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## A PHYLOGENETIC ANALYSIS OF THE BASAL GROUPS OF BIBIONOMORPHA, WITH A CRITICAL EXAMINATION OF THE WING VEIN HOMOLOGY

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(With 5 figures)

### RESUMO

#### **Análise Filogenética dos Grupos Basais de Bibionomorpha, com um Exame Crítico da Homologia da Venação Alar**

Foi realizada uma análise filogenética para os grupos basais tradicionalmente incluídos em Bibionomorpha. Utilizando principalmente caracteres de asa, é apresentado um cladograma para o grupo, no qual um grupo monofilético composto por Perissommatidae, Axymyiidae e Pachyneuridae, denominado Axymyiomorpha, é considerado o grupo-irmão de Bibionomorpha + Brachycera. Os Cramptonomyiiformia, nov., incluindo *Cramptonomyia*, *Haruka* e *Pergratospes*, formam o grupo-irmão dos demais Bibionomorpha. Os Anisopodiformia são o grupo irmão de Bibioniformia + Mycetophiliformia. A posição das espécies fósseis de *Oligophryne*, *Rhaetomyia*, *Protorhyphus*, *Archirhyphus*, *Mesorhyphus*, *Protolbiogaster*, *Eoplecia* e *Mesoplecia* é dada no cladograma e incluída em uma única classificação filogenética para o grupo Axymyiomorpha<sup>†</sup>. Uma análise cladística numérica da matriz de caracteres também foi executada. Os diferentes sistemas para os Bibionomorpha são discutidos.

*Palavras-chave:* Análise filogenética, cladismo, Diptera, Bibionomorpha.

### ABSTRACT

A phylogenetic analysis was performed for the basal groups traditionally placed in the Bibionomorpha. Using mainly wing features, a cladogram is presented, in which a monophyletic group composed of Perissommatidae, Axymyiidae and Pachyneuridae, named Axymyiomorpha, is considered the sister group of the Bibionomorpha + Brachycera. Cramptonomyiiformia, nov., including *Cramptonomyia*, *Haruka*, and *Pergratospes* is the sister group of the remaining Bibionomorpha. The Anisopodiformia is the sister group of the Bibioniformia + Mycetophiliformia. The positions of the fossil species of *Oligophryne*, *Rhaetomyia*, *Protorhyphus*, *Archirhyphus*, *Mesorhyphus*, *Protolbiogaster*, *Eoplecia* and

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*Mesoplecia* are given in the cladogram and included in a single phylogenetic classification for the group Axymyiomorpha<sup>†</sup>. A numerical analysis was also performed for the data matrix. Different systems proposed for the Bibionomorpha are discussed.

**Key words:** Phylogenetic analysis; Diptera; Bibionomorpha.

## INTRODUCTION

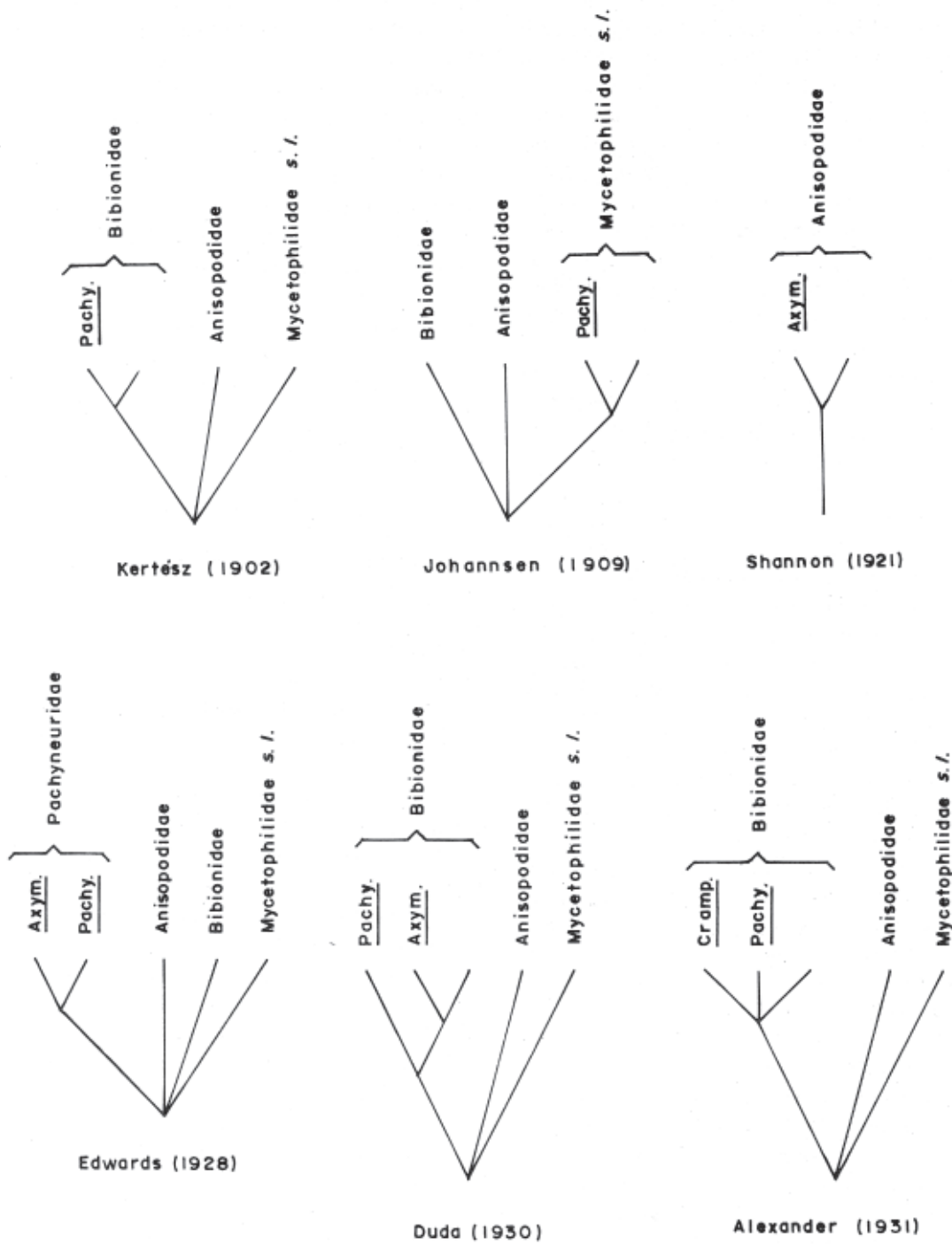
The taxon Bibionomorpha was created by Hennig in 1948, but there has been no consensus on the classification of the group since then. The larger families more frequently included in the group are Anisopodidae, Bibionidae, Scatopsidae, Cecidomyiidae, Sciaridae and Mycetophilidae *s.l.*, the latter family broken into smaller families by many authors. The phylogenetic relationships among these larger families of Bibionomorpha has been rather disputed, but the disagreements about the position of the smaller families also placed in the Bibionomorpha – Pachyneuridae, Axymyiidae, Cramptonomyiidae and Perissomatidae – are still more critical, to say nothing about fossil taxa.

Zetterstedt (1838) created the genus *Pachyneura* for a palearctic species, *P. fasciata*. *Pachyneura* and *Hesperinus* were placed together by Kertész (1902) in the subfamily Pachyneurinae of Bibionidae (see Figs. 1 and 2 for the most important systems proposed). Handlirsch (1908) was the first to consider the group as a family. Williston (1908) basically followed Kertész (1902), but added *Hesperodes* to be subfamily. Johannsen (1909) transferred the Pachyneurinae (including only *Pachyneura*) to the Mycetophilidae. Later, McAtee (1921) described *Axymyia*, with a single Nearctic species, *A. furcata*. Shannon (1921) created the Axymyiinae, including only *Axymyia*, and placed the subfamily in the Anisopodidae. Crampton (1925), in a study of the thoracic sclerites of the "Nematocera", followed Shannon's (1921) position of *Axymyia*. Edwards (1928) accepted Pachyneuridae as a family, also including *Axymyia*, and placed it together with the Anisopodidae. Duda (1930) described a Palearctic species for *Axymyia*, and insisted in the position of the genus in the Bibionidae, including it in the Pleciinae; the Pachyneurinae was also maintained in the Bibionidae. Alexander (1931) described the genus *Cramptonomyia*, with a single Nearctic species, placing it in the Bibionidae, where he also maintained the genus *Pachyneura*. Okada

(1938) described *Haruka*, with a single Japanese species, which he placed in the Pachyneuridae, together with *Cramptonomyia*. Okada (1938) followed Edwards (1928) in accepting a closer relationships between the Pachyneuridae and the Anisopodidae. All these classifications evidently do not reflect phylogenetic relationships inferred through a strict method of analysis.

Hennig (1948) proposed the erection of the Bibionomorpha in a long work about the early stages of Diptera. Later, in the "Flügelgäader", Hennig (1954) included a first general approach on the phylogeny of the Bibionomorpha produced by a strict phylogenetic method, mainly using wing features. Hennig (1954) proposed three major groups for the Bibionomorpha, ranked as infraorders: Anisopodiformia, Bibioniformia and Mycetophiliformia, the first considered the sister-group of the other two. Pachyneuridae, including *Pachyneura* and *Axymyia*, was kept as the sister family of the remaining Mycetophiliformia families. *Mycetobia*, a genus assigned by some authors to the Anisopodidae (Edwards, 1916; Shannon, 1921) and by others to the Mycetophilidae (Crampton, 1925), was placed in the Mycetophiliformia. *Cramptonomyia* was placed in the Anisopodidae.

