1(B)]. He based this view on the symmetrical atelestid hypopygium, which can be interpreted as having the gonocoxae fused into a "periandrium", the condition ascribed to the cyclorrhaphan groundplan by Griffiths (1972). This relationship had been suggested previously by Tuomikoski (1966) and Griffiths (1972), and is supported by the work of Bährmann (1960) and Ulrich (1972). Rohdendorf (1974) also postulated the origin of platypezid flies, the most primitive cyclorrhaphans, from some subgroup of the Empidoidea. Chvála's argument suffers, however, from a lack of explicit analysis treating all the relevant characters and taxa. Most important, male genitalic homologies proposed by Hennig (1970, 1976) and McAlpine (1981) imply instead that similarities in the "periandrium" (interpreted by them as the epandrium or 9th tergum) of the Atelestidae and Cyclorrhapha are symplesiomorphic.

In summary, the placement of the Cyclorrhapha within the Eremoneura has not been resolved by previous studies. Critical questions include empidoid monophyly, the placement of the Atelestidae and the interpretation of the male genitalia in these groups.

Materials and Methods

Two alternatives have been proposed regarding homologies and transformations of cyclorrhaphan male genitalia, the "periandrial" hypothesis of Griffiths (1972) and the "epandrial" hypothesis of Hennig (1976) and McAlpine (1981) (for details see Appendix 1, Male Genitalia). *A priori* assignments of homology using similarity (Remane, 1952; Patterson, 1982) or ontogenetic criteria (conjunction test; Patterson, 1988; Reidl, 1979) have been insufficient to resolve this dispute. In fact, ontogenetic information is completely lacking for the critical brachyceran groups. The most decisive test for homology in any one character should be congruence with phylogeny estimates based on other characters (Hennig, 1966, Patterson, 1988; Kluge, 1989; de Pinna 1991). In this study, data are compiled on as many character systems as possible, for representative empidoid, asiloid and cyclorrhaphan taxa, to test hypotheses about the position of the Cyclorrhapha. By cladistic analysis, under alternative codings of genitalic features reflecting opposing homology theories, and then excluding these features altogether, we can judge whether one genitalic theory is better supported by the evidence as a whole, and how much the debate matters to resolving cyclorrhaphan origins.

THE DATA

We reviewed essentially all morphological characters presumed useful by at least some previous workers, and reinterpreted them based on methods of cladistic character analysis (Wiley, 1981; Mickevich and Weller, 1990). Characters were included without regard to suspected homoplasy in order to present as unbiased a survey as possible of the phylogenetic evidence. Characters which varied markedly within a taxon, such that no groundplan condition could be reasonably assigned, were left unscored, or the variable taxon was subdivided (see below). Forty-nine

morphological characters apparently informative about relationships within the Eremoneura were extracted from the literature and from an extensive specimen survey (Appendix 1). The comparative morphology of the Empidoidea has been studied by many authors, notably Bährmann (1960), Collin (1961), Krystoph (1961), Tréhen (1962), Tuomikoski (1966), Hennig (1970, 1971), Ulrich (1972, 1975, 1976, 1984) and Chvála (1983). Chvála (1983) provided a comprehensive review. For scoring of the complex, highly variable genitalia of the subfamilies of the Empididae *sensu stricto*, we follow Chvála (1983), the most comprehensive account of these structures to date; although ongoing research on these taxa is currently yielding alternative interpretations (Wood, 1990; Cumming and Sinclair, 1990). Detailed descriptions of the interpretation and distribution of characters and their states are given in Appendix 1.

EMPIDOID TAXA STUDIED

The terminal taxa for this study were the families and subfamilies of the Empidoidea, except where there was doubt about monophyly. We follow Hennig (1970, 1971) and Chvála (1981, 1983) for definition of monophyletic groups within the Empidoidea and analyses of Palearctic taxa. Groundplans were constructed, based on the literature and surveys of many North American taxa, for Empidinae, Brachystomatinae, Hemerodromiinae, Clinocerinae, Ceratomerinae, Hybotinae, Tachydromiinae, Ocydromiinae, Microphorinae, Parathalasiinae and Dolichopodidae. Table 1 lists the exemplars of these taxa that were examined as specimens. For the three family group entities whose monophyly was suspect, we included several genera representing their morphological diversity, separately in the analysis. There were, for the Atelestidae, *Atelestus pulicarius*, *Meghyperus sudeticus*, *Acarteroptera occidens* [formerly *Meghyperus occidens* (B. M. Wiegmann, in prep.)], and *Acarteroptera licinia*; for the Oreogetoninae, *Oreogeton*, *Hormopeza* and *Gloma*; and for the Ocydromiinae, *Trichinomyia* and *Bicellaria*. Sources for this material are detailed elsewhere (Wiegmann, 1989; in prep.)

OUTGROUPS

To root the cladogram and polarize character transformations within the Eremoneura (Empidoidea + Cyclorrhapha), outgroups were selected from within the Asiloidea, whose close relationship to Eremoneura was discussed earlier. Representatives of several genera in the apparently paraphyletic Bombyliidae were used, because Bombyliidae *sensu lato* appear to include the most primitive asiloids (Woodley, 1989; Yeates and Irwin, 1992). *Caenotus* Cole appears to match closely the groundplan of the Asiloidea (Woodley, 1989; Griffiths, 1990); it has many primitive characters relative to the Empidoidea, but also has wing venation very similar to that ascribed to the empidoid groundplan by Chvála (1983). Similarly, *Hilarimorpha* Schiner (Hilarimorphidae) was chosen because it exhibits both many plesiomorphic asiloid characters and many derived characters shared with the empidoids; its placement relative to bombyliids and empidoids has been controversial (Woodley, 1989; N. Evenhuis, pers. comm.).

In the survey for possible outgroups, the curious bombyliid *Apystomyia elinguis* Melander was found to possess many empidoid, and possibly cyclorrhaphan,

Table 1

Terminal taxa included in phylogenetic analysis (boldface). Character scorings for each taxon were synthesized from the literature, in conjunction with detailed examination of specimens of representative species listed below.

Asiloidea (outgroups)
Bombyliidae
<i>Caenotus hospes</i> Melander
<i>Apystomyia elinquis</i> Melander
Hilarimorphidae
<i>Hilarimorpha mandana</i> Webb
Eremoneura
Empidoidea
Atelestidae
<i>Atelestus pulicarius</i> Walker, <i>Atelestus dissonans</i> Collin, <i>Meghyperus sudeticus</i> Loew, <i>Acarteroptera</i> occidentens (Coquillett), <i>A. mateus</i> Wiegmann (MS), <i>A. tularensis</i> Wiegmann (MS), <i>A. humeralis</i> Wiegmann (MS), <i>A. peninsularis</i> Wiegmann (MS), <i>A. licinia</i> Collin
Empididae
Empidinae
<i>Empis poplitea</i> Loew, <i>E. spectabilis</i> Loew, <i>E. obesa</i> Loew, <i>Hilara seriata</i> Loew, <i>H. basalis</i> Loew, <i>H. brunnea</i> Roach (MS); <i>Rhamphomyia parva</i> Coquillett, <i>R. fumosa</i> Loew
Clinocerinae
<i>Clinocera binotata</i> Loew, <i>C. conjuncta</i> Loew, <i>Wiedemannia simplex</i> (Loew)
Hemerodromiinae
<i>Neoplasta bivittata</i> (Philippi), <i>Hemerodromia vittata</i> Loew
Brachystomatinae
<i>Brachystoma occidentale</i> Melander
Ceratomerinae
<i>Ceratomerus paradoxus</i> Philippi
Oreogetoninae
<i>Oreogeton basalis</i> Loew, <i>Oreogeton</i> undet. (Chile), <i>Gloma luctuosa</i> Melander, <i>Hormopeza copulifera</i> Melander, <i>H. brevicornis</i> Loew, <i>Iteaphila</i> undet., <i>Apalocnemis oreas</i> Melander
Hybotidae
Hybotinae
<i>Hybos slossonae</i> Coquillett, <i>H. reversus</i> Walker, <i>Ethybus duplex</i> (Walker), <i>Syneches debilis</i> Coquillett, <i>Syndyas polita</i> Loew
Ocydromiinae
<i>Trichinomyia flavipes</i> Meigen, <i>Bicellaria spuria</i> (Fallén), <i>Ocydromia glabricula</i> (Fallén)
Tachydromiinae
<i>Platypalpus xanthopodus</i> Melander, <i>Tachydromia maculipennis</i> Walker
Microphoridae
Microphorinae
<i>Microphor sycophantor</i> (Melander), <i>M. atratus</i> Coquillett
Parathalassiinae
<i>Parathalassius candidatus</i> Melander, <i>P. aldrichii</i> Melander
Dolichopodidae
<i>Dolichopus comatus</i> Loew, <i>Condylostylus flavipes</i> (Aldrich)
Cyclorrhapha
Platypezidae
<i>Opetia nigra</i> Meigen, <i>Platypeza obscura</i> Loew, <i>Microsania imperfecta</i> Loew, <i>Callomyia venusta</i> Snow

characters. *Apystomyia* has the asiloid synapomorphy of an aedeagal sheath formed by fusion of the gonites, and the female retains the three sclerotized spermathecae typical of bombyliids. Like many empidoids and primitive cyclorrhaphans, however, this fly has reduced wing venation, bristle-like setae and, most striking, a broad U-shaped epandrium (9th tergite) extended as a clasper. The latter condition has been until now unknown in the Asiloidea (Fig. 2), and raised the possibility of an eremoneuran sister group within the Asiloidea as currently defined. *Apystomyia* shares the reduction and patterning of the setae with the Eremoneura, but its genitalia clearly retain the plesiomorphic condition of articulated gonocoxae and

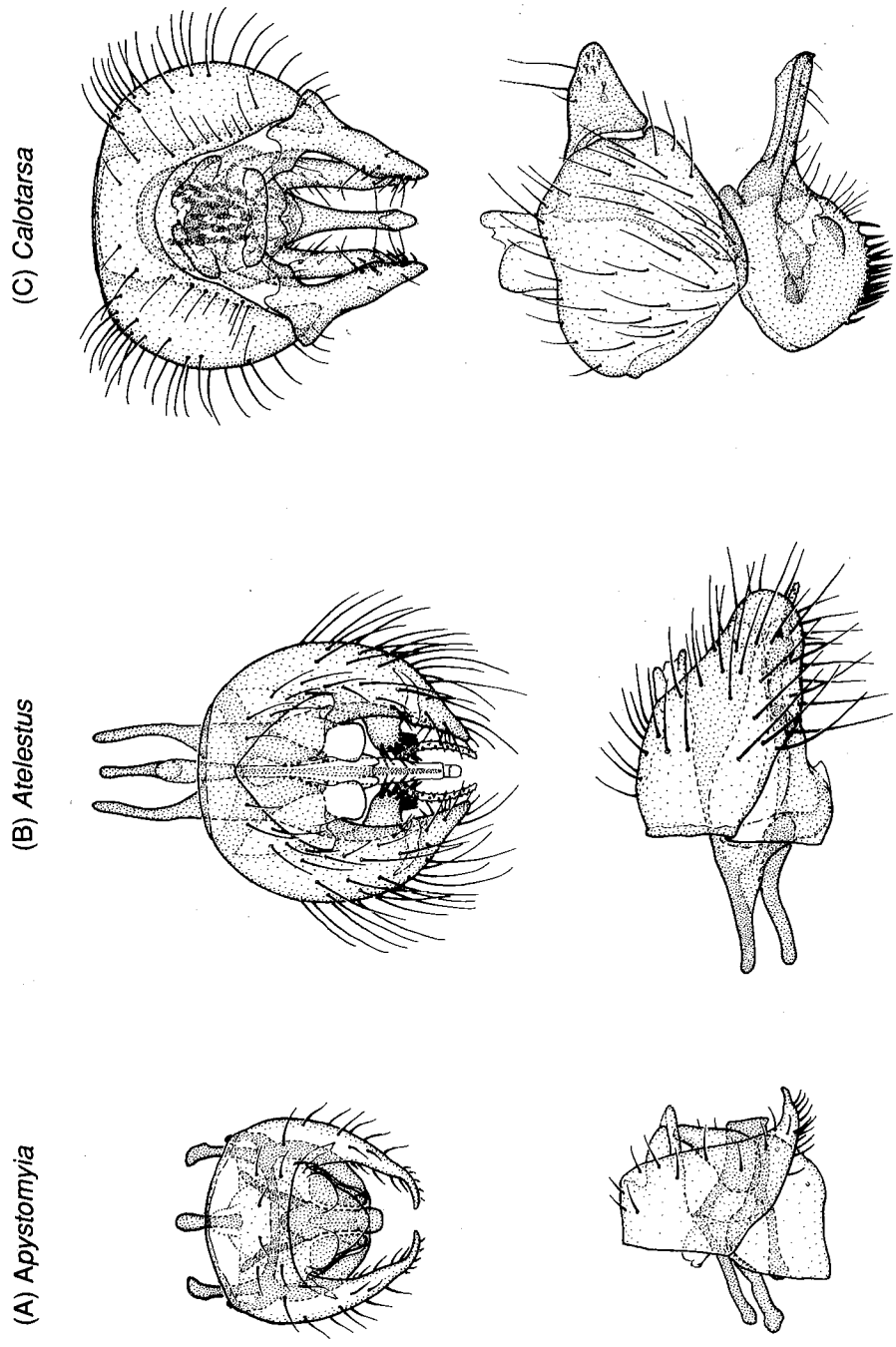


Fig. 2. Dorsal view of male genital capsule (hypopygium) of: (A) *Apystomyia* *etinguis* Melander (Asiloidea); (B) *Atelestus pulicarius* Fallén (Empidoidea); and (C) *Calotarsa insignis* Aldrich (Cyclorrhapha).

gonostyli separate from the epandrium and hypandrium. It also lacks bacilliform sclerites and fusion of the hypandrial bridge across the aedeagus, which conclusively exclude it from the Eremoneura. We included this anomalous fly to test the effects of its unique combination of characters on the placement of the Cyclorrhapha and relationships of the Empidoidea and Atelestidae.

GROUNDPLAN OF THE CYCLORRHAPHA

Assigning groundplan conditions for a group as diverse as the Cyclorrhapha is problematic. Our groundplan estimate is based principally on the Platypezidae, generally regarded to be among the most primitive cyclorrhaphans (Hennig, 1973, 1976; Griffiths, 1972, 1986). The strong similarity of primitive platypezid genera to the empidoid *Atelestus* is one indication of their closeness to the cyclorrhaphan groundplan. We synthesize a cyclorrhaphan groundplan from the literature, primarily the works of Griffiths (1972, 1986, 1990), Chvála (1983) and Hennig (1976), and from detailed examination of the platypezid genera *Melanderomyia*, *Microsania* and *Callomyia*. We also include separately the genus *Opetia* Meigen, whose changing systematic position, ranging from within the Platypezidae (Kessel and Maggioncalda, 1968; McAlpine, 1989), to the stem lineage of Cyclorrhapha (Griffiths, 1986, 1990), even to outside the Cyclorrhapha entirely (Disney, 1987), reflects its transitional position.

EXPERIMENTAL DESIGN

The central goal of this study was to determine the effect of conflicting genitalic homology theories on estimates of eremoneuran relationships, particularly the position of the Cyclorrhapha. A potential complication is additional uncertainty or debate over transformation series in several characters apart from genitalic features, over the most appropriate choice of outgroups for the Eremoneura and over the phylogenetic reliability of many of the characters used in this study. To control for these possible "nuisance" effects on the tree estimate, we adopted a design analogous to a factorial ANOVA. Tree estimates were obtained under each possible combination of choices for these "block" effects, under each of the genitalic homology interpretations.

The 24-block design that results from this procedure is detailed in Table 2. Of three "main effect" data sets, two, designated "EPANDRIAL" and "PERIANDRIAL", incorporate the genitalic homology theories of Griffiths (1972) and Chvála (1983) and of Hennig (1976) and McAlpine (1981), respectively. The third ("NO GENITALIA") is a control from which all the controversial genitalic characters are excluded.

The "block" effects (Table 2, left side) include, first, addition or deletion of the outgroup *Apystomyia* ("APYS"). As noted earlier, this anomalous asiloid was initially included on the possibility that its cyclorrhaphan-like male genitalia indicated true affinity to the Eremoneura. Subsequent work, however (Griffiths, 1990, D. Yeates, pers. comm.), favors a relatively derived position for *Apystomyia* within Asiloidea, by comparison to the other outgroups included here. Under this interpretation, inclusion of *Apystomyia* might actually decrease reliability of the tree estimate, by lowering the mean density of taxon sampling with respect to character change among the outgroups.

Table 2

"Factorial" design of tree calculations and summary of results. Trees were calculated separately for each combination of "block" variables (columns 2-4), under each male genitalic homology coding (columns 5 and 6) and a "control" with controversial genitalic characters removed ("NO GENITALIA"). Each trial was then repeated under successive weighting ("WEIGHT"). Numbers in columns 5-7 denote tree topologies obtained in each experiment, from a total of seven different arrangements among major groups shown in Fig. 7. APYS = outgroup *Apystomyia* included (+) or not (-). TS1 TS2 = alternative transformation series for number of antennal-style segments (character 5) and number of spermathecae (character 40), respectively.

"Block" Effects				Homology theory and resulting topology		
WEIGHT	APYS	TS1	TS2	PERIANDRIAL	EPANDRIAL	NO GENITALIA
-	-	a	a	1	1	1, 5
+	-	a	a	1	1	7
-	+	a	a	1	2, 3	2, 3, 4, 6
+	+	a	a	1	3	4
-	-	b	a	1	1	1, 5
+	-	b	a	1	1	7
-	+	b	a	1	2, 3	2, 3, 4, 6
+	+	b	a	1	3	4
-	-	a	b	1	1	1, 5
+	-	a	b	1	1	7
-	+	a	b	1	2, 3	2, 3, 4, 6
+	+	a	b	1	3	4
-	-	b	b	1	1	1, 5
+	-	b	b	1	1	7
-	+	b	b	1	2, 3	2, 3, 4, 6
+	+	b	b	1	3	4

Second, we have tested the effects of two alternative transformation series for the number of antennal-style segments ("TS1") and the number of spermathecal ducts in the female ("TS2"). The latter is of critical importance to the question of cyclorrhaphan origins since the presence of a single sclerotized spermatheca in many female empidoidea, especially Atelestidae, has been the most convincing evidence for empidoidea monophyly. Placing the cyclorrhaphan origin within the Empidoidea requires either a reversal to the plesiomorphic three-spermathecae condition in the Cyclorrhapha or the acquisition of spermathecae *de novo* from reduced or fused ducts. Detailed descriptions of these characters and their possible transformations are given in Appendix 1 (characters 5 and 36).

A final complication arises from our attempt to include as wide a range of characters as possible. Some of these characters may evolve so rapidly (and homoplasiously) as to be misleading at this level; indeed, most previous treatments of eremoneuran relationships have stressed a select few, presumably reliable, characters. When relationships have been at least partially established based on other evidence, it may be possible to decide *a priori* which characters are likely to be uninformative. For the Eremoneura, however, there is no such prior evidence: all that we know about relationships comes from the same base of morphological information surveyed here. In this circumstance, judgement of the reliability of any one character ultimately rests on concordance with other characters. To gauge the effect of differential reliability of characters, trees were calculated within each "block" of Table 2 both on unweighted characters and under successive weighting in Hennig86 (Farris,

1969) ("WEIGHT+"), in which characters are re-weighted by their agreement with each successive tree estimate until topology and weights stabilize. Successive weighting thus provides a measure of how different the results might have been had we essentially ignored the "bad" characters. In our design its effects can be viewed as analogous to an "error" term due to character selection. In most cases, its effect was to narrow the choice among equally parsimonious trees (Carpenter, 1988).

TREE CALCULATIONS

Most parsimonious trees were calculated using the program packages PHYSYS (Mickevich and Farris, 1984) and Hennig86 (Farris, 1988). In both packages we used heuristic tree search routines combined with branch swapping (DWAG.AS in PHYSYS, mh* and bb in Hennig86). The consistency index (Kluge and Farris, 1969) and retention index (Farris, 1989) are reported as measures of homoplasy.

Results

The initial calculations performed compared the genitalic homology "main effects" under just the combination of the "block" variables considered most plausible. Corresponding to the first row of Table 2, these were alternative (a) for both questionable transformation series and the anomalous outgroup *Apystomyia*

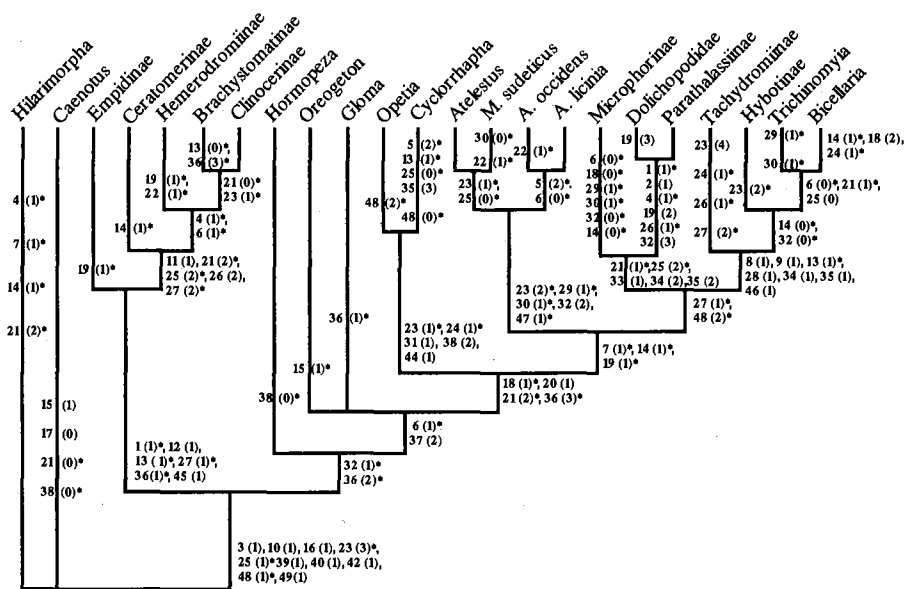


Fig. 3. One of two minimum-length trees obtained from the PERIANDRIAL data set before successive weighting, with *Apystomyia* excluded, and TS1 and TS2 coded with transformation series (a) (Table 2), length (L) = 131, retention index (RI) = 0.75, consistency index (CI) = 0.52, (topology = tree 1, Fig. 7). Synapomorphic characters and their states under ACCTRAN optimization are listed for each node. Characters showing homoplasy on the tree are indicated with an asterisk. Below the *Eremoneura* the rooting is arbitrary (see text).

excluded; successive weighting was not applied. The complex results of the full set of manipulations are most easily presented subsequently, as contrasts to the outcome of this initial experiment.

Under the initial conditions, two nearly identical minimum-length trees were obtained from the PERIANDRIAL data set [Fig. 3; length (L) = 131; consistency index (CI) = 0.52; retention index (RI) = 0.75]. The trees differed only in their support for grouping *Oreogeton* and *Gloma*. The EPANDRIAL data set yielded a single minimum length tree, identical to the first topology for the PERIANDRIAL data (Fig. 4; L = 132; CI = 0.50; RI = 0.74). Seventeen shortest trees were obtained from the NO GENITALIA data set, but resulted in only two alternative placements of the Cyclorrhapha with respect to atelestids and other empidoids; 16 trees place the Cyclorrhapha as sister group to the Atelestidae, whereas a single tree agreed with the genitalic data sets on the placement of the Cyclorrhapha (Figs 5 and 6; L = 118; CI = 0.50; RI = 0.74). The 15 trees not shown here differed from those in Figs 5 and 6 by only minor rearrangements of some empidoid taxa.

To facilitate comparison among these and subsequent results with respect to the central question, all the trees can be expressed in simplified form showing just the position of Cyclorrhapha with respect to five major empidoid lineages that emerged from the calculations (see below). In the 48+ experimental manipulations, only seven different arrangements of these entities were found, of 945 possible topologies for six taxa. In the synopsis of results in Table 2, the numbers refer to the order in which these seven summary topologies are depicted in Fig. 7.

Discussion of the remaining results is organized around the major questions raised in the Introduction.

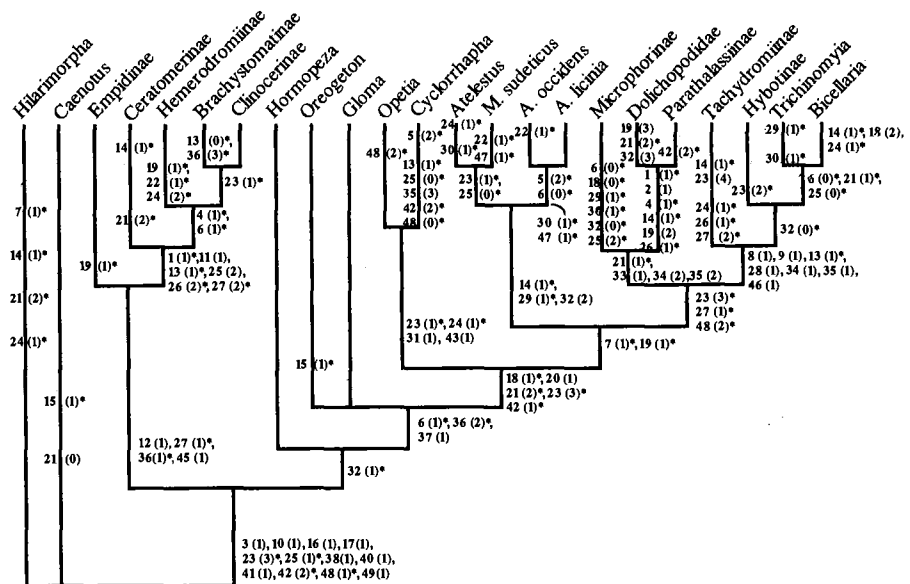


Fig. 4. Minimum-length tree obtained from the EPANDRIAL data set before successive weighting, with *Apystomyia* excluded, and TS1 and TS2 coded with transformation series (a) (Table 2), L = 132, RI = 0.74, CI = 0.50 (topology = tree 1, Fig. 7). Synapomorphic characters and their states under ACCTRAN optimization are listed for each node. Characters showing homoplasy on the tree are indicated with an asterisk. Below the *Eremoneura* the rooting is arbitrary (see text).

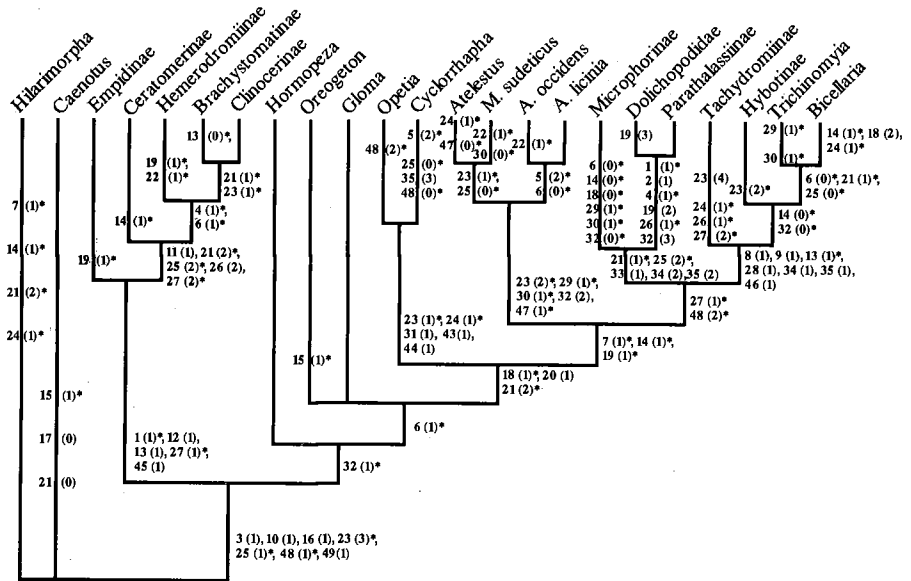


Fig. 5. One of 17 minimum-length trees obtained from the NO GENITALIA data set before successive weighting, with *Apystomyia* excluded, and TS1 and TS2 coded with transformation series (a) (Table 2), $L = 118$, $RI = 0.74$, $CI = 0.50$ (topology = tree 1, Fig. 7). Synapomorphic characters and their states under ACCTRAN optimization are listed for each node. Characters showing homoplasy on the tree are indicated with an asterisk. Below the *Eremoneura* the rooting is arbitrary (see text).