Colless (1962) described the genus *Perissomma*, for which he created the family Perissomatidae, first known only from Australia, but since discovered in Chile (Colless, 1969). Colless (1962) did not precisely indicate the placement of the family. He made an analysis of its possible relationships, calling attention to similarities with adults of *Axymyia*, and recognized the Perissomatidae as a "specialized primitive bibionomorph stock". Rohdendorf (1964) also presented a general system for the Bibionomorpha including most of the known fossils attributed to the group. In general terms Rohdendorf (1964) followed Hennig (1954), the exceptions being the placement of the Perissomatidae as the sister group of Thaumaleidae, the proposal of the Pachyneuridae as the sister group of the Ptychopteridae (both out-



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Fig. 1 — Dendrograms representing the classifications proposed by Kertész (1902), Johannsen (1909), Shannon (1921), Edwards (1928), Duda (1930), and Alexander (1931) for the taxa included in this paper.



side the Bibionomorpha), and accepting the Bolitophiloidea as a basal bibionomorph stem. Mamaev and Krivosheina (1966) described a new genus of Axymyiidae, *Protaxymyia*, based on a Palearctic species, and proposed the creation of a superfamily Axymyioidea, probably near to the Bibionoidea. Mamaev (1968) has proposed the genus *Mesaxymyia* to receive *A. kerteszi* Duda and an additional Palearctic species described by him. Krivosheina and Mamaev (1970) described a new genus, *Pergratospes*, for a single Palearctic species, placed by them in the Cramptonomyiidae, together with *Cramptonomyia* and *Haruka*. They proposed that the Cramptonomyiidae, Pachyneuridae and Hesperinidae should be grouped in the superfamily Pachyneuroidea.

Hennig (1968, 1973) reviewed some of his earlier positions (Hennig, 1954) for wing venation homologies, proposing an infraorder Pachyneuriformia (including Perissomatidae and Pachyneuridae, the latter including *Axymyia*) as the sister group of the remaining Bibionomorpha. Cramptonomyiidae was provisionally placed in the Anisopodiformia, but considered the possible sister group of the Bibioniformia + Mycetophiliformia. *Mycetobia* was placed back into the Anisopodidae. Rohdendorf (1977) also reviewed his own earlier classifications, transferring the Pachyneuridae back to the Bibionomorpha, but leaving the Perissomatidae in the Tipulomorpha. Wood (1981a,b) kept *Cramptonomyia*, *Haruka*, and *Pergratospes* within the Pachyneuridae, the single family of the Pachyneuroidea, placed in the Bibionomorpha, and *Axymyia* was maintained in a family Axymyiidae, belonging alone to the infraorder Axymyiomorpha.

The monophyly of the Bibionomorpha *sensu* Hennig has been questioned by Tuomikoski (1961), who placed Anisopodomorpha as an independent suborder. He basically disagreed with the synapomorphies proposed by Hennig (1954) for the Anisopodomorpha, but did not indicate the relationships between this group and the remaining taxa ranked as suborders of Diptera. Oldroyd (1977) proposed a classification for the Diptera in which the Bibionomorpha (together with the Brachycera families in a taxon named Arescata) appeared as a group, but without the Pachyneuridae. In Oldroyd's classification the

Pachyneuridae was transferred to the Superstata (including only Tipuloidea and Pachyneuridae), and the Perissomatoidea (= Rhaetomyioidea) were placed in the Madescata, a group for the non-tipuloid and non-bibionomorph nematoceran families. Steyskal (1977) fully agreed with Hennig (1973) in respect to the families included in the Bibionomorpha, but maintained only two subordinated major taxa, ranked as superfamilies: Pachyneuroidea and Bibionoidea. Steyskal (1977) used the name Muscomorpha for Brachycera *sensu* Hennig (1954). I prefer to maintain here the name Brachycera, also used more recently by McAlpine *et al.* (1981) and Woodley (1989).

Hackmann and Väisänen (1982), based on cytological features, included the Thaumaleoidea in the Bibionomorpha. Krivosheina (1988) accepted some of the positions of Tuomikoski (1961), using the Anisopodomorpha to include the Anisopodidae and Trichoceridae. Hennig (1954) proposed that the Bibionomorpha would be the sister group of all non-"nematoceros" families of Diptera. This position, with the exception for the displacement of one or another family from the Bibionomorpha, has been accepted by most authors after him (Rohdendorf, 1964; Oldroyd, 1977; Steyskal, 1981; Hackmann and Väisänen, 1982).

A considerably different arrangement for the Bibionomorpha was recently proposed by Wood and Borkent (1989). This is certainly the most important paper concerning the basal evolution of Diptera published after Hennig (1954, 1968, 1973). It has a phylogenetic approach, but the basic features used to erect the system are mostly from immature stages, instead of the wing features (see Discussion, ahead). The phylogeny proposed by these authors is quite different from that of Hennig (1973) in many points. However, the problem of the relationships among the basal groups of Diptera with the Brachycera is unfortunately very superficially analysed by Wood and Borkent (1989). In their system the Anisopodidae, Scatopsidae, Synneuridae, and Perissomatidae were included in the Psychodomorpha, together with Trichoceridae and Psychodidae. The Axymyiidae was placed in an infraorder apart, while the Bibionomorpha includes only Pachyneuridae (with *Cramptonomyia*), Bibionidae

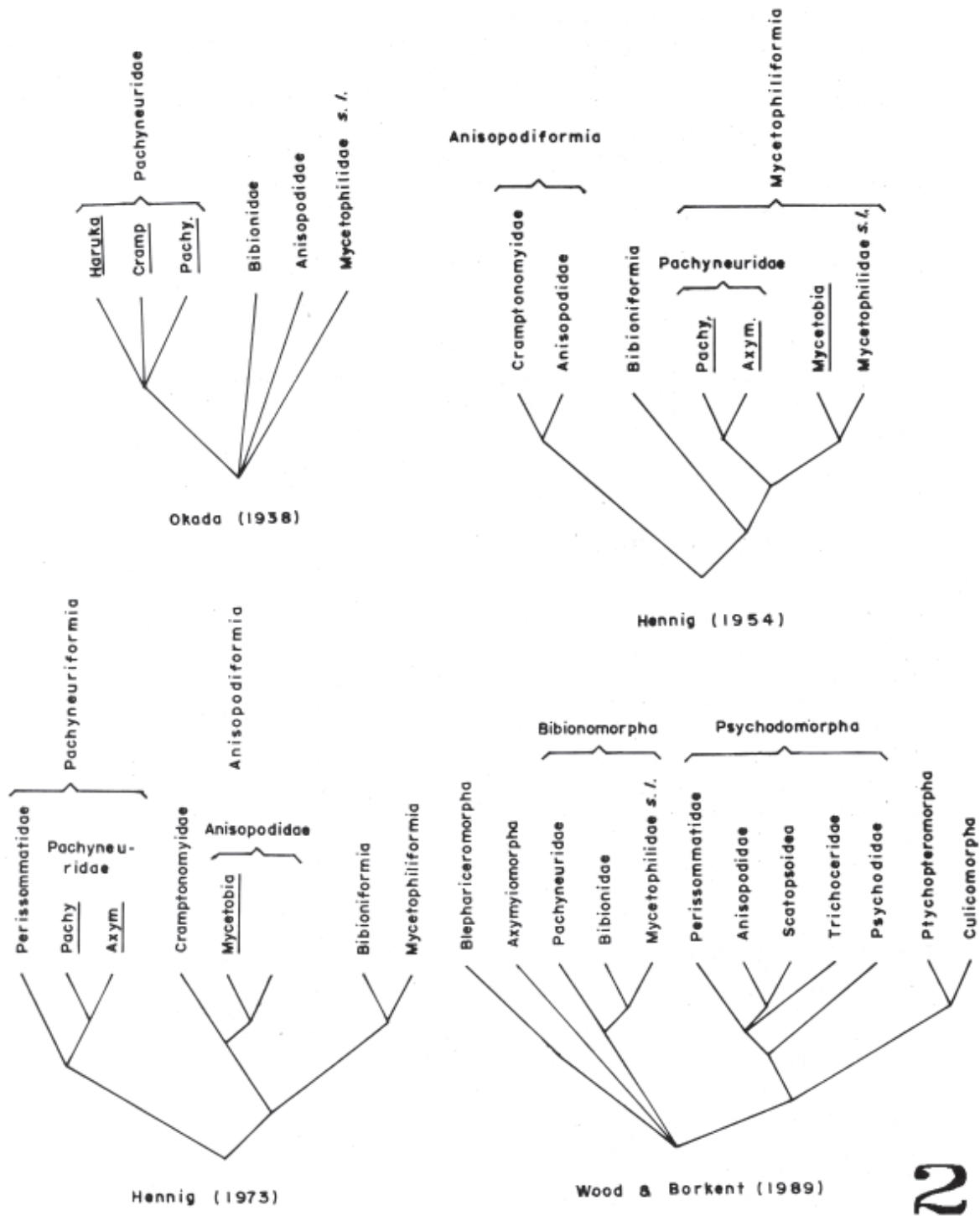


Fig. 2 — Dendrograms representing the classifications proposed by Okada (1938), Hennig (1954), Hennig (1973), and Wood & Borkent (1989) for the taxa included in this paper.

and the "Mycetophiliformia" of Hennig (1973) without the Scatopsioidea.

This brief review of the taxonomic history of the group shows how little agreement there exists about the classification of the Bibionomorpha. Most of the problems regarding the position of the families in the Bibionomorpha, especially before Hennig (1950, 1954, 1966), is a consequence of not discerning among actual synapomorphies, homoplasies, and plesiomorphic similarities. Even Hennig seems to have been confused in distinguishing between homologous and homoplastic similarities (contrast Hennig, 1954 with 1968, 1973).