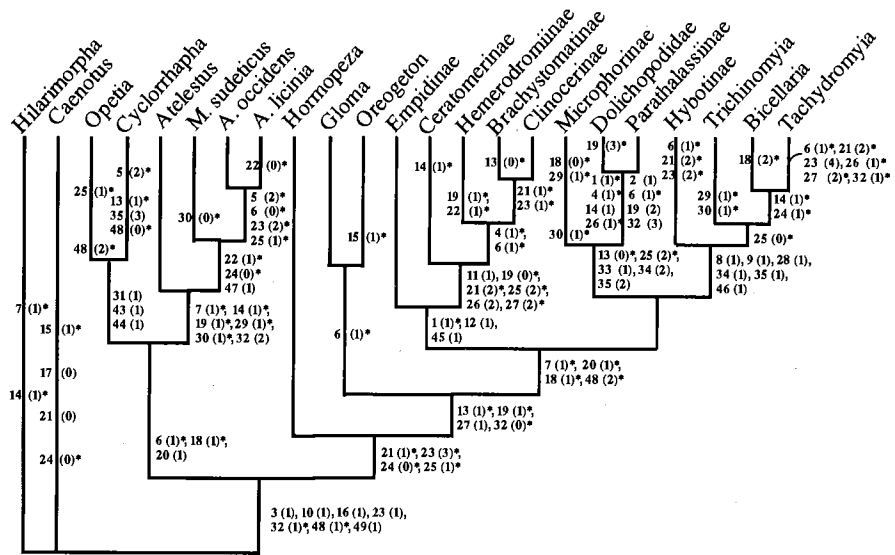


Fig. 6. Second, equally parsimonious tree obtained from the NO GENITALIA data set before successive weighting, with *Apystomyia* excluded, and TS1 and TS2, coded with transformation series (a) (Table 2), $L = 118$, $RI = 0.74$, $CI = 0.50$ (topology = tree 5, Fig. 7). Synapomorphic characters and their states under Acctran optimization are listed for each node. Characters showing homoplasy on the tree are indicated with an asterisk. Below the *Eremoneura* the rooting is arbitrary (see text).

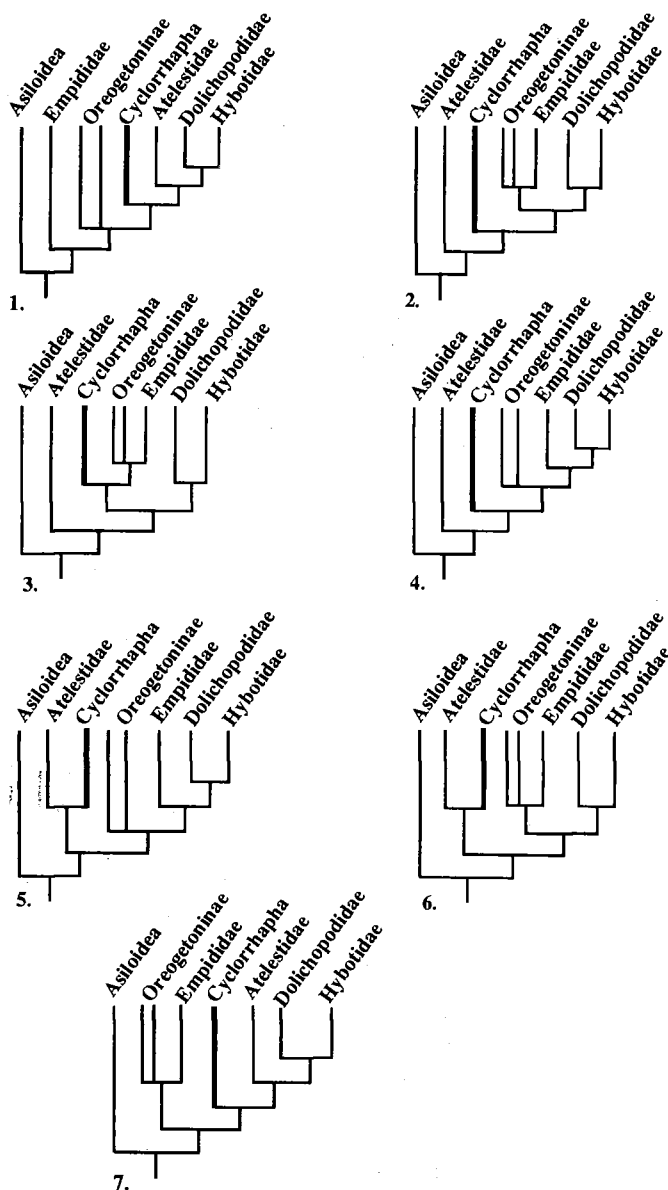


Fig. 7. Summary of all topologies obtained for the placement of the Cyclorhapha (bold) and the relationships of empidoid taxa. Nodes are collapsed to show only those subgroups of the Eremoneura which were consistently monophyletic. Names given terminals are descriptors and do not necessarily represent valid taxon group names. No consistently occurring synapomorphy supported the monophyly of the subfamily Oreogetoninae, consequently the relationships of its members with respect to the remaining Eremoneura are represented here as unresolved. Labeled terminals include the following taxa: Asiloidea—*Caenotus*, *Hilarimorpha*, *Apystomyia*; Empididae—Empidinae, Ceratomerinae, Brachystomatinae, Hemerodromiinae, Clinocerinae; Oreogetoninae—*Hormopeza*, *Gloma*, *Oreogeton*; Cyclorhapha—*Opetia*, Platypezidae; Dolichopodidae—Microphorinae, Parathalassiinae, Dolichopodidae; Hybotidae—Hybotinae, Tachydromiinae, Ocydromiinae (*Bicellaria*, *Trichinomyia*), Atelestidae—*Atelestus*, *Meghyperus*, *Acarteroptera*.

ORIGIN OF THE CYCLORRHAPHA

Opetia Meigen is placed as the sister group to the Cyclorrhapha *sensu stricto* in all trees obtained. Synapomorphies for this grouping include the loss of the discal cell [24(1)], a shortened and recurved vein CuA2 [23(1)], a free ejaculatory apodeme not fused to the base of the aedeagus [43(1)] and the absence of abdominal plaques [31(1)]. The wing venation characters also occur in several empidoid and platypezid genera; however, the latter two synapomorphies are strong support for Griffith's (1986, 1990) inclusion of *Opetia* in the Cyclorrhapha as its most plesiomorphic extant taxon. In all subsequent references to the Cyclorrhapha, we assume the broad meaning of the term to include *Opetia*.

In all manipulations, the Cyclorrhapha originate from within the Empidoidea, in the broad sense, and in nearly all cases they are placed close to the Atelestidae. Thus, our results do not support the monophyly of the Empidoidea. The strongest evidence for empidoid monophyly has been reduction to a single sclerotized spermatheca in primitive empidoids (Chandler, 1981, Woodley, 1989). On our trees, the higher number seen in Cyclorrhapha must always be interpreted as a reversal, rather than retention of the primitive condition, under both plausible codings for this character ("TS2", Table 2). If the relationships indicated by the other "fundamental" characters were simply obscured by the inclusion of many less-reliable characters, one might have expected empidoid monophyly to emerge after successive weighting, but this did not happen.

Two primary alternative placements of the Cyclorrhapha are evident among the summary topologies in Fig. 7. In trees 1 and 7, the Atelestidae and Cyclorrhapha are primitive members of the Ocydromioinea lineage of the Empidoidea, which includes the Microphoridae, Dolichopodidae and Hybotidae. This is similar to the phylogeny suggested by Chvála (1983) [Fig. 1(B)]. In four of the remaining five trees, the atelestids are placed as the most primitive members of the Eremoneura, with the Cyclorrhapha as their sister group (trees 5 and 6), or as the basal lineage of the remaining Eremoneura (trees 2 and 4). In tree 3, the Cyclorrhapha are placed as sister group to the Oreogetoninae + Empididae.

The variation in the estimated placement of the Cyclorrhapha just described arises in part from the conflicting interpretations of their male genitalia, but in a complex way. Had the outgroup *Apystomyia* not been examined, one would have concluded that choice between homology theories made little difference, provided that the genitalic characters were included in some form. Data sets with both PERIANDRIAL and EPANDRIAL homology interpretations consistently yield tree 1, under both scorings for the number of antennal-style segments and of sclerotized spermathecae, and with or without successive weighting. Under the PERIANDRIAL theory, the loss of the epandrium and fusion of the gonocoxae across the dorsum forming a periandrium, as well as trends in wing venation, place the Cyclorrhapha as the sister group to Atelestidae, Microphoridae + Dolichopodidae and Hybotidae. Similarly, under the EPANDRIAL theory, fusion of the genostyli to the gonocoxae [38E (1)] and several non-genitalic characters, especially R4+5 unbranched [20(1)], a single medius from the discal cell 21(2) and costa ending at M1 [18(1)], although homoplasious elsewhere on the tree, corroborate these genitalic synapomorphies to some degree, allowing the higher flies to group with the ocydromioid lineage of the Empidoidea.

Non-controversial characters by themselves, however, do not consistently support any single topology. The "NO GENITALIA" data set yields all seven summary topologies in Fig. 7. This is likely the result of homoplasy, as successive weighting narrowed the outcome for these data to trees 7 and 4 of Fig. 7. Trees 7 and 4, however, are never obtained from PERIANDRIAL or EPANDRIAL data sets. Thus, the most consistent set of characters that are independent of the two competing homology theories do not support either theory over the other.

The picture changes somewhat, and a difference between the homology theories emerges, when *Apystomyia* is included as an outgroup. Under the EPANDRIAL codings, but not the PERIANDRIAL ones, similarities of *Apystomyia* to Atelestidae and Cyclorrhapha, most notably the U-shaped clasping epandrium [36E(2)], patterned notal setae [16(1)], reduced number of ocellar setae [3(1)] and single-segmented maxillary palpus [10(1)], place *Apystomyia* adjacent to the Eremoneura and alter relationships within the latter (Fig. 8). On the basis of similarities to *Apystomyia*, Atelestidae drop to a basal position within Eremoneura. Cyclorrhapha are placed either as the next oldest lineage (tree 2 of Fig. 7), the remaining empidoidea sharing a two-branched medial vein [21(1)] and reduced CuA2 [23(3)], or as sister group to the Oreogetoninae + Empididae (Fig. 8; tree 3 of Fig. 7). The latter relationship is supported most consistently by the presence of surstyli on the epandrium [42(2)], homologs of tergum 10 under Hennig's (1976) EPANDRIAL interpretation (but see Appendix 1). Both trees are equally parsimonious for genitalic characters, requiring character reversals in the remaining empidoidea. Successive weighting consistently selected tree 3 over tree 2, and alternative scorings for antennal-style segmentation and spermathecal number yields both trees.

Under the PERIANDRIAL codings, the tree (1 in Fig. 7) is unaffected by *Apystomyia*, with both Atelestidae and Cyclorrhapha remaining in relatively derived

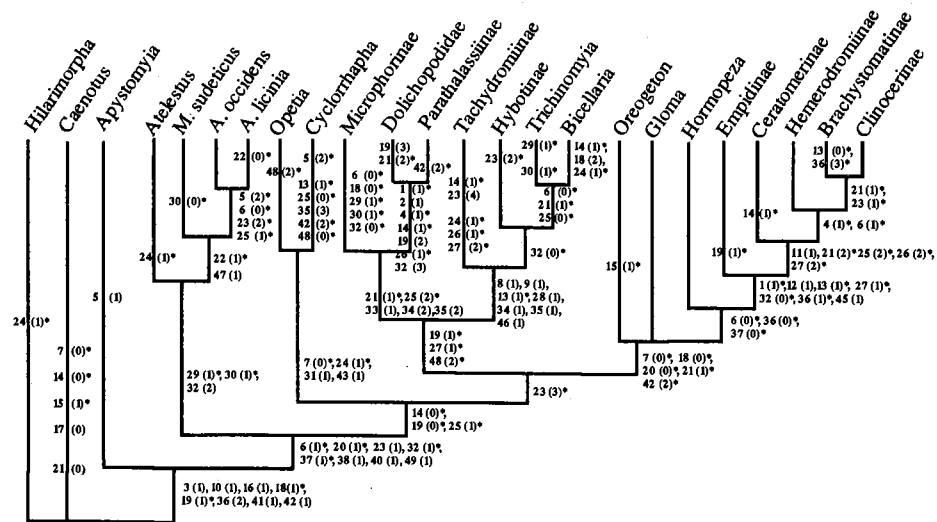


Fig. 8. One of eight Minimum-length trees obtained from the EPANDRIAL data set before successive weighting, with *Apystomyia* included, and TS1 and TS2, coded with transformation series (a) (Table 2), $L = 137$, $RI = 0.75$, $CI = 0.510$ (topology = tree 2, Fig. 7). Synapomorphic characters and their states under Acctran optimization are listed for each node. Characters showing homoplasy on the tree are indicated with an asterisk. Below the Eremoneura the rooting is arbitrary (see text).

position, related to the ocydromioid empidids. This is supported by the fusion of the gonocoxae across the dorsum to form the perianthrium [36P(2)], and the reduction of the gonostyli [37P(1)].