This paper is a re-analysis of the evolution of the groups traditionally placed in the Bibionomorpha based especially on a critical reexamination of the homology of the wing veins obtained from literature and from specimen examination.

#### MATERIAL AND METHODS

For most characters the Tipulidae were used as an outgroup, but it was necessary for some characters to compare with the conditions found in Mecoptera or and/or Trichoptera. Data from the wing of Pachyneuridae, Axymyiidae, Cramptonomyiidae, and the fossils were obtained from the literature. Other taxa have had the specimens directly examined. The data matrix was submitted to hand-made analysis first, and then to a series of runs using the Hennig86 numerical analysis program (Farris, 1989; see also Platnick, 1989).

#### GROUND-PLAN CONDITION FOR WING VEINS OF DIPTERA

Hennig (1973: 254, fig. 5) was probably the first to formally propose a complete ground-plan condition for the wing of Diptera. The basic structure of wing venation of his proposal has been followed by McAlpine *et al.* (1981) with a modified interpretation of homology and terminology for some veins. I accept here the homology system and terminology used by McAlpine *et al.* (1981). Veins supposed to exist in the ancestral Diptera are: costa (C); subcosta (Sc), with a basal connection to C, the humeral vein (Hu), and a distal connection (sc-r) to R<sub>1</sub>; the radial veins, composed of

R<sub>1</sub> and the radial sector (Rs), with R<sub>2</sub> and R<sub>3</sub> in an anterior fork, and R<sub>4</sub> and R<sub>5</sub> in a posterior fork, all reaching the wing margin; a r-m connection stemming from R<sub>5</sub> to reach bM along cell d; the medial system is composed of M<sub>1</sub> and M<sub>2</sub> forking together, M<sub>3</sub>, a connection between M<sub>2</sub> and M<sub>3</sub> closing cell d (m-m), and a connection between M<sub>3</sub> and CuA<sub>1</sub> (actually the basis of M<sub>4</sub>, supposedly fused to CuA<sub>1</sub>); the cubital system, composed of an anterior fork, with a long stem (CuA), branching into CuA<sub>1</sub> and CuA<sub>2</sub>, and a posterior branch CuP, visible only as an isolated, scarcely sclerotized furrow posterior to CuA<sub>2</sub>; the anal system, with a basal fork separating A<sub>1</sub> and A<sub>2</sub> (A<sub>2</sub> reaching wing margin only in the Tipulomorpha). Figures 3 and 4 illustrate the wings of most important groups included in this study.

#### RESULTS

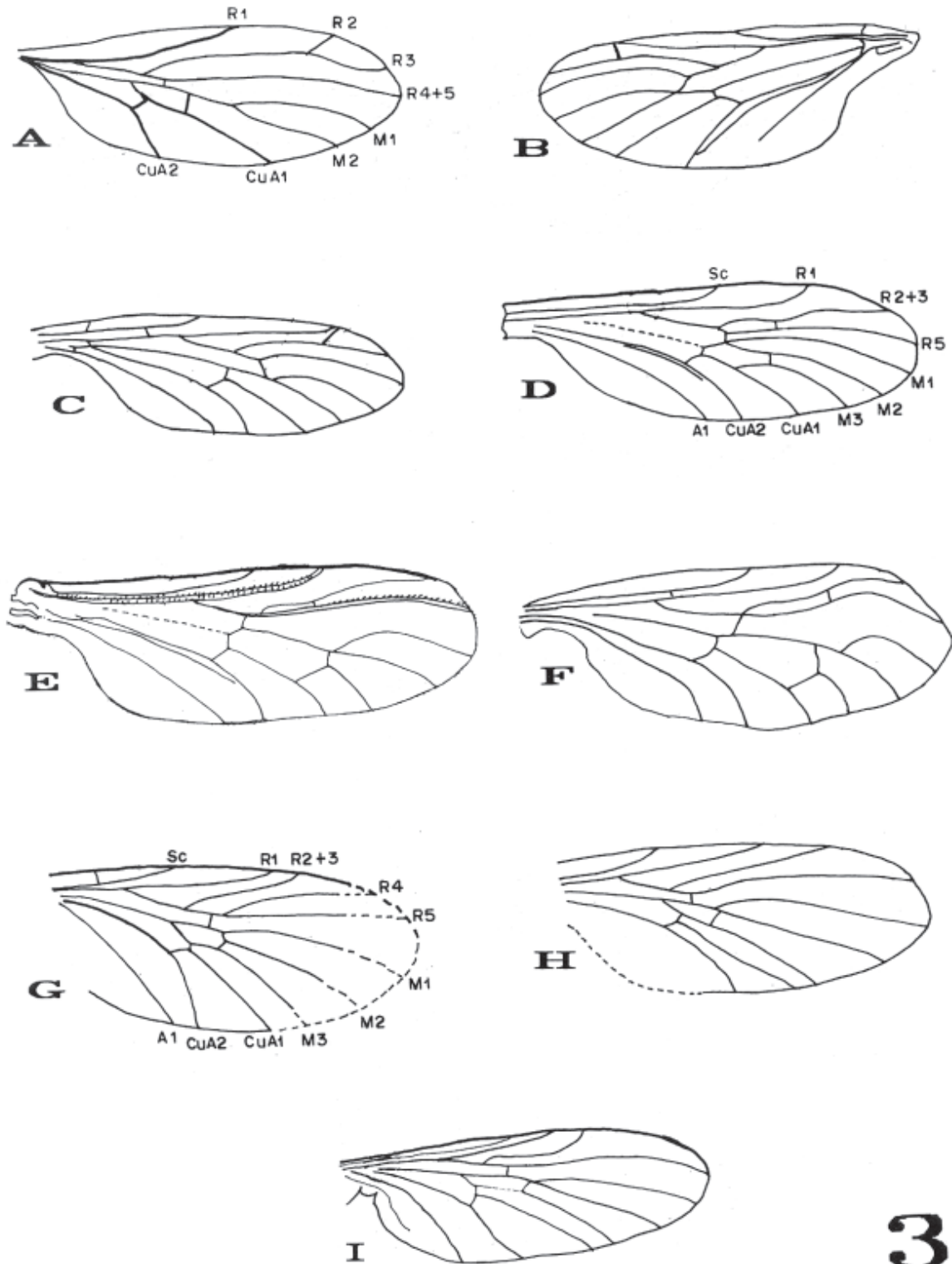
A list of the characters present in the cladogram (Fig. 5) is given below. Comments are included whenever necessary to clarify problems of homology. The plesiomorphic condition of each character is given first, separated by a bar from the respective apomorphic state(s). When more than one step exist, the apomorphic steps are successively designated by letters a, b, and c. I use the group<sup>+</sup> artifact (Amorim, 1982) to refer unambiguously to unnamed inclusive groups of the sequenced classification. Table I shows the condition of each term of the cladogram for each character listed below.

##### Adult characters

1. Number of flagellomeres: 15 / a. 14 / b. less than 14.

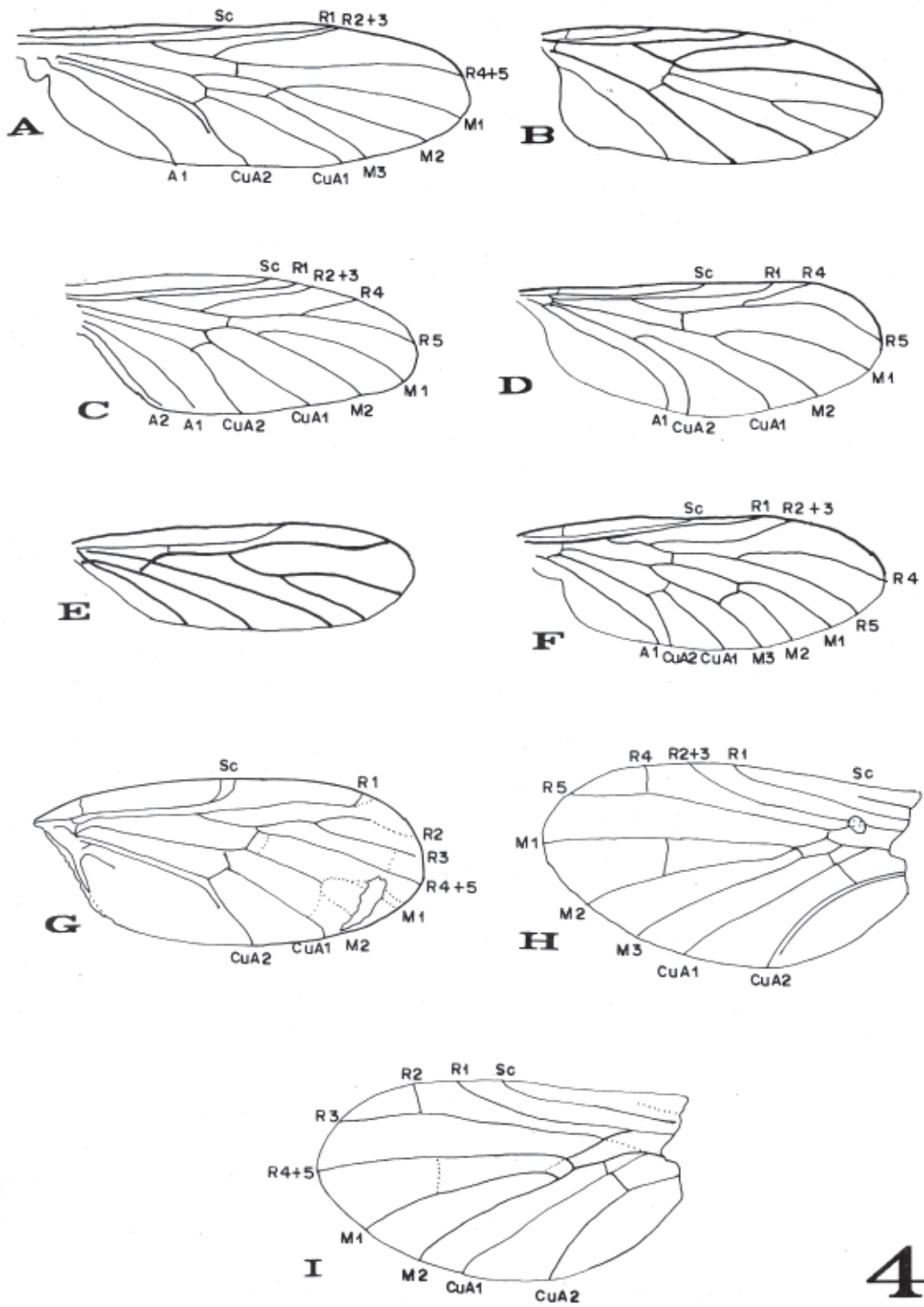
The number of flagellomeres probably had an independent reduction in many groups of Diptera. The plesiomorphic condition, with 16 or more flagellomeres, is found in some Tanyderidae, Tipulidae, and Trichoceridae. Pachyneuridae is the only member of the group Axymyiomorpha<sup>+</sup> that still has 15 flagellomeres. There has occurred a reduction to 14, and later to 9, in the Axymyioidea, and to 14 in the basis of the group Bibionomorpha<sup>+</sup>. All Brachycera have at most 8 flagellomeres, while in the Bibionomorpha the Cramptonomyiidae have 13, and the Bibioniformia have at most 10.





**3**

Fig. 3A-I — Wing of species of Axymyiomorpha, and Bibionomorpha. Axymy A. *Perissomma congrua* Colless (after Colless, 1969); B. *Mesaxymyia kert* Mamaev & Krivosheina, 1966); C. *Pachyneura fasciata* Zetterstedt (aft Bibionomorfa — D. *Cramptonomyia spenceri* Alexander (after Krivosheina E. *Pergratospes holoptica* Krivosheina & Mamaev, 1970 (ibidem); F. *Haru* (ibidem); G. *Protorhyphus stigmaticus* Handlirsch (after Handlir *Mesorhyphus anomalus* Handlirsch (ibidem).



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2. Eye undivided / a. with a clear line separating a ventral and a dorsal portion / b. ventral and dorsal halves of eye clearly separated by a sclerotized area.

This is an important character, since it is not a common feature in Diptera (maybe also known only in *Trisopsis* and related genera in the Cecidomyiidae, and the rhagionid *Liptoletis*). The difference in sclerotization between Perissomatidae and Axymyiidae, as observed Colless (1962), "is only one of degree", so the division of the eyes in these two families is here considered homologous.

3. Maxillary-palpi 5-segmented / a. 3-segmented / b. 2-segmented.

A reduction of the number of palpomeres occurred in many groups of Diptera. At the level of analysis here considered, there are synapomorphies for the Perissomatidae and a very clear synapomorphy for the Brachycera. The major subgroups of Bibionomorpha have 5-segmented palpi as a ground-plan character. Independent reductions also occur in subgroups of Mycetophiliformia.

4. Maxillary palpi with palpomeres longer than wide / palpomeres about as long as wide.

The maxillary palpi of the Perissomatidae are 3-segmented and the palpomeres are considerably reduced. In the Axymyiidae the palpi are 5-segmented, but the palpomeres are short, different from the ground-plan condition for this structure, for example, as found in *Olbiogaster*, *Cramptonomyia*, most Mycetophiloidea, and many genera of Tipulomorpha, Psychodomorpha and Culicomorpha. The reduction in the length of the palpomeres is considered a synapomorphy for the Axymyioidea.

5. Mandibles present in the adult / absent.

There are sclerites in the mouthparts of females of some groups of Brachycera and of Culicomorpha considered homologous to mandibles. This character seems to have been lost in the Tipulomorpha, the Psychodomorpha, part of the Culicomorpha, and part of the Brachycera.

This is evidently not a very reliable character for inferring phylogenetic relationships. If the Axymyiomorpha and the Bibionomorpha are really not sister-group, the mandibles must have been lost at least twice at this level.

6. C continuing all around the wing / C ending at or shortly after R<sub>5</sub>

This character has been cited by Hennig (1954: 290; 1973) as a synapomorphy for the Bibionomorpha. I must disagree with him, since most basal groups of Brachycera do not present C clearly produced after M<sub>1</sub>. Therefore, it is probable that this is a synapomorphy for the Axymyiomorpha<sup>+</sup>. The few cases in the Brachycera in which C is produced after M<sub>1</sub> should be interpreted as a non-homologous secondary production.

7. Sc reaching at least half of the wing / Sc shorter than half of the wing.

The reduction in the length of Sc occurred independently in many groups. At this level of the analysis, Sc has become shorter than half of the wing length in the Axymyiomorpha, although the fact that Sc is incomplete in the Perissomatidae makes it difficult to determine what would be its actual length. Sc is also reduced in the Protorthyphidae and in many subgroups of Brachycera.

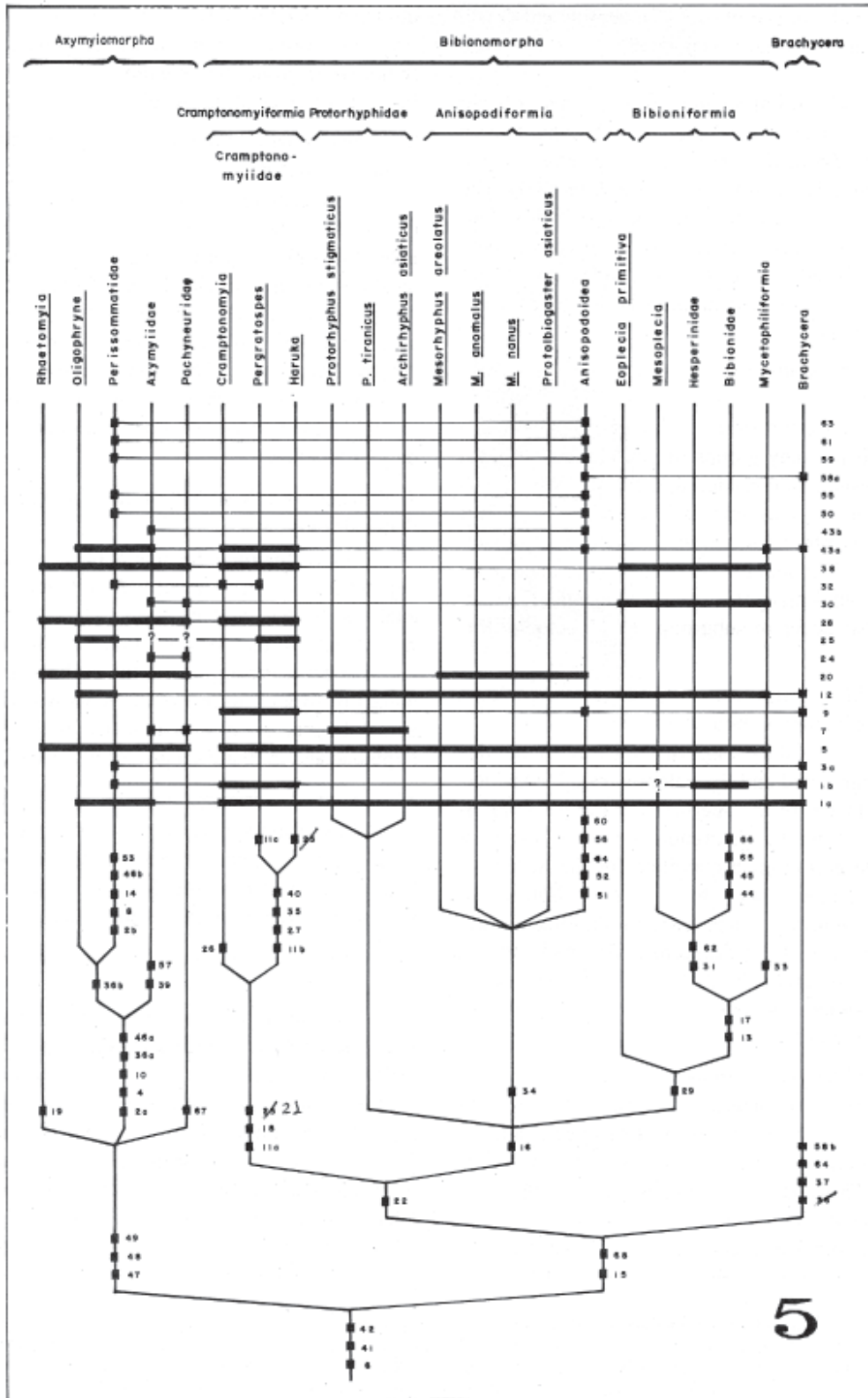
8. Sc complete / incomplete.

This character, as some of the preceding ones, certainly appeared many dozens of times in Diptera. However, at this level it seems to be a synapomorphy for the Perissomatidae.

9. sc-r beyond origin of R<sub>s</sub> / sc-r basal to origin of R<sub>s</sub>.