Although *Apystomyia* is probably aberrant, as noted earlier, its effects raised the question of whether our initial sampling of outgroups was adequate. To get a better estimate of the groundplan of the Asiloidea, six additional outgroups were subsequently sampled and added to the data sets. These included five diverse asiloids: *Psilocephala*, *Apsilocephala* (Therevidae), *Dioctria* (Asilidae), *Epacmus*, *Bombylius* (Bombyliidae); plus a homeodactylus brachyceran, the rhagionid *Rhagio*. Addition of these outgroups did not affect either polarity assignments within the Eremoneura or the trees obtained from the "main effects" data sets, suggesting that these results were not dependent on the initial choice of outgroups.

In sum, morphological evidence subjected to differing homology interpretations, outgroup inclusion and character codings consistently places the Cyclorrhapha near the Atelestidae within the Empidoidea, making the latter a paraphyletic group. No single arrangement is supported by characters for which homology assignments are non-controversial; addition of the controversial genitalic characters generally narrows the choice to the same 1 or 2 trees under both homology theories.

EMPIDOID MONOPHYLY VS PARAPHYLY: A SIGNIFICANCE TEST

While our results consistently favor an origin of Cyclorrhapha from within Empidoidea over monophyly for the latter, the difference in fit is relatively small: constraining empidooids to be monophyletic adds only 1–6 steps to the tree length (Table 3). Is this degree of difference decisive, or might it represent error due to homoplasy, leaving the hypothesis of empidooid monophyly still viable? As a heuristic significance test, we applied Faith's (1991) permutation test for non-monophyly. The null model for this test is independence of character state distributions from each other and from phylogeny, simulated by random permutation of the observed states for each character across the taxa. For determining whether the data depart from this model in the direction of hierarchical structure specifically favoring empidooid non-monophyly over monophyly, our test statistic (Faith, 1991) is the difference in length between the shortest tree in which the empidooids are monophyletic, and the shortest tree in which they are not. To approximate the null distribution for this difference, we generated an initial 20 random permutations of each main effects data set, with and without *Apystomyia*. Minimum tree length was estimated for each permuted data set using heuristic search with branch swapping

Table 3

Difference in length (No. of steps) between shortest tree with Empidoidea monophyletic, and shortest trees in which they are not. *P* values are frequencies with which a difference as great or greater than the observed difference was obtained under 20 random permutations (following Faith, 1991).

	Data set		
	PERIANDRIAL	EPANDRIAL	NO GENITALIA
<i>Apystomyia</i> excluded	6, <i>P</i> = 0.65 n.s.	3, <i>P</i> = 0.90 n.s.	2, <i>P</i> = 1.00 n.s.
<i>Apystomyia</i> included	3, <i>P</i> = 0.90 n.s.	1, <i>P</i> = 1.00 n.s.	1, <i>P</i> = 1.00 n.s.

in Hennig86 (mh*; bb), with and without the constraint of empidoid monophyly. The observed length differences were then compared to the corresponding permutation distributions.

As Table 3 shows, in no case does the observed difference approach significance. Because 65% or more of the length differences under the initial permutations were greater than the observed difference, further simulations seemed unnecessary. This does not mean that the data lack phylogenetic structure: the minimum-length trees for the original data are always 80 to 90 steps shorter than any trees obtained from their permutations, a highly significant "PTP" test result (Faith and Cranston, 1991). However, it appears that that fraction of the character variation which bears on just the placement of Cyclorrhapha with respect to empidoidea cannot be distinguished from random.

While the logical foundations of permutation and other significance tests for phylogenies need clarification (Farris, 1991; Carpenter, 1992), this outcome suggests that the hypothesis of empidoid paraphyly with respect to Cyclorrhapha, while best supported by the available evidence, should not be taken as firmly established.

MONOPHYLY AND RELATIONSHIPS OF THE EREMONEURA

Our results provide some additional corroboration for the working hypothesis of monophyly for the Eremoneura. That is, in all our trees, all the outgroups join the remaining taxa (i.e. eremoneurans) through a common stem (Farris, 1972), despite the fact that little effort was made to include characters bearing just on relationships among the outgroups. The Eremoneura were supported in all trees by the loss of the female 9th tergite [49(1)], patterned notal setae [16(1)], reduced number of ocellar setae [2(1)], a one-segmented maxillary palpus [10(1)] and reduction to a single sclerotized spermatheca [48(1)]. In the Cyclorrhapha, which have three sclerotized spermathecae, this last character must be interpreted as a reversal to the primitive condition. The organization of notal setae into distinct patterns is a derived feature of many groups outside of the Eremoneura, for example in some Rhagionidae and Asilidae and in the genera *Apystomyia* and *Apsilocephala* among others, and consequently cannot be considered a strong synapomorphy for the Eremoneura.

The status of other possible eremoneuran synapomorphies remains unclear, either because they depend on a particular genitalic hypothesis, or because more extensive homoplasy renders their point of origin unclear. Under the PERIANDRIAL genitalic codings only, the Eremoneura are interpreted as uniquely possessing paired processes of the hypandrium [39P(1)] and as having lost the male 10th tergite [42P(1)]. The following other characters appeared in some trees but not others to define the Eremoneura: fusion of the hypandrial bridge across the dorsum of the aedeagus [40(1)]; presence of bacilliform sclerites [41(1)]; incomplete vein A1 [25(1)]; vein R4+5 unbranched [20(1)]; vein CuA2 recurved [23(3)]; 8th abdominal tergite a reduced band [32(1)]; and in tree 2 only, an aristate style.

PHYLOGENY OF THE EMPIDOIDEA

Since the limited goal of the study was to determine the effects of genitalic homology interpretations on the placement of the Cyclorrhapha and Atelestidae,

morphological evidence sufficient to resolve fully the phylogenetic relationships of all subgroups of Empidoidea was not obtained. This would require a much more detailed treatment of these groups. Nonetheless, our analysis did consistently support several previously hypothesized groupings within the Empidoidea.

Although the exact placement of the Atelestidae remains uncertain, especially with respect to the origin of the Cyclorrhapha (Fig. 7), all of our trees corroborate the monophyly of this family. The most consistent synapomorphies for the Atelestidae are: [29(1)] a clavate hindtibia and [32(2)] 8th abdominal tergite in the form of a U-shaped band. Atelestid monophyly may also be supported by unusually broad folds of the perianthrium, but this character, cited by Chvála (1983), was excluded here due to difficulty in scoring it. In the PERIANDRIAL results, the Atelestidae were also supported by [23(2)] vein CuA2 meeting the anal vein at an approximate 90-degree angle near the length of the basal cells, and [14(1)] proepisternum, bare; and, in the NO GENITALIA results, by [19(1)] subcosta incomplete and [20(1)] R4+5 unbranched. While any or all of these latter characters may be synapomorphies of the Atelestidae, they occur independently in several empidoid lineages, and thus cannot be considered unambiguous evidence for atelestid monophyly. There is as yet insufficient character evidence satisfactorily to resolve phylogeny within the Atelestidae. Lower-level atelestid relationships are treated in detail elsewhere (Wiegmann, 1989; in preparation).

The family Hybotidae, erected by Chvála (1983) to include the Hybotinae, Tachydromiinae and Ocydromiinae, is a well-defined monophyletic group, appearing in all our trees and supported by the following synapomorphies also recognized by Chvála (1983): [8(1)] maxillary palpi attached to a sclerotized palpifer; [9(1)] maxillary lacinia absent, [28(1)] front tibia with sensory gland; 34(1) hypandrium asymmetrical; [35(1)] hypandrium rotated 90 degrees; [46(1)] aedeagus attached to the inner wall of the hypandrium. Our data do not suffice, however, to distinguish among the possible arrangements of the subfamilies. In part, this is because the highly specialized Tachydromiinae could not be scored for many characters due to the variability of their states. Our trees invariably place the Hybotidae as sister group to the Dolichopodidae plus Microphoridae, as proposed by Chvála (1983). The synapomorphies for this grouping are a reduced alula [27(1)] and loss of the sclerotized spermathecae in the female [48(2)].

Within the dolichopodid/microphorid clade, the Microphoridae (*sensu* Chvála 1983) are made paraphyletic by the placement of the subfamily Parathallasiinae as sister group to the Dolichopodidae. This relationship, proposed by Hennig (1971), was evident in all our trees and is supported by the following synapomorphies: [1(1)] eyes dichoptic in males; [2(1)] eyes haired; [4(1)] antennae inserted high on face; [19(2)] subcosta reduced; [26(1)] anal lobe reduced. More detailed study of the subgroups of Microphoridae is needed better to define the family and its probable relationship with Dolichopodidae (Ulrich, 1991).

The Empididae s.s. (Chvála, 1983) and Oreogetoninae were consistently closely associated on all of the trees, but no single arrangement with respect to other empidoids was obtained. The empidids are a well-defined monophyletic group, sharing a fused prosternum [12(1)], reduced alula [27(1)], split epandrium [36(1)] and a long slender upcurved aedeagus [45(1)]. The Oreogetoninae are clearly a paraphyletic assemblage with no apparent synapomorphy, although the representative genera included in this study, *Oreogeton*, *Hormopeza* and *Gloma*, were

closely associated on all trees. A more thorough study of the Oreogetoninae and Empididae is necessary to resolve the relationships within these large and diverse taxa.

Discussion

The purpose of this study was to evaluate the two leading hypotheses on the origins of higher flies, and to determine the bearing on these of the debated homologies of cyclorrhaphan male genitalia. Even with weighting against homoplasious characters, our evidence from adult morphology invariably supports the hypothesis of Chvála (1983) in placing *Cyclorrhapha* within Empidoidea near the Atelestidae, over the hypothesis of a sister-group relationship between Empidoidea and *Cyclorrhapha* (Hennig, 1958; Griffiths, 1990). Moreover, presuming that the cyclorrhaphan-like genitalia in several species of Asiloidea represent convergence, the estimated placement of the *Cyclorrhapha* appears independent of which interpretation of their clasping organs is adopted, provided that these characters are included in some form. Thus, the question of clasper homologies appears unresolved by the appeal to concordance with other characters, but does not appear critical to the larger issue of cyclorrhaphan origins.

For several reasons, however, these conclusions should be regarded as provisional, serving primarily to focus further study.

First, our result that the *Cyclorrhapha* originates from within the Empidoidea is not strongly supported. Trees in which the Empidoidea are monophyletic are only a few steps longer, and a permutation test shows these differences to be far from statistically significant. Therefore, even a small amount of undetected homoplasy could explain our result, and the number of corroborating characters necessary to overturn it would be few. Conversely, however, many opposing characters indeed would be needed to establish empidoid monophyly convincingly. We doubt that adult morphology can settle the issue.

Second, characters of the immature stages were not included, as these are not yet available for critical empidoid and asiloid groups, such as Atelestidae and *Apystomyia*. Such characters might lead to a different result; for example Woodley (1989) and Sinclair (1992) cite larval characters in support of empidoid monophyly.

Third, the synthesized adult groundplans for the terminal taxa included here may change as relationships within these entities become better known. Our results suggest that the asiloid groundplan is particularly critical to placement of the *Cyclorrhapha*. The monophyly of the Asiloidea, supported by three adult synapomorphies (Griffiths, 1986) and a single larval synapomorphy (Woodley, 1989; but see Yeates and Irwin, 1992), appears reasonably well established. It thus seems unlikely that a partially cyclorrhaphan-like male clasper, seen in *Apystomyia* and several other groups bearing the defining asiloid characters, could be primitive; this would require reversion to the primitive dipteran condition in the vast majority of asiloids and, independently, in empidoids. However, the potential effect, were this reasonable assumption (or that of asiloid monophyly) to be proven wrong, is simulated by calculations that include *Apystomyia* but do not include asiloid characters that would presumably place it in a derived position. Our results suggest that *Cyclorrhapha* and/or Atelestidae might then be inferred to be basal or nearly so within Eremoneura, with the clasper homologies re-emerging critical to exact placements; under these

conditions, moreover, the evidence against a monophyletic Empidoidea becomes considerably weaker.

Regarding resolution of cyclorrhaphan genitalic homologies, perhaps the most promising source of additional evidence would be detailed analyses of muscle insertions, which may reveal the segmental identity of particular modified sclerites (Ulrich, 1975; Ovchinnikova, 1989). Detailed studies of the development and fate of individual sclerites might be definitive, but face daunting obstacles for the critical groups, which are small and almost all unknown as immatures.

Regarding further resolution of cyclorrhaphan origins, apart from discovery of additional immatures, and clarification of asiloid relationships, molecular sequence data, which we have begun to collect, may be the most promising additional source of evidence. This is especially true given the seemingly high rates of diversification and morphological change in flies, which have made morphological study of their origins so difficult.

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Appendix 1. Character Distributions and Scoring

Characters and character states used in the phylogenetic analysis are described in detail below with their numerical coding. Alternative transformation series (a, b) for characters 5 and 48 correspond to columns "TS1" and "TS2" in Table 2. For male genitalic characters 36-39, P denotes scorings for PERIANDRIAL data sets (Table 2), E denotes EPANDRIAL scorings. Characters 36-42 were removed in the NO GENITALIA data set.

HEAD

1. Eye contiguity. Holoptic (0) or dichoptic (1). The shape of the head in the Empidoidea is, in part, determined by the size of the eyes. As in most swarming Diptera in which the males locate and capture the female in flight (Downes, 1969), the ommatidia on the upper 1/2-2/3 of the male eye are greatly enlarged, and the eyes, comprising nearly the entire head, are contiguous on the frons above the antennae (holoptic). Females have smaller eyes which never touch on the frons (dichoptic). Males in some solitary and predaceous empidoid groups which have lost the swarming habit, often revert to the primitive dichoptic condition (Chvála, 1976) and, like females, almost always have uniform ommatidia. These include Clinocerinae, Hemerodromiinae, some Tachydromiinae, Parathalassinae and most Dolichopodidae. In some of these groups, especially Tachydromiinae here coded as "unknown" (?), eye contiguity is highly variable and is clearly more useful below the subfamily level.

Chvála dismissed this character, doubting its phylogenetic utility because of its clear functional dependence on the swarming habit. However, he repeatedly cites the holoptic condition as a synapomorphy for his groupings. Hennig (1971) and Chvála (1981, 1983) use the dichoptic condition of the male as evidence for the sister-group relationship between Parathalassinae and Dolichopodidae.