This small vein probably has a history of many homoplastic modifications in Diptera, especially its loss (character 10). A particular problem here is that it is a very small vein and in the drawings of many authors it is simply not represented. In the fossils, it can be seen only in *Mesoplecia*. I have included in the data matrix the condition "non-comparable" for all fossils, except *Mesoplecia*. This vein is absent in the Perissom-

Fig. 4A-I — Wings of Bibionomorpha and Brachycera, and of fossil Bibionomorpha. A. *Sylvicola fascipennis* (Macq.) (after Hennig, 1954); B. (original); C. *Mycetobia pallipes* Mg. (after Hennig, 1954); D. *Eoplecia* (after Handlirsch, 1921); E. *Hesperinus imbecillus* Loew (after Hen *Corynoscelis eximia* Boh. (ibidem); Brachycera — G. *Rhagio* sp. (after Axymyiomorpha — H. *Rhaetomyia necopinata* Rohd. (after Rohdendorf, 1964) *fungivoroides* Rohd. (ibidem); I. same, but venation reinterpreted (su represented as dotted lines).



matidae and Axymyiidae, so it is also "non-comparable" for the placement of the vein in the Axymyioidea. The apomorphic condition for this character is here considered to be shared by the Cramptonomyiidae, the Anisopodoidea, and the Brachycera.

10. sc-r present / absent.

11. Rs first fork midway between  $R_1$  and r-m / a. fork of Rs very near to r-m / b. at the point of origin of r-m / c. first fork of Rs beyond r-m.

In the genera of Cramptonomyiidae the first fork of Rs is not found in its original position, but has been displaced to more distal positions in the wing. The first apomorphic step of this character is also found in the Mycetobiidae.

12. First fork of Rs at about half of wing / first fork of Rs more basal than half of wing.

In the Perissommatidae there is a retraction of most forks to the base of the wing, including cell d. This character seems to be clearly present in *Olygophryne*. All Bibionomorpha except Cramptonomyiidae also present the apomorphic condition for this character.

13. Length of Rs between its origin and r-m more than 4 times r-m / less than 3 times r-m.

14.  $R_1$  long, reaching C beyond half of the wing length /  $R_1$  short, not longer than half of the wing.

This character shows the clear reduction of  $R_1$  in the Perissommatidae, very different from the plesiomorphic conditions found in Axymyiidae and Pachyneuridae.

15.  $R_{2+3}$  forked / unforked.

A whole discussion of the evolution of Rs veins is given ahead under character 20. I stress that virtually no Brachycera has  $R_{2+3}$  forked. The asilid genera *Andrenosoma* and *Promachus* have a vein between  $R_4$  and  $R_{2+3}$ , but this is most certainly a secondary feature appearing within the Asilidae.

16.  $R_{2+3}$  reaching C quite apically / ending at C rather near to  $R_1$ .

Analysing the basic-plan of the wing in Diptera, we may see that  $R_3$  continues in a quite straight line beyond the fork of  $R_{2+3}$ , and  $R_2$  reaches C obliquely, more basally than  $R_3$ . It is

quite clear that in all the Bibionomorpha<sup>+</sup>  $R_{2+3}$  is unforked by loss of  $R_2$ . The position in which  $R_{2+3}$  reaches C varies between different groups. In *Protorhyphus*, the Anisopodoidea, *Mesorhyphus*, and *Eoplecia*, the unbranched  $R_{2+3}$  reaches C much nearer  $R_1$  than in the Cramptonomyiidae or in the Axymyiomorpha. In the Bibioniformia<sup>+</sup> it is non-comparable.

17.  $R_{2+3}$  present / lost (see character 20).

18.  $R_{2+3}$  straight / sinuose.

19. Fork of  $R_{2+3}$  short / long.

20.  $R_{4+5}$  forked /  $R_4$  absent as a free vein.

If the cladogram herein proposed for the Axymyiomorpha<sup>+</sup> is correct, in two closely related groups the 4-branched Rs (admitted as a ground plan feature for the group) has derived to a 3-branched condition in two different ways. On the one hand, the Axymyiomorpha clearly show  $R_{2+3}$  forked and  $R_{4+5}$  unforked, and on the other hand the loss of  $R_2$  would be a synapomorphy for the Bibionomorpha<sup>+</sup>. Within the Bibionomorpha, the 2-branched condition of Rs was also achieved through two independent transformation series. In the basic plan of Diptera the first fork of Rs ( $R_{2+3}/R_{4+5}$ ) is placed quite before r-m, whereas  $R_{4+5}$  apparently branches just before r-m. However, in most families in which  $R_{2+3}$  and  $R_4$  are present, the fork of  $R_{4+5}$  is clearly beyond r-m. In the 2-branched condition of the Anisopodiformia Rs forks clearly before r-m, suggesting a loss of  $R_4$ . On the other hand, in all Bibioniformia and Mycetophiliformia, the anterior branch of Rs originates clearly after r-m. Therefore, the 2-branched condition in the group Bibioniformia<sup>+</sup> seemingly resulted from the loss of  $R_{2+3}$ . Interestingly, *Eoplecia* and the Protorhyphidae maintain both veins  $R_{2+3}$  and  $R_4$ , the former arising before and the latter beyond r-m, as in the ground-plan. To admit a single loss of either  $R_4$  or  $R_2$  for a group composed of Anisopodiformia + Bibioniformia + Mycetophiliformia would demand the exclusion of the Protorhyphidae and *Eoplecia* from such a group and also an additional apomorphy to remove  $R_{2+3}$  from its original, quite basal position to a very distal point in relation to r-m (or to remove  $R_4$  to a much more basal posi-

Fig. 5 — Cladogram for the group Axymyiomorpha<sup>+</sup>. Numbered characters are presented and discussed in the text.



TABLE I

Data matrix for characters and taxa. Characters are numbered as they are in the list of characters. Names of taxa are abbreviated and placed in the same sequence they appear in the cladogram. Question marks refer to three situations in which the information cannot be assessed: (1) information not available in the literature, (2) structure modified in a way that comparisons are not possible, or (3) the character refers to immature stages, but there is information available only from adult. The asterisks refers to taxa in which the ground-plan condition is plesiomorphic for the character, but the apomorphic condition is found in part of its members.

characters	00000	00001	11111	11112	22222	22223	33333	33334	44444	44445	55555	55556	66666	666
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	678
TAXA														
ANCEST	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
RHAETO	?????	100??	00000	00011	00000	00100	00000	??0??	?????	?????	?????	?????	?????	???
OLIGOP	?????	100??	01000	00001	00100	00000	20?0?	?????	?????	?????	?????	?????	?????	???
PERISS	22111	101?1	01010	00001	00001	00100	01000	20100	11100	11111	00101	?0011	10100	00?
AXYMYI	11011	110?1	00000	00001	0001?	0?101	00000	10110	11200	21110	00000	01000	00000	00?
PACHYN	00001	11000	00000	00001	0001?	0?101	00000	00100	11000	01110	00000	00000	00000	01?
CRAMPT	20001	10010	10001	001?0	11000	10000	01000	00100	11100	00000	00000	00000	00000	00?
PERGRA	20001	10010	30001	001?0	11001	01000	01001	00101	11100	00000	00000	00000	00000	00?
HARUKA	20001	10010	20001	001?0	11101	01000	00001	00101	11?00	0????	?????	?????	?????	???
PROTST	?????	110??	00001	100?0	01000	00000	00000	00?0?	?????	?????	?????	?????	?????	???
PROTTI	?????	110??	00001	100?0	01000	00000	00000	00?0?	?????	?????	?????	?????	?????	???
ARCHIR	?????	110??	00001	100?0	01000	00000	00000	00?0?	?????	?????	?????	?????	?????	???
MESOAR	?????	100??	00001	100?1	01000	00000	00010	00?0?	?????	?????	?????	?????	?????	???
MESOAN	?????	100??	00001	100?1	01000	00000	000?0	?0?0?	?????	?????	?????	?????	?????	???
MESONA	?????	100??	00001	100?1	01000	00000	000?0	00?0?	?????	?????	?????	?????	?????	???
PROTOL	?????	100??	00001	100?1	01000	00000	000?0	00?0?	?????	?????	?????	?????	?????	???
ANISOP	10001	1*010	00001	100?1	?1000	0*0**	0*010	00*0*	11200	00001	11011	10111	10100	001
EOPLEC	?????	100??	00001	100?0	0100?	00111	00000	0000?	?????	?????	?????	?????	?????	???
MESOPL	?????	10000	0?101	?10?0	?100?	00111	10000	00?0?	1????	?????	?????	?????	?????	???
HESPER	20001	10000	??101	?10?0	?100?	00111	10000	00100	11000	00000	00000	00000	01000	001
BIBION	20*01	1000*	??101	?10?0	?100?	00111	10000	00100	11011	00000	00000	00000	01001	101
MYCETO	1**01	1*0**	??1*1	?10?0	?100?	00111	**100	*010*	11100	00000	*00**	*0***	*0*00	001
BRACH	202**	1*01*	01*01	*00?*	0*000	0*0**	00000	*1000	11100	00000	00000	00200	00010	001

tion). I believe this would be a very unpar-simonious interpretation. All three Axymyiomorpha families have a forked anterior branch of Rs and an unforked posterior branch. This has probably influenced many systematists to place these families near the Anisopodidae, where R<sub>4+5</sub> is also unbranched. However, if a direct relationship between those four families is accepted, we would have to admit that R<sub>2+3</sub> became un-

branched in at least 3 or 4 different levels. In the interpretation presented here R<sub>4</sub> is lost only twice, and R<sub>2</sub> and R<sub>2+3</sub> only once each. The condition of Rs in the Cramptonomyiidae also had different interpretations. The longitudinal veins reaching C from R<sub>2+3</sub> and from R<sub>4+5</sub> seem to be, respectively, R<sub>3</sub> and R<sub>5</sub>. It is thus more probable that the contact between both longitudinal veins of Rs in the Cramptonomyiidae corresponds to R<sub>4</sub> stemming

from R<sub>5</sub>, rather than R<sub>3</sub> from R<sub>2</sub> (see character 21). The interpretation accepted here for R<sub>s</sub> is in conformity to that of Edwards (1928: 5) and also of Hennig (1968, 1973). Hennig (1973) believed in the monophyly of the Bibionomorpha including the "Pachyneuriformia", so he admitted that R<sub>2+3</sub> was lost twice at this level: in the Anisopodiformia<sup>+</sup> and in the Brachycera. In the cladogram here proposed R<sub>2+3</sub> is lost only once.

21. R<sub>4</sub> ending free / fused to R<sub>2+3</sub>.

22. R<sub>5</sub> reaching C at or beyond wing apex / before wing apex.

The condition indicated here as apomorphic is present in all Bibionomorpha (in the sense used here), and the plesiomorphic condition is found in the Axymyiomorpha and in most members of Brachycera.

23. R<sub>5</sub> straight / R<sub>5</sub> bent near apex.

24. r-m transverse or ending at M<sub>1</sub> basal to origin in R<sub>4+5</sub> / r-m oblique, ending at M<sub>1</sub> in a position distal to origin at R<sub>s</sub>.

This transformation occurred twice within the Axymyiomorpha.

25. m-m connected to M<sub>2</sub> / connected to M.

26. M<sub>1</sub> arising at apex of cell d / M<sub>1</sub> forking very basally on cell d (in some drawings of the wing of *Cramptonomyia spenceri* (e.g., Wood, 1981b) it actually arises from r-m).

27. M<sub>1</sub> gently curved beyond origin / M<sub>1</sub> strongly arched.

28. M<sub>3</sub> present as a free vein / M<sub>3</sub> partially or completely fused to CuA<sub>1</sub>.

Cell d is present in the Perissommatidae but in this family M<sub>3</sub> is clearly absent. Cell d is present in this group because there is a "m-m" connection between M<sub>2</sub> and CuA<sub>1</sub>, which would be a good indication that M<sub>3</sub> is not actually lost in that group, but rather fused to CuA<sub>1</sub>. In Axymyiidae and Pachyneuridae neither M<sub>3</sub>, nor m-m are present. It has been considered here that the fusion of M<sub>3</sub> to CuA<sub>1</sub> occurred at the level of the Axymyiomorpha and that m-m has been lost twice (see character 29). In the Cramptonomyiidae there is a clear fusion of part of M<sub>3</sub> to CuA<sub>1</sub>, since CuA<sub>1</sub> is part of the posterior vein in cell d.

29. M<sub>3</sub> present / absent.

The loss of M<sub>3</sub> is presented here as a feature independent from the fusion of M<sub>3</sub> to CuA<sub>1</sub> (character 28). The apomorphic condition of this character is found in all members of the group *Eoplecia*<sup>+</sup>. Hennig (1954) and Rohdendorf (1964) have placed *Mycetobia* in the Mycetophiliformia, probably based on this character and on character 34, position later revised by Hennig (1973).

30. m-m present / absent.

In most cases where M<sub>3</sub> is lost there is no trace of m-m (group *Eoplecia*<sup>+</sup>). In the members of the Perissommatidae the disappearance of M<sub>3</sub>, by probable fusion to CuA<sub>1</sub> (see character 28), did not imply the loss of m-m. Axymyiidae and Pachyneuridae, on the other hand, present neither M<sub>3</sub>, nor m-m. The possible monophyly of the Axymyiidae + Perissommatidae forces either the conclusion that M<sub>3</sub> and m-m were both lost twice or that M<sub>3</sub> was fused to CuA<sub>1</sub> once, at the base of the Axymyiomorpha, and m-m lost twice. This second interpretation is here preferred.

31. bm-cu oblique, posterior end of vein placed distal to anterior end / bm-cu transverse.

Crossvein bm-cu originally runs between CuA<sub>1</sub> and M<sub>3</sub>. If McAlpine's (1981) interpretation for wing homology is correct, than "bm-cu" is actually the base of M<sub>4</sub>. When M<sub>3</sub> is lost, a very basal part of the vein is kept, connecting bm-cu to bM. The original position of the vein, with its posterior end quite distal to the anterior end, can be easily visualized in the wings with cell d. In the groups without cell d, bm-cu can be seen in the original position, as in *Eoplecia* and *Paleoplatyura*, or in a modified transverse position, as in the Bibioniformia and many subgroups of the Mycetophiliformia.

32. bM present / scarcely produced.

This character has produced much confusion in the literature. Even in very basal groups of the Axymyiomorpha<sup>+</sup>, as the Perissommatidae, and two genera of Cramptonomyiidae a scarcely sclerotized bM can be found; in *Mycetobia* bM is also very faint and in *Mesochria* it is nearly absent. In most Mycetophiliformia bM is completely absent, but a faint bM is certainly present at least in the Mycetophiliformia genera *Bolitophila* (*Bolitophilidae*), *Arachnocampa*, *Paleoplatyura* and *Platyura* (*Keroplastidae*). From a strictly numerical parsimony point of view (just counting steps), the distribution of the apomorphic condi-



tion would possibly indicate that bM was lost at the level of Mycetophiliformia, and secondarily produced in such genera. However, the reappearance of wing veins in a condition essentially similar to the plesiomorphic one seems to me quite improbable, in the sense that the reappearance would involve the occurrence of very specific mutations, switching genes on and off. The disappearance of features hypothetically can be reached by a quite higher number of possible different ways (see also Christoffersen, 1988). The scope of this paper does not allow a longer discussion about the evolution of this vein in the Mycetophiliformia. I am now including it as a synapomorphy for Perissommatidae, *Cramptonomyia* and *Pergratospes*. The problem in the Mycetophiliformia is left to be discussed in more detail elsewhere.

33. Length of bM between r-m and bm-cu longer than r-m / shorter than r-m.

When cell d is present, bm-cu has a more basal position in the wing than r-m. The loss of M<sub>3</sub> in principle would not alter the position of bm-cu, a condition still observable in the Bibionidae and *Eoplecia*, but in all Mycetophiliformia bM is very short or completely absent between r-m and bm-cu.

34. CuA<sub>2</sub> convex midway to margin / CuA<sub>2</sub> with a mesal concavity.

The apomorphic condition of this character is present in all recent genera of the Anisopodiformia, although it is not well represented in some published drawings (Edwards, 1928, Fig. 4; Carrera, 1941, Fig. 1). *Mesorhyphus areolatus* seems to be apomorphic for this character, but it cannot be verified in the wings of the remaining species of *Mesorhyphus*, as well as in *Protolbiogaster*, so it is difficult to determine whether it is a synapomorphy for the Anisopodoidea or for all Anisopodiformia. It is here provisionally adopted as a synapomorphy for the Anisopodiformia.

35. CuA<sub>2</sub> gently curved posteriorly near margin / CuA<sub>2</sub> with a quite strong backward curve near margin.

36. A<sub>1</sub> reaching wing margin / a. A<sub>1</sub> incomplete, not reaching margin / b. A<sub>1</sub> nearly absent.

This is certainly a character that arose many times in the evolution of Diptera. However, the occurrence of the first step of this series in the

Axymyiidae and Perissommatidae is congruent with other characters, so it is interpreted as an actual synapomorphy at that level.

37. A<sub>1</sub> reaching wing margin at some distance from CuA<sub>2</sub> / reaching margin very near or actually fused to CuA<sub>2</sub> (see Woodley 1989).

38. A<sub>2</sub> incomplete, but produced / very reduced.

This feature is cited by Hennig (1954) as a synapomorphy of the Bibionomorpha. However, A<sub>2</sub> is very clearly produced in *Olbiogaster* and *Sylvicola*, and in the basal subgroups of Brachycera, as Xylophagidae, Tabanidae, and Therevidae. I prefer to understand that this reduction occurred independently in the Axymiomorpha, in Cramptonomyiidae, in the group Bibioniformia<sup>+</sup> (A<sub>2</sub> seems to be clearly present in *Eoplecia*, but it is not verifiable in the wing drawings of species of *Protorhyphus* and *Mesorhyphus*) and inside the Brachycera.

39. Anal lobe produced, posterior margin rather gently curved / anal lobe well produced, posterior margin with an incision.

40. Wing membrane entirely hyaline / wing membrane dark with white markings.

41. Second laterotergite small / enlarged (Hennig, 1973).

42. Postphragma divided / undivided (Hennig, 1973).

#### Larval characters

43. Larva holopneustic, with two pairs of thoracic and eight pairs of abdominal spiracles / a. metathoracic spiracle lost / b. abdominal spiracles vestigial or absent.

44. Body surface of the larva covered only with setae / larvae with conspicuous fleshy projections.

Krivosheina and Mamaev (1967) cite that *Pachyneura* and *Hesperinus* share the conditions here considered plesiomorphic for the characters 44, 45, 65, and 66.

45. Posterior spiracle on abdominal segment VIII / spiracle on segment IX (Krivosheina and Mamaev, 1967)

47. A posterior respiratory siphon absent in the larvae / a. a small siphon present / b. siphon very long.

Colless (1962) has described a short breathing tube for the Perissommatidae, and Mamaev



and Krivosheina (1966) described the larvae of Axymyiidae with a long siphon. Although Hennig (1973) included *Axymyia* in the Pachyneuridae, he has referred to both structures as "breathing tube". They are here considered homologous. The fact that there is a siphon in both families reinforces the idea that they actually compose together a monophyletic unity.

47. Mandible of larvae without any external tooth / an external tooth present on the mandible.

This feature is apparently known only in the Axymyiomorpha families.