2. Eye hair. Absent (0) or present (1). The presence of microscopic hairs between the facets of the compound eye is commonly considered a derived character

- throughout the Diptera. In the Empidoidea, this character was used by Hennig (1971) and Chvála (1981, 1983) as evidence of the close relationship of the parathalassiinae genera *Microphorella* and *Parathalassius* to Dolichopodidae, all of which have pubescent eyes.
3. Ocellar vestiture. Many scattered hair-like setae (0) or few ordered pairs of thicker bristle-like setae (1). The Empidoidea and Cyclorrhapha are characterized by the reduction and ordering of undifferentiated scattered hairs (occurring in orthorrhaphous Brachycera) into sets of bristle-like setae. This trend occurs on almost all haired external body regions (see characters 13–17). The ocellar tubercle of Brachycera is normally raised above the level of the eyes, bearing three ocelli. This tubercle is covered with scattered setulae in most Bombyliidae, but these setulae are reduced to a single, long, usually divergent pair of ocellars and a normally convergent pair of post-occellars in *Apystomyia*, Empidoidea and most Cyclorrhapha. Griffiths (1986) considered this reduction a synapomorphy for the Eremoneura, but it also occurs in the orthorrhaphous Brachycera with clearly parallel origins in Bombyliidae, Asilidae and Empidoidea.
 4. Antennal insertion. Antennae inserted at or near middle of face (0) or antennae inserted high on face (1). The antenna of most Empidoidea and primitive Asiloidea is inserted near the middle of the head when viewed laterally. The genus *Microphorus* and several other isolated genera have the antenna inserted slightly lower. Parathalassinae and Dolichopodidae have the antenna inserted high on the head, a condition that also occurs in *Dolichocephala* and several other Clinocerinae, as well as in Hemerodromiinae and Brachystomatinae. Hennig viewed this character as an additional synapomorphy for the Parathalassiinae/Dolichopodidae sister-group relationship, but considered it functionally dependent on the elongation of the compound eyes subsequent to the fusion of the clypeus and prefrons (Hennig, 1971).
 5. Style articulation. Two (0) or one (1) or three (2); (a) 2–0–1, (b) 2–1–0. A reduction in the number of flagellar style subsegments is a general trend in the Diptera. The style of the Empidoidea is two-articulated, whereas more primitive orthorrhaphous Brachycera have three or more subsegments, and most Cyclorrhapha have a three-articulated aristate style. For a time, Hennig (1970, 1981) considered the two-articulated style of Empidoidea (Empidiformia) and some Asiloidea (Asiliformia) a synapomorphy for these groups, and the three-articulated condition in the Cyclorrhapha a plesiomorphy. The discovery of a three-articulated style in *Meghyperus* and *Acarteroptera* of the Atelestidae, however, provided evidence that the three-articulated condition of Cyclorrhapha could be independently derived from the two-articulated empidoid style. Indeed, the ampulliform basoflagellomere of *Meghyperus sudeticus* and *Atelestus* suggests a transformation series in which the small protruding section of the basoflagellomere buds off to become the 3rd article. Chvála and Griffiths consider the three-articulated cyclorrhaphan condition derived from the two-articulated empidoid condition, and we concur. However, to test the effects of both of these interpretations on the placement of the Cyclorrhapha, we score both transformations (cyclorrhaphan condition primitive or independently derived; TRANSFORMATION SERIES 1) and analyze the effects of the two scorings in conjunction with all other evidence.

A reduction to a single segment has occurred in *Anthalia* and *Euthyneura* (ocydromiinae). Many Empidoidea have a small terminal bristle at the apical tip of the style; unlike Chvála (1983), we do not consider this a flagellar article as it is clearly a socketed seta.

6. Antennal-style type. Stylate, equal to or less than the length of the basoflagellomere (0) or aristate, greater than 2× the length of the basoflagellomere (1). Chvála (1983) described two general trends in the development of the empidoid antenna: the enlargement of the basoflagellomere with a smaller style-like arista, a condition already established in the primitive Asiloidea; and the elongation of the style into a long slender arista with the retention of a smaller basoflagellomere. An aristate style has arisen several times in the Empidoidea and is clearly convergent. We have somewhat arbitrarily defined a "style" as nearly equal to or less than the length of the basoflagellomere, and an "aristate" style (arista) as greater than 2× the length of the basoflagellomere.
7. Scape vestiture. Setae present (0) or setae absent (1). Primitively, the scape is a large visible segment with scattered hairs or setae. Some empidoid groups, *Apystomyia* and *Hilarimorpha*, however, have a reduced scape which is never haired or setose. Tuomikoski (1966) and Hennig (1970) considered this a synapomorphy for the Ocydromioinea group of subfamilies.
8. Maxillary palpus attachment. Not attached to a sclerotized palpifer (0) or attached to sclerotized palpifer (1). Krystoph (1961), Tuomikoski (1966), Hennig (1970) and Chvála (1981, 1983) all recognized the presence of a distinct sclerotized palpifer at the base of the maxillary palp as synapomorphic for the Hybotinae, Tachydromiinae and Ocydromiinae [Ocydromioinea (in part) of Hennig, 1970; Hybotidae of Chvála, 1983]. All other empidoids, and bombyliids, have a membranous base to the palps.
9. Maxillary lacinia. Present (0) or absent (1). In addition to the presence of a sclerotized palpifer, Chvála's "Hybotidae" are characterized by the loss of the maxillary lacinia (Krystoph, 1961; Tuomikoski, 1966; Hennig, 1970; Chvála, 1981, 1983). Primitively these are long blade-like stylets of the maxilla.
10. Maxillary palpus segmentation. Two-segmented (0) or one-segmented (1). The Empidoidea and Cyclorrhapha are characterized by a one-segmented club-like palpus, a reduction from the more primitive, two-segmented, asiloid condition, Griffiths (1987) considers this a synapomorphy for the Eremoneura (Empidoidea + Cyclorrhapha). Some bombyliids, Hilarimorphidae and *Apystomyia* also have developed a single-segmented palpus. The length of the palpus is correlated with that of the proboscis and does not appear phylogenetically useful.
11. Pseudotracheae. Present (0) or absent (1). A fleshy labellum derived from the labial palpus, with pseudotracheae for sponging liquid food, is a ubiquitous dipteran feature. Many specialized groups, especially those with strict predatory habits, have lost the pseudotracheae. This is true of the specialized subfamilies Hemerodromiinae and Clinocerinae and may be considered evidence for their relationship (Chvála, 1983). Brachystomatinae and Tachydromiinae are polymorphic for this character and are thus scored as "?".

THORAX

12. Prosternum type. Separate sclerite between the surfaces of the forecoxae (0) or fused to the proepimeron and proepisternum (1). The prosternum is a small,

separate, saddle-shaped sclerite between the anterior surfaces of the forecoxae. It has traditionally been an important character in the classification of the Empidoidea. Collin (1961), Tuomikoski (1966) and Chvála (1983) agree that its occurrence in atelestids, microphorids, hybotids (including presumably the groundplan of the Tachydromiinae), some Oreogetoninae and Cyclorrhapha is symplesiomorphic. In the subfamilies Empidinae, Hemerodromiinae, Clinocerinae, Ceratomerinae, Brachystomatinae and some Tachydromiinae, this sclerite is fused to the proepimeron and proepisternum across the base of the coxae. Hennig (1970) called this the precoxal bridge and suggested tentatively that the small separate prosternum was derived from elements of the katepisternum and represents an apomorphic condition. Outgroup comparison makes this seem unlikely, as a small prosternum is present in the majority of orthorrhaphous Brachycera. We were unable to score the groundplan condition in the Dolichopodidae and Parathalassiinae as a fused prosternum has presumably evolved independently in several genera.

13. Proepimeron vestiture. Haired (0) or bare (1).
14. Proepisternum vestiture. Haired (0) or bare (1).
15. Laterotergite vestiture. Bare (0) or haired (1). Characters 13–15 describe the presence or absence of setae or hairs on the proepimeron, proepisternum and laterotergite (metapleuron). These characters have been traditionally used in keys to sets of genera in many taxa (Collin, 1961; Steyskal and Knutson, 1981; Chvála, 1983). The presence of setae on the laterotergite has long been a useful feature in the Empidinae. In general, the presence of scattered undifferentiated hairs is plesiomorphic with a reduction to several bristle-like setae or complete loss of setation apomorphic. Setation characters seem to vary greatly within taxa, however, and several taxa were left unscored. They may prove more useful within general or tribes. Our scorings are provisional and based on surveys of North American taxa.
16. Notal setae type. Randomly scattered (0) or arranged in pattern (1). Primitively, the asiloid notum is covered with randomly scattered undifferentiated hairs. Organization of these hairs into a specific ordered pattern of dorsocentral and acrostichal setae has long been considered an important character within the Cyclorrhapha (McAlpine, 1989) and Empidoidea (Chvála, 1983). Apparently parallel reductions have occurred sporadically in the Nematocera and orthorrhaphous Brachycera.
17. Postalar vestiture. Many (0) or single (1). In Empidoidea, most Cyclorrhapha, there is a single long postalar seta. The postalar region is covered with scattered hairs in most Asiloidea, and this character follows the general pattern of notal setae reduction described above. McAlpine (1989) considered reduction of postalar seta number an apomorphic condition of the schizophoran Cyclorrhapha.

WING VENATION

Wing venation (characters 18–26) has been critical to the classification of the Empidoidea, especially at the level of genus and subfamily. Collin (1961) used these features in his keys, and Hennig (1970, 1971) and Chvála (1983) used them in phylogenetic analyses. With some emendations, we have followed the traditional interpretations of Chvála and Hennig. Venation change is sometimes difficult to

characterize, especially gain and loss of crossveins, and some veins seem to be gained or lost repeatedly in some groups. We follow Hennig and Chvála in adopting the venation of the oldest known fossil empidid, *Protempis antennata* (Usachev, 1968) from the Jurassic, as the estimated groundplan wing venation for the Empidoidea (Chvála, 1983). This fossil has venation similar to that of many primitive bombyliids.

18. Coastal termination. Circumambient (0) or ending at M1 (1) or ending at R4+5 (2). In *Protempis* and primitive Asiloidea, including *Hilarimorpha* (Webb, 1981), the costal vein runs entirely around the wing, providing support for the wing veins reaching the costa. Reduction in the number of wing veins in the Empidoidea and higher Diptera is associated with shortening of the costa, which extends only to the tip of M1 in atelestids, Cyclorrhapha and most Hybotidae. The costa ends at R4+5 in *Bicellaria* and many Empidinae.
19. Subcostal termination. Complete, reaching costa (0) or incomplete, not reaching costa (1) or reduced, never longer than 1/2 the length of the basal cells (2) or recurved, meeting R1 (3). Primitively, the subcosta extends to the wing margin, as in most orthorrhaphous Brachycera, *Protempis* and primitive empidoids (Oreogetoninae, Brachystomatinae, Clinocerinae). The subcosta commonly ends short of the wing margin in atelestids and Hybotidae and is further reduced in some Tachydromiinae and in *Parathallasius*, to less than 1/2 the length of the basal cells. In Dolichopodidae, the subcosta is very short and recurrent, often meeting or fused with R1. We interpreted these successive reductions as steps in a transformation series. Some groups showed marked variation in this character and were left unscored (e.g. Tachydromiinae). *Opetia* and Cyclorrhapha have a complete subcosta, suggesting either reversal or a primitive origin for these groups.
20. R4+5 type. Branched (0) or unbranched (1). A branched R4+5 is a primitive trait present in *Protempis*, orthorrhaphous Brachycera and primitive Empidoidea. The loss of this branch is common to the Hybotidae, *Atelestus*, Microphoridae, Dolichopodidae and all higher Diptera. Only in the Empidinae is the character variable, the large genus *Rhamphomyia* having a simple unbranched R4+5.
21. Medial branch number. Three (0) or two (1) or one (2). A reduction in the number of branches of the medial vein from 3 to 2 has been regarded a synapomorphy for the Eremoneura (Lameere, 1906; Hennig, 1958; Griffiths, 1987). This reduction also occurs independently in many Bombyliidae, Hilarimorphidae, Asilidae and Scenopinidae. Within the Empidoidea, the interpretation of this character is made difficult by conflicting terminologies. The vein which extends from the base of the discal cell to the wing margin is referred to as M3+4 by Chvála (1983), but as CuA1 by McAlpine (1981). The groundplan wing of the Diptera indeed has four medial branches (McAlpine, 1981), but these have been already lost in most Asiloidea. For this reason, we prefer the view that the vein labeled M3+4 in Chvála (1983) is an extension of the cubitus and should be labeled CuA1.

There are three branches of M from the discal cell in most primitive Brachycera, two primitively in the Empidoidea, *Apystomyia* and Hilarimorphidae, and a single unbranched medius in *Atelestus*, *Acarteroptera*, *Opetia*, Cyclorrhapha, Hybotidae, Dolichopodidae and Microphoridae.