48. Tergite of larvae smooth or only with setae / some spines present on the abdominal tergites of larvae.

49. Mandible, clypeus and maxilla with setae / mouthpieces with tufts of setae.

50. Prostheca present / absent (Wood and Borkent, 1989).

This, as characters 51 to 56 and 58 to 62, were extracted from the extensive and very useful discussion of Wood and Borkent (1989). Most of these characters have their apomorphic condition shared by Perissommatidae and Anisopodidae, or by these two families and Synneuridae + Scatopsidae. I discuss below the incongruences of such larval characters with adult features.

51. Hypostomal bridge: present / absent (Wood and Borkent, 1989).

52. Tentoria: not much developed / heavily sclerotized (Wood and Borkent, 1989).

53. Anteroventral margin of heap capsule of larva only with setae / with long spicules (Wood and Borkent, 1989).

54. Labrum: bilobate / apically rounded or pointed (Wood and Borkent, 1989).

55. Premandibles: unadorned sclerites / with a row of teeth (Wood and Borkent, 1989).

56. Torma: fused with the dorsal labral sclerite / articulated with the dorsal labral sclerite (Wood and Borkent, 1989).

57. Anal papillae absent / present, well developed.

58. Mandibles moving horizontally / a. moving obliquely / b. moving vertically (Wood and Borkent, 1989; Woodley, 1989).

This character is one of the features that has a similar condition shared by the families placed

by Wood and Borkent (1989) in the Psychodomorpha. However, the evolution of the character still cannot be considered definitely understood. The Culicomorpha, Ptychopteromorpha, and the Blephariceromorpha (using Wood and Borkent's (1989) system) also seem to share the oblique movement of the mandibles, as certainly do the Brachycera, in which the movement is actually vertical. The arguments exposed by Wood and Borkent (1989) to establish the horizontal movement as the plesiomorphic condition seem fully acceptable. However, it is difficult to determine, in this context, whether the horizontal movement also found in some of the families of Bibionomorpha is a retained symplesiomorphy or a reversion. If we accept the monophyly of the Axymyiomorpha<sup>†</sup>, the first possibility (symplesiomorphy) would imply at least three gains in Diptera (considering the remaining hypothesis of the cladogram of Wood and Borkent (1989) correct): Psychodidae + Culicomorpha + Ptychopteromorpha, Anisopodidae, and Brachycera. The second possibility would imply in at least three different reversals – Axymyiomorpha, Cramptonomyiidae, and Bibioniformia<sup>†</sup>. The first option is provisionally assumed here. Actually, the description of the character in terms of inclination of the mandibles seems to be unprecise to solve such a complex problem of homology, and a more detailed study of the mandibles in the various basal families of Diptera is necessary to solve this question.

59. Mandibles with teeth restricted to the apex / a subbasal inner projection projected towards the apex giving the mandible the appearance of a chela (Wood and Borkent, 1989).

60. Apex of mandible solidly fused to the base / presence of a line of weakness between the base and the apex of the mandible (Wood and Borkent, 1989).

61. Cardo: well sclerotized / membranous, poorly defined (Wood and Borkent, 1989).

62. Abdominal intersegmental fissures: continuous around the body / ventral and dorsal intersegmental fissures not meeting laterally (Wood and Borkent, 1989).

63. Maxillary palpus well developed / reduced (Wood and Borkent, 1989).

64. Posterior portions of larval head capsule: short, at most only slightly under segment 1 of thorax / elongated posteriorly into thorax (Woodley, 1989).

#### Pupal characters

65. Pupae with antennal sheaths long / short (Krivosheina and Mamaev, 1967).

66. Pupae with basis of antennal sheaths near each other / spread apart (Krivosheina and Mamaev, 1967).

67. Pupae with posterior margin of tergites straight / posterior margin of tergites with posterior projections.

#### Cytogenetic characters

68. Chiasmata formed in the autosomal chromosomes during meiosis / no chiasmata formed.

The cytogenetic data now available is still insufficient to fully understand the chromosomal evolution in Diptera. White (1949, 1973) has gathered cytogenetic data and Hackman and Väisänen (1982) reanalysed it under a phylogenetic approach. Particularly, the absence of chiasmata during the meiosis is observed in very distant groups as a plant species, protozoans, molluscs, and arthropods (White, 1973). The presence of chiasmatic meiosis is certainly the plesiomorphic condition, in Diptera found in most Tipulidae, Psychodidae, Culicidae, Chironomidae, Dixidae, Simuliidae. The achiasmatic meiosis is assumed to be general in the Anisopodidae, Bibionidae, Scatopsidae, Cecidomyiidae, Sciaridae, Mycetophilidae, as well as in Thaumaleidae, Blephariceridae, and the Brachycera. White (1973: 488) comments that "it is possible, and indeed probable, that achiasmatic male meiosis has been acquired independently on a number of occasions in the Diptera". The results from Rothfels and Mason (1975) correspond indeed to evidences that within the Simuliidae the chiasmatic condition has been lost more than once. However, the fact that this (as any other) character has appeared homoplasically many times is not *per se* an argument against the possibility of it being synapomorphic at more restrict levels. In this sense, I agree with the interpretation of Hackman and Väisänen (1982) who proposed

that the achiasmatic male meiosis would be homolog in all Bibionomorpha. A considerable number of morphological features indicate that the Thaumaleidae most certainly belong to the Culicomorpha, and that the Blephariceridae do not belong to the Bibionomorpha, so I prefer to see their condition of this characters as originated homoplasically. White (1973) interpret that the achiasmatic meiosis may have been originated only once in the Brachycera, the apparently plesiomorphic condition in Phoridae being a reversal. Although more data would be desirable to confirm the homolog condition of the achiasmatic meiosis in all Brachycera, I take White's (1973) generalization for the Brachycera as correct and I unite this group to the Bibionomorpha on the basis of this character. This would be certainly the more parsimonious decision face the data at hands. Since there is no data available about this character for the Axymyiomorpha (the data in Colless (1962) for the Perissomatidae are inconclusive), it is not possible for the time being to firmly hold whether it is a synapomorphy for the Bibionomorpha<sup>+</sup> or for the Axymyiomorpha<sup>+</sup>.

#### DISCUSSION

The data matrix was first submitted to a non-numerical hand analysis. Further it was submitted to a series of runs using the Hennig86 program. In the first run with the "ie" option, using all data and all taxa, 2250 trees of equal length (108 steps) were produced. A shorter matrix was made excluding *Rhaetomyia*, one of the species of Protorhyphidae, three of the fossil species of Anisopodiformia, and *Mesoplecia*. A run with the "ie" option for this new matrix resulted in 3 trees of equal length (107 steps), in which the relationships for the recent groups are always the same: (Axymyiomorpha (Bibioniformia<sup>+</sup> (Cramptonomyiiformia (Brachycera + Anisopodiformia))). This cladogram is according to the suggestion of Woodley (1989) about the position of the Brachycera. A run without characters 9, 12, and 38 (option "ccode; ie") produced 9 trees of equal length, which referred to 4 trees with different topologies for the recent taxa: (Brachycera (Axymyiomorpha + Cramptonomyiiformia) + Anisopodiformia<sup>+</sup>); (Axymyiomorpha (Bibionomorpha + Brachycera)); (Brachycera (Axymyiomorpha + Bibionomorpha); and



(Axymyiomorpha + ((Brachycera + Cramptonomyiiformia) + Anisopodiformia<sup>+</sup>)). The cladogram accepted here has 110 steps (Fig. 5), and is a consensus for 3 of these 9 trees. The option for this tree actually corresponds to a subjective weighting against characters 1, 43, and 58. This last character refers to the way the mandibles move.

It is out of the scope of this paper to study all the basal groups of Diptera, as have made Wood and Borkent (1989). As the monophyly of the Bibionomorpha has been questioned by these authors (*i.e.*, that characters 6, 41, 42, 15, 68, 22 may not be synapomorphies), the restrictions of the scope of this study recommends that the results herein proposed for the larger groups should not be considered definite.

In the final cladogram adopted here (Fig. 5) there are polychotomies at the levels of Axymyiomorpha, Protorhyphidae, Anisopodiformia, Bibioniformia, and of the relationships among Protorhyphidae, Anisopodiformia, and Bibioniformia<sup>+</sup>, all of which involve fossils. The cladogram for recent groups is fully resolved. At the moment it seems quite difficult to present any further solution for these polychotomies. On the other hand, there are some levels of the cladogram for which the synapomorphies obtained seem to give great strength to the hypotheses of monophyly proposed, as the Axymyiomorpha, the Brachycera, the Cramptonomyiidae, the Harukinae, *nov.*, the group *Eoplecia*<sup>+</sup>, and the group Bibioniformia<sup>+</sup>. There is an incongruence between apomorphic characters shared by the Axymyiidae and Perissomatidae and by Axymyiidae and Pachyneuridae. In view of the data set presently at hand, it seems more probable that the similarities in the wing venation between Axymyiidae and Pachyneuridae are due to symplesiomorphies and homoplasies, particularly the loss of cell d. In any case, the position of the Pachyneuridae in the Cramptonomyiidae, as have proposed Wood and Borkent (1989), is very unparcimonious. The monophyly of the Bibionidae (without *Hesperinus*) seems nearly sure, and the monophyly of the Bibioniformia has been reinforced by character 62, proposed by Wood and Borkent (1989). All apomorphic features shared by Hesperinidae and Bibionidae refer to larval characters, so it is not possible to determine more

precisely the position of *Mesoplecia* within the Bibioniformia. A similar situation occurs with *Rhaetomyia*.