22. Distal medius type. Unbranched (0) or branched (1). A two-branched medius in which the fork is distal to the discal cell, is present in the atelestid genera *Merghyperus* and *Acarteroptera*; it also occurs in *Hemerodromia*, and, most likely by convergence, in *Opetia* and *Hilarimorpha*. The latter two taxa are scored unknown (?) under the assumption that the branched M1 in these groups is not homologous with that of the aforementioned empidoidea. The primitive condition, occurring in nearly all other Empidoidea, is an unbranched M1 connecting the discal cell and edge of the wing.
23. CuA2 curvature. Straight, joining A1 at or near the wing margin (0) or recurved, joining A1 at an angle greater than 90 degrees, cell CuP longer than 2nd basal cell (1) or equal, joining A1 at approximate 90-degree angle, cell CuP equal to length of 2nd basal cell (2) or reduced, joining A1 at less than 90-degree angle, cell CuP less than length of second basal cell (3) or lost (4). In some primitive Brachycera, as in the dipteran groundplan, vein CuA2 reaches the wing margin. In Bombyliidae the primitive condition is retained, but in some taxa it joins vein A1 at the wing margin. A stepwise reduction in the length of this cell is evident in the Empidoidea, brought about by the migration of CuA2 toward the base of the wing in its attachment to A1. We have scored this transformation as a progressive reduction in the length of the cell, described by the shape of CuA2. *Protempis*, some bombyliids and primitive Platypezidae (Cyclorrhapha) have a straight CuA2 which joins A1 at or near the wing margin. As CuA2 moves toward the wing base, the cell becomes shorter and CuA2 becomes recurved in its attachment to A1; *Apystomyia*, atelestids, some Hybotinae and Brachystomatinae, all have an anterior cubital cell longer than the basal cells. Most Hybotidae have a more highly recurved CuA2 which with the anterior cubital cell approximately equal in length to the basal cells. Microphoridae and Dolichopodidae have even further reduced anterior cubital cells which are much shorter than the basal cells. Many specialized groups with very reduced wing venation, such as the Tachydromiinae, have lost the anterior cubital cell.
24. Discal cell. Present (0) or absent (1). A discal cell created by the crossvein dm-cu is a common feature in Diptera. The loss of dm-cu, and consequently of the discal cell, occurs in many specialized groups with reduced wing venation (e.g. Tachydromiinae) and also in *Atelestus*, *Opetia* and some primitive Cyclorrhapha (e.g. Platypezidae: *Melanderomyia*, *Microsania*), constituting a possible synapomorphy for these groups.
25. A1 termination. Complete, reaching wing margin (0) or incomplete, ending before wing margin (1) or lost (2). In primitive Brachycera and nearly all Bombyliidae, the anal vein (A1) is complete, extending to the wing margin. In the Empidoidea, the shortening of the A1 is loosely correlated with the general reduction of the anal area of the wing. The vein is lost in Brachystomatinae, Clinocerinae, Hemerodromiinae and Ceratomerinae, which have a greatly reduced anal area. In other empidooid groups variation in length is considerable, with most groups having the vein fading before reaching the wing margin. A reversal to the complete condition in some atelestids and primitive Cyclorrhapha may be a synapomorphy for these groups since purportedly more primitive groups, e.g. Oreogetoninae, have incomplete anal veins.
26. Anal lobe type. Developed, axillary angle acute or right (0) or reduced, axillary

- angle obtuse (1) or lost (2). The anal area of the wing is reduced in some Empidoidea through a gradual flattening of the anal lobe. Discrete states are difficult to recognize for this character which we have quantified by using the axillary angle formed by the lobe and its connection to the base of the wing. We have somewhat arbitrarily distinguished a well-developed lobe, corresponding to an acute or right angle, from a reduced lobe, corresponding to an obtuse anal angle. The anal lobe is lost in Hemerodromiinae, Brachystomatinae, Clinocerinae and Ceratomerinae, which have slender, nearly parallel-sided wings.
27. Alula type. Developed (0) or reduced (1) or lost (2). The alula is well developed in primitive Brachycera, Bombyliidae and primitive Empidoidea. As with many wing characters, it tends to be reduced or lost as the anal area of the wing decreases, as in the Brachystomatinae. However, the alula is also lost or reduced in many groups with well-developed anal lobes, and thus appearing to provide at least partial independent support for relationship.

LEGS

28. Foretibial gland. Absent (0) or present (1). The presence of a distinct gland near the base of the foretibia, not found in any other groups, is a well-recognized synapomorphy of the Hybotidae (Tuomikoski, 1966; Smith, 1969; Hennig, 1970; Chvála, 1983). The function of the gland is unknown. The opening of the gland is often raised on a tubercle surrounded by conspicuous hairs or spines.
29. Hindtibia shape. Slender, equal in width to fore- and midtibiae (0) or clavate, greater than 3× the width of fore- and midtibiae (1).
30. Hind basitarsomere shape. Slender, equal in width to fore- and mid-basitarsomere (0) or dilated, greater than the width of fore- and mid-basitarsomere (1). In the Atelestidae, Platypezidae and several isolated genera, e.g. *Microphorus* and *Trichinomyia*, the male hindtibia is clavate and compressed, presumably for holding the female during mating (Chvála, 1983). Additionally, some groups have dilated hindtarsi, particularly *Acarteroptera* and *Atelestus*. The expansion of the hindtibia and tarsus in male atelestids may represent a stage in the development of the large flattened hindtibia and tarsus which occurs in the Platypezidae.

ABDOMEN

31. Abdominal plaques. Present (0) or absent (1). Stoffolano et al. (1988) have recently shown that the cuticular plaques found on the abdomen of Nematocera and Orthorrhaphous Brachycera are not sensory pits but the external remnant of attachment sites for muscles of the pupa. This character, then, is an indirect indicator of the method of pupation. Cyclorrhaphans, which have an immobile obtect pupa inside the puparium, lack these muscles and consequently the plaques. The obtect puparium has long been considered a synapomorphy for the group. The presence of the plaques in *Atelestus* is additional evidence that it is not a cyclorrhaphan and that its larva and pupa, though unknown, retain empidoid features (Stoffolano et al., 1988). *Opetia nigra* lacks muscle plaques, indicating that its unknown pupa may have already acquired the cyclorrhaphan puparium.

32. 8th abdominal tergite shape. Band, nearly equal to the length of sternite 7 (0) or reduced band, approximately 1/2 the length of sternite 7 (1) or U-shaped band, much less than 1/2 the length of sternite 7 with ventral posterior projection (2) or reduced band fused to tergite 7 (3):

0-1-2
1
3

Primitive Brachycera and many empidoids (Hybotidae) have a complete 8th abdominal sclerite nearly equal in length to the 7th tergite. Bährmann and Chvála noted the reduction of this band to 1/2 the length of the 7th tergite in most Oreogetoninae and "Empididae". Its further reduction to a thin band with lateral L-shaped projections occurs in the Atelestidae, a possible synapomorphy for the group. In Dolichopodidae, the 8th tergum is reduced and fused with the 7th tergite. This character is highly variable, reduced or sometimes fused in primitive cyclorrhaphans. Due to this variability, we have left the cyclorrhaphan groundplan condition undetermined.

33. 8th abdominal tergite placement. Dorsal (0) or pleural (1) or ventral (2). Rotations of the hypopygium are common in the Diptera (Griffiths, 1972; McAlpine, 1981). Often this rotation also affects the position of the sclerites of segment 8, although to varying degrees. In nearly all Empidoidea the 8th tergite remains in its primitive dorsal position. In the Microphoridae, Parathalasiinae and Dolichopodidae it is shifted laterally resulting from the torsion and 180-degree rotation of the hypopygium (Ulrich, 1976). Griffiths (1972) and Chvála (1983) describe a ventral 8th tergum and dorsal 8th sternum, an inversion which occurs with the first 180 degrees of a 360-degree rotation, or circumversion, in the Cyclorrhapha. However, inversion of the 8th tergum does not occur in many Platypzidae, but is shifted in other primitive Cyclorrhapha, e.g. *Lonchoptera*, consequently we have scored the cyclorrhaphan groundplan as "unknown" (?) for this character. We have scored both the pleural position of the 8th tergite in microphorids and dolichopodids, and the inverted condition of the Cyclorrhapha as derived independently from the primitive dorsal position.

MALE GENITALIA

The complexity of the male genitalia in the Empidoidea has led to considerable debate over the homologies and transformations of structures in the transition from "orthorrhaphous" to cyclorrhaphous Brachycera. At issue are the homologies of the dorsal and ventral sclerites of segments 9-11 (hypopygium), and their associated appendages. Two major competing hypotheses have emerged, conflicting in the interpretation and terminology of structures, and differentially affecting the phylogenetic reconstruction of various dipteran lineages. Specifically these are the "periandrial" hypothesis of Griffiths (1972) and "epandrial" hypothesis of McAlpine (1981), following Hennig (1976). Their differences result from conflicting interpretations of the segmental origin of the clasping structures of the higher Diptera. These are separate biarticulated appendages in primitive Diptera, but in some Empidoidea and all Cyclorrhapha are a single expanded saddle-shaped sclerite. The details of these hypotheses have been reviewed by Griffiths (1972,

1981, 1983, 1984, 1986, 1987), McAlpine (1981), Chvála (1983) and Michelsen (1988), along with analyses of the fate of individual associated hypopygial structures.

Chvála (1983) provided the most thorough analysis to date of the structures of the male hypopygium in the Empidoidea. His study of the Palearctic taxa builds on the work of Bährmann (1960), Ulrich (1975), Hennig (1976) and Griffiths (1972). The proposed homologies and terms used by each of these authors for the controversial hypopygial segments are discussed separately below as they pertain to characters in the phylogenetic analysis.

The purpose of this study is not to resolve the controversy over dipteran hypopygial homologies. Rather, our purpose is to examine their consequences for the phylogeny problem when analyzed in conjunction with all other evidence available.

We have included here only those characters for which the variation can be coded into discrete, easily recognized states for large groups of taxa. To avoid the bias of choosing either system (periandrial vs epandrial), we have constructed two separate data sets for characters which differ in interpretation. Transformation series are constructed following Chvála (1983) and Griffiths (1984, 1986, 1987) and alternatively following McAlpine (1981). These transformations are illustrated and summarized schematically in Fig. A1 and detailed in the descriptions of characters 36–44.

34. Hypopygial symmetry. Symmetrical (0) or hybotid asymmetry (1) or microphorid asymmetry (2); 1–0–2. The hypopygium is symmetrical in nearly all primitive Diptera, primitive Empidoidea, Atelestidae and primitive Cyclorrhapha. Complex asymmetrical hypopygia are present in Hybotidae, Microphoridae, Parathalassiinae and Dolichopodidae (but see Bickel, 1987). Chvála (1983) considered this asymmetry a synapomorphy for these groups, but the development of this complexity is clearly independent in the two lineages. Chvála (1983) himself attributed the hybotid asymmetry to the 90-degree right rotation of the hypopygium and that of the microphorid line to torsion of the pregenital segments. Griffiths (1972) believes the complex asymmetrical hypopygia are instead the result of flexion of the terminalia for protection. Unlike Chvála (1983), we have scored the two asymmetries as separate states arising from symmetrical hypopygia since their origin and the development of their complexity is clearly non-homologous.
35. Hypopygial rotation. Not rotated (0) or rotated 90 degrees (1) or rotated and ventroflexed (2) or rotated 360 degrees (3):

1–0–2
|
3

In many dipteran groups, rotation and flexion of the hypopygium occurs as an adaptation to facilitate mating and for protection of the genitalia (McAlpine, 1981). As stated above (character 33), the position of the 8th abdominal tergum is often affected by this rotation, but in a complex way and to varying degrees; in some groups the 8th tergum seems to have shifted with the twisting of the abdomen, while in others the two seem independent. For this reason, we treat the final position of the genital capsule as independent

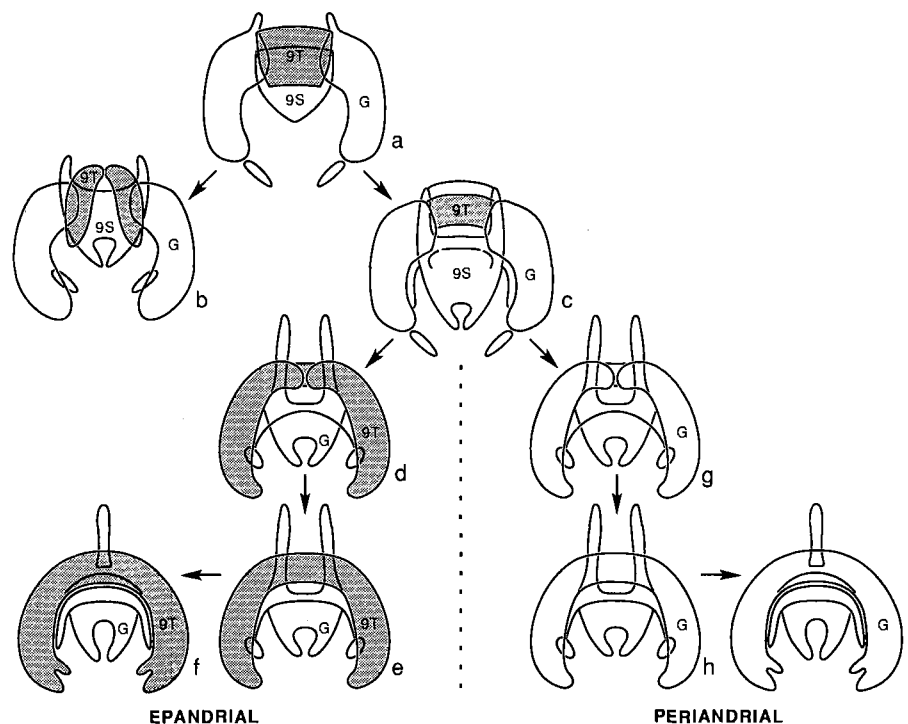


Fig. A1. Schematic representation of competing interpretations of hypopygium evolution in the Asiloidea and Eremoneura. (a) Primitive asiloid hypopygium with a separate well-developed 9th tergite (9T) and sternite (9S) with gonocoxae and gonostyli performing the clasping function (G); (b) typical empidid hypopygium (Chvála, 1983) with the epandrium (9T) split dorsally and gonocoxae (G) retaining the clasping function; (c) hypopygium of *Hormopeza* Zetterstedt with a small epandrium (9T) fused to the gonocoxae (G); (d)–(f) EPANDRIAL interpretation of Hennig (1976) and McAlpine (1981): the epandrium (9T) expands laterally, as in Atelestidae (d), to become the genitalic clasping structure in the higher Diptera (f). The gonocoxae (G) and gonostyli are reduced and fused to the hypandrium (9S); (g)–(i) PERIANDRIAL interpretation of Griffiths (1972) and Chvála (1983): the epandrium (9T) is reduced and lost with a correlated dorsal expansion and fusion of the gonocoxae (G) to form the periandrium or clasping structure of some Empidoidea [e.g. *Atelestus* (g)] and all Cyclorrhapha (i).

from the final position of tergum 8, although the relationship between the two features may indeed be more complicated than this scoring implies.

In primitive Brachycera and Empidoidea, including Atelestidae, the hypopygium is not rotated, although rotation does occur independently in most advanced Bombyliidae and some Asilidae (Dasypogoninae). In almost all Hybotidae the hypopygium is rotated 90 degrees to the right and in the microphorid and dolichopodid lines rotation is 90–180 degrees with a latero-ventral flexion of the genital capsule (Chvála, 1983). Griffiths (1972) and Chvála (1983) recognized the 360-degree rotation of the Cyclorrhaphan hypopygium as a synapomorphy for the group evidenced by the twisting of the vas deferens, nerves and tracheal system around the hindgut (Griffiths, 1972; McAlpine, 1981). Disney (1987) favors excluding *Opetia nigra* from the Cyclorrhapha since its genital ducts are seemingly too short for this twisting to occur.

36P. Epandrium type. Single unmodified sclerite (0) or split into two dorsal sclerites (1) or fused to the gonopods (2) or lost (3); 3–2–0–1.

36E. Single unmodified sclerite (0) or split into two dorsal sclerites (1) or clasper, elongate, U-shaped (2); 2-0-1. The 9th tergum or epandrium is a simple unmodified tergite in the Nematocera and primitive Brachycera. The fate of this sclerite within the Empidoidea and Cyclorrhapha is the central conflicting feature between Griffiths' (1972) periandrial hypothesis and McAlpine's (1981) epandrial hypothesis. In the transformation series proposed by Griffiths (1972) and Chvála (1983), the 9th tergum is lost in the Atelestidae, Hybotidae, Microphoridae, Dolichopodidae and all Cyclorrhapha. In these groups, the large saddle-shaped sclerite posterior to segment 8 is believed to be the dorsally fused bases of the gonocoxae, appendages of the 9th sternite. This hypothesis is based on continuity of function for the gonocoxae, the clasping structures of all primitive Diptera. Griffiths (1972) regarded the loss of the epandrium and fusion of the gonocoxae forming a periandrium a synapomorphy for the Eremoneura (Empidoidea + Cyclorrhapha). However, the discovery of a well-developed epandrium and separate gonocoxae in *Hormopeza*, *Iteaphila* and most "Empididae" (*sensu* Chvála, 1983) reveals that the reduction of parts actually occurred within the Empidoidea (Chvála, 1983). Both Chvála and Griffiths recognized this transformation as evidence for a possible close relationship of *Atelestus* and the Cyclorrhapha.

Griffiths (1986, 1987) now believes the periandrial similarities of *Atelestus* and cyclorrhaphous flies are the result of convergence, with fusion of the gonocoxae a groundplan character of the Eremoneura which is reversed in the Atelestidae and Hybotidae.

We have scored the epandrium as interpreted by Chvála (1983) for most empidoid groups. The epandrium of *Hormopeza* is a distinct simple sclerite lying between and fused to the bases of the gonocoxae. This fusion of the epandrium to the gonocoxae in *Hormopeza* has been scored as a step in the formation of the periandrium in PERIANDRIAL data sets, but as a separate sclerite in the EPANDRIAL data sets since the gonocoxae of *Hormopeza* retain their clasping function. In *Oreogeton* the epandrium is larger and also seemingly fused to the gonocoxae. Dorsally, the epandrium (or periandrium) of *Oreogeton* appears to be the fusion product of two sclerites. This is very similar to the condition in *Atelestus*, in which the periandrium appears to be formed by the fusion of two large sclerites with an easily visible suture between them. Under the EPANDRIAL hypothesis these structures are interpreted as a single, large, U-shaped sclerite with presumably no fusion of structures. The interpretation of the dorsal suture in these taxa as a result of the fusion of the gonocoxae across the dorsum or splitting of the epandrium subsequently affects the homologization of additional hypopygial structures. Bährmann (1960) and Chvála (1983) interpreted the paired dorsal lamellae of *Iteaphila*, Empidinae, Hemerodromiinae, Clinocerinae and Ceratomerinae as the 9th tergum (epandrium) split into two separate tergites. The epandrium has been lost independently in the Brachystomatinae (Chvála, 1983). Consequently, the transformation series proposed by Chvála, in which the single 9th tergum of *Hormopeza* and primitive groups is split in the "empidid" lineage, or fused with the gonocoxae in intermediate forms (*Oreogeton*), or lost as in all Hybotidae, Microphoridae, Dolichopodidae, Atelestidae and Cyclorrhapha, conforms to the periandrial hypothesis of Griffiths (1972). In contrast, Hennig (1976) and

subsequently McAlpine (1981) have concluded that the epandrium is expanded in the Cyclorrhapha, with the gonopods reduced and becoming fused to the hypandrium (9S), the epandrium (9T) taking over the clasping function. We have used an alternative scoring for this "epandrial" theory which accounts for this retention and transformation of the 9th tergite.

The interpretation of the presence or absence of the epandrium is not the only point of conflict in the theories, but its scoring affects the homologies of the more complex structures of the hypopygium. Griffiths (1981, 1983, 1984) has argued that Hennig's (1976) and McAlpine's (1981) thesis results in far too many *ad hoc* assumptions for the origin and homologies of the processes of the hypandrium and aedeagus (pregonites and postgonites). Hennig's (1976) views are the result of evidence from muscle insertions which show an association of the gonopods and hypandrium in Cyclorrhapha and Empidoidea.

- 37P. Gonopod type. Separate appendages articulating with segment 9 (0) or fused dorsally with visible seam (1) or fused dorsally without seam (2); 0-1-2.
- 37E. Separate appendages articulating with segment 9 (0) or fused to hypandrium (1); 0-1. Interpretation of the biarticulated appendages of sternum 9, gonocoxae and gonostyli is highly dependent on the interpretation of the fate of the epandrium (9T). Since opinion varies on the homology of this character, we score it as two separate transformation series here. As stated above, under the periandrial hypothesis the gonocoxae fuse across the dorsum in the Cyclorrhapha and similarly, or in parallel, in Atelestidae, Hybotidae, Microphoridae and Dolichopodidae. In *Atelestus* and some *Oreogeton* spp., there is a visible dorsal seam between the bases of the gonocoxae, perhaps constituting additional evidence for the PERIANDRIAL theory. Hennig (1976) and McAlpine (1981) argue that the gonopods are reduced and fused to the hypandrium in the Cyclorrhapha. Michelsen (1988) interprets the pregonites of the Schizophora, sclerotized structures associated with the base of the phallus, as derivations of the gonopods; however, tracing the homology of the pregonites in order to observe this transition within the Empidoidea is very difficult. We could not identify the homologs of the gonocoxae in the highly derived hypopygium of Brachystomatinae, and have scored it as "unknown" (?).
- 38P. Gonostyli articulation. Articulating distally with gonopods (0) or articulating proximally with gonopods, within genital capsule (1) or fused to gonopods (2); 0-1-2.
- 38E. Separate, articulating distally with gonopods (0) or fused to gonopods (1); 0-1. The distal articles of the gonopods, the gonostyli (telomeres of Griffiths, 1972), are the apical clasping structures of most primitive Diptera, including orthorrhaphous Brachycera (excl. Hilarimorphidae) and *Hormopeza*. Under the periandrial hypothesis, they are reduced and move anteriorly within the periandrium in Atelestidae and related empidooids, and represent the clasping lobes which have usually (but incorrectly according to this hypothesis) been called surstyli in the Cyclorrhapha and *Opetia*.

Hennig (1976), McAlpine (1981) and Michelsen (1988) believe the surstyli are derived from the 10th tergum and have replaced the gonostyli as claspers. In this view, the gonostyli have become fused with the gonocoxae, the gonopods thus losing their biarticulated condition. Michelsen (1988), following Hennig (1976), believes the pre- and postgonites of the schizophoran

aedeagus are derived from the gonocoxae and gonostyli, but McAlpine (1981) homologizes these with the parameres of more primitive Diptera. We have not been able to trace the homology of these structures within the Empidoidea, which have a diverse array of paramere-like structures used in guiding the aedeagus and aiding copulation.

- 39P. Hypandrium type. Without paired processes (0) or with paired processes (1); 0-1. Not scored in EPANDRIAL data set (=gonopods). The hypandrium, or 9th sternite, is primitively a ventral plate protecting the aedeagus and genital complex. In the Empidoidea, this plate is complex in form and fused internally with various sclerites and appendages of other hypopygial structures. This has resulted in conflicting interpretations of this structure (McAlpine, 1981; Griffiths, 1981, 1982, 1984; Chvála, 1983). Primitively, the hypandrium is an unmodified 9th sternite in orthorrhaphous Brachycera including Bombyliidae. In the Empidoidea and Cyclorrhapha, the hypandrial complex consists of a ventral plate protecting the aedeagus (9S) with a pair of posteriorly projecting processes, a hypandrial bridge which joins the gonocoxae internally across the dorsal surface of the aedeagus and paired gonocoxal apodemes. Griffiths (1986) considered the presence of the paired processes a synapomorphy for the Eremoneura. He believes the presence of similar processes in some asilids to be due to convergence. McAlpine (1981) interprets these processes as the gonocoxae and gonostyli fused to the hypandrium, consequently this character is not included in the "epandrial" dataset.
40. Hypandrial bridge. Absent, anterior corners of the hypandrium and gonocoxites not fused dorsally across the aedeagus (0) or present, anterior corners of the hypandrium and gonocoxites fused dorsally across the aedeagus (1). Hennig (1976) recognized a dorsal bridge (dorsal Brücke) with paired apodemes extended dorsally across the aedeagus. This he interpreted as the internal fusion of the anterior corners of the hypandrium with the fused gonocoxae and their associated gonocoxal apodemes. Both Hennig (1976) and Griffiths (1981, 1982, 1984) consider this fusion a synapomorphy for the Eremoneura. However, Griffiths (1986, 1987) now believes the periandrial similarities of Atelestidae and Cyclorrhapha are probably the result of parallelism (fusion of the gonocoxae across the dorsum having occurred independently in different lineages). The hypandrium and gonocoxal bridge are separate in orthorrhaphous Brachycera, including Bombyliidae, and fused in all Empidoidea and in primitive Cyclorrhapha.

The transformation series leading to this fusion and the true origin of the hypandrial complex are disputed. Hennig (1976) saw the hypandrium of Eremoneura (Empidoidea + Cyclorrhapha) as the fusion product of the 9th sternite, gonocoxae, gonostyli, gonocoxal bridge and gonocoxal apodemes. Griffiths (1981, 1982, 1984, 1986), however, believes that the gonocoxal bridge and apodemes secondarily separate from the gonocoxae with the bacilliform sclerites (see below), and they alone fuse to the hypandrium. As stated above, the homology of the gonocoxae and gonostyli is integral to these interpretations. Griffiths cites ontogenetic and muscular evidence for his views, but both theories require several *ad hoc* assumptions of fusion or separation for various structures. The differences in these transformation series are reflected in the alternative scorings of characters in the two genitalic data sets.

- 41P. Bacilliform Sclerites. Absent (0) or present (1).
- 41E. 10th Sternite. Absent (0) or present (1). The homology of the rod-shaped bacilliform sclerites (interparameral sclerites, Skleritleiste, intergonopodal sclerites, processus longi or intergonocoxal sclerites) of the schizophoran Cyclorrhapha has been difficult to trace back to the Empidoidea and Platypozidae. Griffiths (1986) believes these are the inner surfaces of the gonopods which separate with the gonocoxal bridge and articulate distally with the gonostyli (Fig. A1). Hennig (1976) and McAlpine (1981) also interpret these same structures as homologs of the bacilliform sclerites, but believe instead that they are the remnant of sternite 10. In Griffiths' system sternite 10 is a proctiger plate present in most primitive empidoids and orthorrhaphous Brachycera. We have observed neither bacilliform sclerites nor a proctiger plate in *Apystomyia*. Although the ontogenetic origin of the bacilliform sclerites is disputed, both systems consider their origin in the Eremoneura to be a synapomorphy for this group.
- 42P. 10th tergite. Present (0) or absent (1). Tergite 10.
- 42E. Single unmodified sclerite (0) or split into two sclerites articulating with the inner surface of the epandrium (1) or surstylus, fused to the epandrium (2). The homology of tergite 10 is also difficult to infer. It is present in some orthorrhaphous brachycerans, including many Asilidae. Griffiths (1986) considers tergite 10 present in the groundplan of the Heterodactyla, and its absence as a discrete sclerite in the Empidoidea and Cyclorrhapha an additional synapomorphy for the Eremoneura. Conversely, Yeates (pers. comm.) believes tergite 10 to be lost in all Asiloidea. Hennig (1976) and McAlpine (1981), however, believe the clasping surstyli of Cyclorrhapha actually represent the 10th tergite which is split in the Empidoidea (gonostyli of Griffiths and Chvála) and subsequently fused to the epandrium as the surstyli. Consequently, it is scored as present or absent in PERIANDRIAL datasets, and unmodified, split or fused to form surstyli in EPANDRIAL datasets. We scored tergite 10 "present" for the asiloid outgroups, corresponding to the groundplans proposed by Griffiths (1986) and McAlpine (1981) (see Appendix 2). Scoring tergite 10 "absent" in Asiloidea (Yeates, pers. comm.) did not affect the results.
- 43P. Ejaculatory apodeme. Fused to the base of the aedeagus (0) or not fused to the base of the aedeagus (1).
- 43E. Present (0) or absent (1).
- 44P. Aedeagal apodeme fusion. Gonocoxal apodemes not fused to form aedeagal apodeme (0) or gonocoxal apodemes separated from gonocoxae and fused forming aedeagal apodeme (1). (Not scored in EPANDRIAL data set = Ejaculatory apodeme). The ejaculatory apodeme (*sensu* McAlpine, 1981) of orthorrhaphous Brachycera and Empidoidea occurs at the base of the aedeagus providing both the sperm pump mechanism and an articulation point for movements of the aedeagus (Hennig, 1976). Hennig (1976) and Griffiths (1972, 1986) refer to this structure as the "aedeagal apodeme". The ejaculatory apodeme and sperm pump of Cyclorrhapha are separated from the base of the aedeagus, without muscular connections to the body wall, and are connected to the aedeagus only by a sperm duct. In the Cyclorrhapha, there is also an apodeme at the base of the aedeagus providing for movement. Hennig (1976), McAlpine (1989) and Griffiths (1981) agree that the separate, free ejaculatory apodeme

is a synapomorphy of the Cyclorrhapha; however, the origin of this structure is unclear. Hennig (1976) suggested that in Cyclorrhapha the basal aedeagal apodeme and ejaculatory apodeme are homologous, having arisen from the fission of the basal ejaculatory apodeme of Empidoidea and primitive Brachycera. Griffiths challenges this assumption in favor of continuity of function for the endogenous ejaculatory apodeme (character 43P), hypothesizing instead that the aedeagal apodeme of the higher Diptera secondarily arose from the separation and fusion of the paired gonocoxal apodemes (character 44). McAlpine (1981) considers the aedeagal apodemes of orthorrhaphous Brachycera and Cyclorrhapha homologous, with the ejaculatory apodeme and sperm duct an apomorphic acquisition of the Cyclorrhapha (character 43E). Character 44 is not scored in the EPANDRIAL data sets since it is not part of the hypotheses proposed by Hennig (1976) and McAlpine (1981).