Some additional comments must be made now about the phylogeny of the basal groups of Diptera proposed by Wood and Borkent (1989). There is an obvious incongruence between adult (mainly wing) features believed by Hennig (1973) to be synapomorphies and features of the larva which Wood and Borkent (1989) considered synapomorphies. It is my opinion that Wood and Borkent's paper furnishes indeed a splendid contribution to the understanding of the evolution of larval and pupal structures in the basal groups of Diptera, and it certainly stimulates a new approach on the study of the evolution of the immature stage characters in Dipterology. However, it seems to me that their work will pass now through a process of point to point critical review, as also occurred with Hennig's (1954) paper on wing venation. There are potential problems concerning the polarization of transformation series, the discernment between synapomorphies and similar but independently derived apomorphies, and the arisal of reversions in immature structures in their paper (see also Griffiths, 1989). This would certainly affect some points in their phylogeny.

Wood and Borkent (1989) include a very detailed discussion for each character they use, and in many instances they show that different options are possible. They actually recognized that the data base supporting the results is still provisional: "As noted in our analysis, many of our hypothesis of polarity of character stages are tenuous" (1989: 1367). This does not mean that very radical changes will occur, but rather that there is a probability that different arrangements for at least some of the monophyletic groups proposed may be more parsimonious. This may be the case of the Bibionomorpha. However, I believe that it is not possible to make now a strictly rational (*i.e.*, parsimonious) decision favoring my concept of the Bibionomorpha or that of Wood and Borkent (1989), since the data base for an objective analysis is still insufficient. So at this time I prefer to provisionally consider that the similarities used to gather the Psychodomorpha *sensu* Wood and Borkent are due to homoplasies and/or to symplesiomorphies, rather than synapomorphies. This means to overweight my



characters numbered 15, 16, 22, 67, and underweight those larval features that sustain the Psychodomorpha. As I have not dealt with the problem of the Scatopsoidea in this paper, I prefer to assume here a more conservative position and maintain this group in the Mycetophiliformia, separated from the Anisopodidae, until a further analysis.

It is also interesting to note that a very detailed study of the homology and evolution of wing venation of recent groups becomes a very powerful tool to understand the position of fossils. The fossil species with well preserved wings may be quite easily included at least in the higher levels of the classification. On the other hand, doubts on the homology of veins in not well preserved fossil wings can be much more easily solved in view of present phylogenetic knowledge. There are two important cases at the levels of the analysis herein included to be solved. One of them is that of *Rhaetomyia necopinata* Rohd. (Fig. 4), placed by Rohdendorf (1964) in the Tipulomorpha, near the Chironomoidea. The wing of this species has very clearly a branched anterior stem of Rs, arising before r-m, most certainly R<sub>2+3</sub>. The posterior branch of Rs, supposedly R<sub>4+5</sub>, is unbranched. This data is sufficient to include the genus in the Axymyiomorpha. The reduction of A<sub>1</sub> and the absence of M<sub>3</sub> corroborate this position. The "forked" apex of Sc and of R<sub>1</sub> seem to be artifacts. A dotted line between M<sub>2</sub> and M<sub>3</sub> is indicated in the drawing of Rohdendorf (1962: 163, Fig. 54). The position of such a vein, connecting anteriorly to M<sub>2</sub>, corresponds very closely to the plesiomorphic condition of m-m in cell d, so it is possibly not an artifact. Two other plesiomorphic features in the wing of *Rhaetomyia* – r-m with its posterior end basal to its origin, and a quite short M<sub>1+2</sub> "fork" –, would indicate that the genus would be the sister group of all known recent Axymyiomorpha. The relatively long fork of R<sub>2+3</sub> may be an autapomorphy of that species.

The other fossil with a problematic classification is *Oligophryne fungivoroides* Rohd., included by Rohdendorf (1964) in the Anisopodoidea. The basic problem here is that there is supposedly an incomplete longitudinal vein posterior to the C, interpreted by Rohdendorf (1962: 204, Fig. 66) as Sc. If this is the case, the next longitudinal veins reaching the wing margin

would be R<sub>1</sub>, R<sub>2+3</sub>, R<sub>4</sub>, R<sub>5</sub>, M<sub>1</sub>, M<sub>2</sub>, M<sub>3</sub>, CuA<sub>1</sub>, and CuA<sub>2</sub> (Fig. 4H). If the distal connection between M<sub>2</sub> and M<sub>3</sub> is the m-m cross-vein (in quite an atypical position), cell d would be present and, in this case, a more basal closed cell would be an artifact. The inverse interpretation for this vein is also possible – the distal m-m vein may be an artifact. The position of a taxon with such a wing venation would be quite difficult to determine. Even if we consider the species a very specialized stem, its position in the Cramptonomyiiformia or in the Anisopodiformia would hardly be acceptable: The wing of *Oligophryne* differs very strongly from the basic-plan of any of these groups (i.e., it would be very unparsimonious). On the opposite way, if the line posterior to the C is not the Sc, but an artifact, the longitudinal veins would be Sc, R<sub>1</sub>, R<sub>2</sub>, R<sub>3</sub>, R<sub>4+5</sub>, M<sub>1</sub>, M<sub>2</sub>, CuA<sub>1</sub>, and CuA<sub>2</sub>. This is the typical venation of the Axymyiomorpha, from which the wing of *Oligophryne* would not differ very much. In this case, the connection between R<sub>5</sub> and M<sub>1</sub> would most certainly be an artifact. The region around cell d seems quite confused. If the distal connection between CuA<sub>1</sub> and bM is actually homologous to m-m (as in *Perissomma*, but in a still more basal position), cell d would be present and the genus would compose a monophyletic group with the Perissomatidae. However, if such a connection and also the more oblique basal connection between CuA<sub>1</sub> and bM are artifacts, the group would seem to be quite close to the Pachyneuridae. As R<sub>1</sub> in *Oligophryne* is indeed quite shorter than the condition seen in the Pachyneuridae and the Axymyiidae, I prefer to understand that *Oligophryne* has a closer relationship with the Perissomatidae. In Fig. 4I a reinterpretation of the wing venation of *Oligophryne* is proposed.

Not much can be advanced about the age of the group Axymyiomorpha<sup>†</sup>. The wings of *Rhaetomyia* and *Protorhyphus* show that both taxa were already present at the Lower Jurassic. The Pleciofungivoridae, correctly associated by Kovalev (1987) to the Bolitophilidae, were also already present at that time (Rohdendorf, 1964; Kovalev, 1987). *Crosaphis* Evans from the Upper Triassic/Lower Jurassic of Australia has been shown by Kovalev (1983) to be the sister group of *Mycetobia* (Anisopodoidea). The Keroplatidae are

also believed to be differentiated into subgroups at the Cretaceous (Matile, 1990). As the Bolitophilidae are a quite specialized group of the Mycetophiliformia, there must have existed a history of divisions of the Bibionomorpha before the Upper Triassic, in such a way that subgroups of Plecofungivoridae already existed as specialized and diversified entities at that time. It is not possible to determine now how long before the Upper Triassic the Bibionomorpha would have had its origin, but I believe that this, maybe reach the Permian.

A phylogenetic classification is presented below, using the sequencing convention proposed by Nelson (1972), the *sedis mutabilis* label proposed by Wiley (1979) to distinguish polichotomies in sequenced classifications from more than two sequenced stems, the name "Plesion", suggested by Patterson and Rosen (1977), as substitute categories for the Linear ranks in the case of extinct taxa, the square bracket convention proposed by Christoffersen (1988) to indicate redundant nominal taxa in the classification, and the conventions of group<sup>+</sup> (Amorim, 1982), and group\* (Amorim, 1989) to indicate unnamed inclusive groups in sequenced classifications.

- group Axymyiomorpha<sup>+</sup>
    - Suborder Axymyiomorpha
      - Plesion *Rhaetomyia necopinata* Rohdendorf, *sedis mutabilis*
      - Pachyneuroidea, *sedis mutabilis*
        - Pachyneuridae [*Pachyneura fasciata* Zetterstedt]
      - Axymyioidea, *sedis mutabilis*
        - Axymyiidae
          - Plesion *Olygophryne fungivoroides* Rohdendorf
          - Perissommatidae [*Perissomma* Colless]
    - Suborder Bibionomorpha
      - Infraorder Cramptonomyiiformia, nov.
        - Cramptonomyiidae
          - Cramptonomyiinae [*Cramptonomyia spenceri* Alexander]
          - Harukinae nov.
            - Haruka* Okada [*Haruka elegans* Okada]
            - Pergratospes* Krivosheina and Mamaev [*P. holoptica* Kriv. & Mamaev]
- group Protorhyphidae\*
  - Plesion Protorhyphidae

- Plesion *Protorhyphus stigmaticus* Handlirsch, *sed. mut.*
- Plesion *Protorhyphus turinicus* Handlirsch, *sed. mut.*
- Plesion *Archirhyphus asiaticus* Rohdendorf, *sed. mut.*
- Infraorder Anisopodiformia
  - Plesion *Mesorhyphus fittoni* Brod., *sed. mut.*
  - Plesion *Mesorhyphus anomalus* Handlirsch, *sed. mut.*
  - Plesion *Mesorhyphus nanus* Handlirsch, *sed. mut.*
  - Plesion *Protolbiogaster rhaetica* Rohdendorf, *sed. mut.*
  - Anisopodoidea, *sed. mut.*
- group *Eoplecia*<sup>+</sup>
  - Plesion *Eoplecia primitiva* Handlirsch
- Infraorder Bibioniformia
  - Plesion *Mesoplecia* Rohdendorf, *sed. mut.*
  - Hesperinidae [*Hesperinus* Walker], *sed. mut.*
  - Bibionidae, *sed. mut.*
- Infraorder Mycetophiliformia
- Suborder Brachycera

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