45. Aedeagus shape. Not upcurved (0) or upcurved (1). Chvála (1983) suggested that the distally upcurved slender aedeagus present in the subfamilies Empidinae, Clinocerinae, Ceratomerinae and Brachystomatinae is a synapomorphy for these subfamilies ("Empididae" *sensu* Chvála, 1983). Nearly all other empidooids, except for some Ocydromiinae, bombyliids and cyclorrhaphans, have short, straight aedeagi.

The empidooid aedeagus is a complex, obviously rapidly evolving structure which could potentially provide many useful characters. Much of the variation in this structure, however, occurs below the subfamily level and finer sampling is required to interpret its transformations. The slender, upcurved aedeagus of the "empidid" subfamilies may represent evidence for their close relationship.

46. Aedeagal connection. Free, not attached to inner wall of hypandrium (0) or attached to inner wall of hypandrium (1). Chvála (1983) recognized the attachment of the aedeagus to the inner wall of the hypandrium in many members of the Ocydromiinae and Hybotinae. He considered this a synapomorphy for his family "Hybotidae". In most other Empidoidea, Orthorrhaphous Brachycera and Cyclorrhapha the aedeagus is free, not connected to the hypandrium.
47. Parameral apodemes. Absent (0) or present (1). The aedeagus of the atelestid genera *Meghyperus* and *Acarteroptera* is flanked by sclerotized parallel rod-like appendages articulating with a parameral hood (for illustrations see Chvála, 1983). The genitalic apparatus of these groups is clearly homologous. The transformation series leading to the great aedeagal diversity among empidooids are not easily discernable. However, the extraordinary long apodemes of the parameres in *Meghyperus* and *Acarteroptera*, seem to be good evidence for a relationship between these genera.

FEMALE GENITALIA

48. Spermathecae number. (a) Three (0) or one (1) or zero (2); 0-1-2. (b) Three (0) or two (1) or one (2) or zero (3); 0-1-2-3. The most conclusive synapomorphy for the Empidoidea has been the presence of a single sclerotized spermatheca in almost all "primitive" members of the superfamily. The discovery of a single spermatheca in *Atelestus* by Chandler (1981) affirmed its place in the Empidoidea. The primitive dipteran condition is three sclerotized spermathecae,

a feature retained in most primitive Brachycera including bombyliids (including *Apystomyia*) and in Cyclorrhapha. Three sclerotized spermathecae with three separate ducts is the groundplan condition for the Asiloidea; however, in many groups the number of spermathecae is secondarily reduced. *Caenotus*, for example, has only two spermathecae. Indeed, the condition of the Cyclorrhapha might more accurately be described as two, since two of the three spermathecae, in some groups, share a common duct. The effects of scoring the number of spermathecae in the Cyclorrhapha as three or two (one composed of two spermathecae which share a common duct) are tested by including both interpretations in the experimental design (TRANSFORMATION SERIES 2).

Parallel loss of the spermathecae occurs throughout the Diptera. In the Empidoidea, the spermathecae are lost in Tachydromiinae, Hybotidae, Microphorinae, Parathalassiinae and Dolichopodidae. They are also apparently lost in the transitional pre-cyclorrhaphan genus *Opetia*.

49. 9th tergite. Present (0) or absent (1). Griffiths (1986) believes the loss of the sclerites of the 9th abdominal segment in the female to be a synapomorphy for the Eremoneura. The 9th tergite and genital furca of more primitive groups are lacking in most Empidoidea [with the exception of some *Hilara* (Lobanov, 1985)] and in Cyclorrhapha. The groundplan terminalia of the female eremoneuran is interpreted as having lost the sclerites of segment 9, and possessing a full tergite and sternite 10, and a pair of single segmented cerci. According to Griffiths (1986), citing ontogenetic evidence, many of the Figures in Chvála (1983) have the 10th tergite misinterpreted as the 9th. We follow Griffiths interpretation in scoring this character.

The presence of acanthophorites, thick spines, on tergite 10 occurs in at least some members of all families of Asiloidea and is considered a synapomorphy for the superfamily (Griffiths, 1986; Woodley, 1989). They are also found in some Dolichopodidae, Microphoridae, Clinocerinae and Brachystomatinae, but have usually been considered a convergent acquisition in these groups for ovipositing in sand (McAlpine, 1981; Chvála, 1983). Since the presence of acanthophorites is highly variable within these families/subfamilies, it could not be included here as evidence of phylogenetic relationships within the Empidoidea.

Appendix 2. Data Sets

PERIANDRIAL DATA SET

Character	1	11111	11112	22222	22223	33333	33334	44444	4444	
Taxon	12345	67890	12345	67890	12345	67890	12345	67890	12345	6789
	*						**	*		
<i>Oreogeton</i>	00100	10001	00001	11000	10301	00000	01000	22111	11000	0011
<i>Gloma</i>	00100	10001	00000	11000	10301	00000	01000	12111	11000	0011
<i>Hormopeza</i>	00100	00001	00000	11000	10301	00000	01000	20011	11000	0011
<i>Atelestus</i>	00100	11001	00010	11111	20110	00011	02000	32111	11000	0011
<i>M. sudeticus</i>	00100	11001	00010	11111	21100	00010	02000	32111	11000	0111
<i>A. occidentis</i>	00102	01001	00010	11111	21201	00011	02000	32111	11000	0111
<i>A. licinia</i>	00102	01001	00010	11111	20201	00011	02000	32111	11000	0111
<i>Trichinomyia</i>	00100	01111	00100	11111	10300	01111	00011	32111	11000	1021
<i>Bicellaria</i>	00100	01111	00110	11211	1?310	01100	00011	32111	11000	1021
Tachydromiinae	?0100	11111	?0110	111?1	2041?	12100	01011	32111	11000	1021
Hybotinae	00100	11111	00100	11111	20201	01100	00011	32111	11000	1021

Appendix 2:—contd.

Taxon	Character	1		11111	11112	22222	22223	33333	33334	44444	4444
		12345	67890	12345	67890	12345	67890	12345	67890	12345	6789
		*						* **	*		
Microphorinae	00100	01001	00000	11011	10302	01011	00122	32111	11000	0021	
Dolichopodidae	11110	11001	0?0??	11131	1030?	11000	03122	32111	11000	0021	
Empidinae	?0100	00001	01?00	1101?	10301	01000	00000	10111	11001	0011	
Hemerodromiinae	10110	10001	11100	11010	21302	22000	00000	10111	11001	0011	
Brachystomatinae	10110	10001	?1000	11000	10102	22000	00000	3?111	11001	0011	
Clinocerinae	10110	10001	11100	11000	10102	22000	00000	10111	11001	0011	
Ceratomerinae	10100	00001	11110	11000	20302	22000	00000	10111	11001	0011	
<i>Apystomyia</i>	00101	01001	?0010	10110	20000	00000	00000	00000	00000	0000	
<i>Hilarimorpha</i>	00000	01000	00?10	00000	2?010	00000	00000	00100	00000	0000	
<i>Opetia</i>	00100	10001	00000	11101	2?111	00000	11000	32211	11110	002?	
Cyclorrhapha	00102	10001	001?0	11101	20110	000??	1??03	32211	11110	0001	
Parathalassinae	11110	11001	0??10	11121	1030?	11000	0?122	32111	11000	0021	
<i>Caenotus</i>	00000	00000	?0001	00000	00000	00000	00000	00000	00000	0000	

Characters marked with an asterisk are multifurcating transformation series. Assigned states for these are shown above, but were coded in binary for Hennig86.

EPANDRIAL DATA SET

Taxon	Character	1		11111	11112	22222	22223	33333	33334	44444	4444
		12345	67890	12345	67890	12345	67890	12345	67890	12345	6789
		*						* **	*		
<i>Oreogeton</i>	00100	10001	00001	11000	10301	00000	01000	211 1	120 0	0011	
<i>Gloma</i>	00100	10001	00000	11000	10301	00000	01000	211 1	120 0	0011	
<i>Hormopeza</i>	00100	00001	00000	11000	10301	00000	01000	001 1	120 0	0011	
<i>Atelestus</i>	00100	11001	00010	11111	20110	00011	02000	211 1	110 0	0011	
<i>M. sudeticus</i>	00100	11001	00010	11111	21100	00010	02000	211 1	110 0	0111	
<i>A. occidentis</i>	00102	01001	00010	11111	21201	00011	02000	211 1	110 0	0111	
<i>A. licinia</i>	00102	01001	00010	11111	20201	00011	02000	211 1	110 0	0111	
<i>Trichinomyia</i>	00100	01111	00100	11111	10300	01111	00011	211 1	110 0	1021	
<i>Bicellaria</i>	00100	01111	00110	11211	1?310	01100	00011	211 1	110 0	1021	
Tachydromiinae	?0100	11111	?0110	111?1	2041?	12100	01011	211 1	110 0	1021	
Hybotinae	00100	11111	00100	11111	20201	01100	00011	211 1	110 0	1021	
Microphorinae	00100	01001	00000	11011	10302	01011	00122	211 1	110 0	0021	
Dolichopodidae	11110	11001	0?0??	11131	2030?	11000	03122	211 1	110 0	0021	
Empidinae	?0100	00001	01?00	1101?	10301	01000	00000	101 1	120 1	0011	
Hemerodromiinae	10110	10001	11100	11010	21302	22000	00000	101 1	120 1	0011	
Brachystomatinae	10110	10001	?1000	11000	10102	22000	00000	2?1 1	120 1	0011	
Clinocerinae	10110	10001	11100	11000	10102	22000	00000	101 1	120 1	0011	
Ceratomerinae	10100	00001	11110	11000	20302	22000	00000	101 1	120 1	0011	
<i>Apystomyia</i>	00101	01001	?0010	10110	20000	00000	00000	200 0	??0 0	0000	
<i>Hilarimorpha</i>	00000	01000	00?10	00000	2?010	00000	00000	000 0	000 0	0000	
<i>Opetia</i>	00100	10001	00000	11101	2?111	00000	11000	211 1	111 0	0021	
Cyclorrhapha	00102	10001	001?0	11101	20110	000??	1??03	211 1	121 0	0001	
Parathalassinae	11110	11001	0??10	11121	1030?	11000	0?122	211 1	120 0	0021	
<i>Caenotus</i>	00000	00000	?0001	00000	00000	00000	00000	000 0	000 0	0000	

Characters marked with an asterisk are multifurcating transformation series. Assigned states for these are shown above, but were coded in binary for Hennig86.

Appendix 2:—contd.

NO GENITALIA DATA SET

Taxon	Character	1		11111	11112	22222	22223	33333	33334	44444	4444
		12345	67890	12345	67890	12345	67890	12345	67890	12345	6789
		*						* **	*		
<i>Oreogeton</i>	00100	10001	00001	11000	10301	00000	01000			000	0011
<i>Gloma</i>	00100	10001	00000	11000	10301	00000	01000			000	0011
<i>Hormopeza</i>	00100	00001	00000	11000	10301	00000	01000			000	0011
<i>Atelestus</i>	00100	11001	00010	11111	20110	00011	02000			000	0011
<i>M. sudeticus</i>	00100	11001	00010	11111	21100	00010	02000			000	0111
<i>A. occidentis</i>	00102	01001	00010	11111	21201	00011	02000			000	0111
<i>A. licinia</i>	00102	01001	00010	11111	20201	00011	02000			000	0111
<i>Trichinomyia</i>	00100	01111	00100	11111	10300	01111	00011			000	1021
<i>Bicellaria</i>	00100	01111	00110	11211	1?310	01100	00011			000	1021
Tachydromiinae	?0100	11111	?0110	111?1	2041?	12100	01011			000	1021
Hybotinae	00100	11111	00100	11111	20201	01100	00011			000	1021
Microphorinae	00100	01001	00000	11011	10302	01011	00122			000	0021
Dolichopodidae	11110	11001	0?0??	11131	1030?	11000	03122			000	0021
Empidinae	?0100	00001	01?00	1101?	10301	01000	00000			001	0011
Hemerodromiinae	10110	10001	11100	11010	21302	22000	00000			001	0011
Brachystomatinae	10110	10001	?1000	11000	10102	22000	00000			001	0011
Clinocerinae	10110	10001	11100	11000	10102	22000	00000			001	0011
Ceratomerinae	10100	00001	11110	11000	20302	22000	00000			001	0011
<i>Apystomyia</i>	00101	01001	?0010	10110	20000	00000	00000			000	0000
<i>Hilarimorpha</i>	00000	01000	00?10	00000	2?010	00000	00000			000	0000
<i>Opetia</i>	00100	10001	00000	11101	2?111	00000	11000			110	002?
Cyclorrhapha	00102	10001	001?0	11101	20110	000??	1?03			110	0001
Parathalassiinae	11110	11001	0??10	11121	1030?	11000	0?122			000	0021
<i>Caenotus</i>	00000	00000	?0001	00000	00000	00000	00000			000	0000

Characters marked with an asterisk are multifurcating transformation series. Assigned states for these are shown above, but were coded in binary for Hennig86.