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Phylogeny of the subfamilies of Chironomidae (Diptera)

O. A. SÆTHER
Museum of Zoology, Department of Zoology, University of Bergen, Norway

Abstract. The phylogeny of the subfamilies of Chironomidae are cladistically analysed using parsimony. A data matrix is presented and some characters discussed. Different outgroup taxa, constraints and options are used, characters unordered or ordered, weighted or unweighted, the results reweighted or not and the results discussed. Telmatogetoninae in all cladograms forms the sister group of the remaining subfamilies. Aphroteniinae in some cladograms forms the sister group of all subfamilies except Telmatogetoninae, whereas in other cladograms, including the preferred cladogram, it is part of Tanypodoinae, which otherwise includes Podonominae, Usumbaromyiinae and Tanypodinae. Chilenomyiinae is basal in Tanypodoinae in some cladograms. In most cladograms, including the preferred cladogram, it is basal in Chironomoinae, which also includes Buchonomyiinae, Diamesinae, Prodiamesinae, Orthocladiinae and Chironominae. The preferred cladogram is compared with the relationships between different subfamilies suggested by previous authors.

Introduction

A first attempt at evaluating the relationships between subfamilies and groups of Chironomidae was by Goetghebuer (1914). At that time, there were only two subfamilies, Tanypodinae and Chironominae (including the presently recognized Diamesinae, Prodiamesinae, Orthocladiinae and Chironominae). He thought that Orthocladiinae, as then defined, was what we today call paraphyletic and that his *Chironomus* group (Chironominae of today) had arisen from within his *Orthocladius* group (Orthocladiinae + Prodiamesinae excluding the *Corynoneura* group).

Edwards (1929) separated Diamesinae and Clunioninae as subfamilies distinct from Orthocladiinae, whereas Brundin (1956) regarded them merely as tribes of Orthocladiinae. Brundin (1966) provided phylogenies for each of Podonominae, Aphroteniinae and Diamesinae, using a traditional Hennigian scheme of argumentation. He regarded Tanypodinae as the apomorphic sister group of Podonominae plus his newly erected Aphroteniinae and these three subfamilies together as the sister group of Diamesinae + Telmatogetoninae + Orthocladiinae + Chironominae, with the two first closely related. Chironominae was thought to form the sister group of Diamesinae + Telmatogetoninae + Orthocladiinae. Sæther (1976) accepted the sister-group relationship of Diamesinae and Telmatogetoninae, but argued that his new subfamily Prodiamesinae, together with Orthocladiinae and Chironominae, formed a monophyletic unit.

Although both Fittkau (1962) and Brundin (1956) followed Hennig's principles, Sæther (1977) made the first complete phylogenetic scheme of argumentation of all the subfamilies recognized at that time, combined. The scheme of argumentation was based on forty-one characters arranged in fourteen trends. As many as seventeen of these were based on characters from the female genitalia, twelve on other imaginal characters, four on pupal and eight on larval characters. Telmatogetoninae was regarded as the sister group of the remaining subfamilies, which could be divided into two groups, one consisting of Tanypodinae + Aphroteniinae + Podonominae and one consisting of Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae in phyletic sequence. To have the classification accurately reflect the hypotheses of genealogical descent by phyletic sequencing and subordination, Sæther (1983) gave the two main groups of chironomids the rank of semifamilies as Tanypodoinae and Chironomoinae.

Buchonomyia was described by Fittkau (1955) in Podonominae, but later transferred to Orthocladiinae (Fittkau *et al.*, 1967). Assuming that the genus belonged either in Diamesinae or Prodiamesinae, Sæther (1977) stated that it at least belonged in the monophyletic unit Chironominae + Orthocladiinae + Prodiamesinae + Diamesinae. Buchonomyiinae was erected for the genus by Brundin & Sæther (1978), who

Correspondence: O. A. Sæther, Museum of Zoology, Department of Zoology, University of Bergen, Muséplass 3, N-5020 Bergen, Norway. E-mail: Ole.Sather@zmb.uib.no

made a revised synapomorphic diagram for the subfamilies of Chironomidae, in which Buchonomyiinae was placed as the sister group of the remaining Chironomoinae. Murray & Ashe (1981, 1985) and Ashe (1985), however, suggested that the genus was an integral member of Tanypodoinae. Their critique was met by Sæther (1990b), who, although agreeing with some of their findings, retained his interpretation of the placement of the subfamily in Chironomoinae. Brundin (1983) erected the subfamily Chilenomyiinae for the single species *Chilenomyia paradoxa* Brundin and placed it in a scheme of argumentation as the sister group of Tanypodoinae + Chironomoinae. Most recently, Andersen & Sæther (1994) erected Usumbaromyiinae for the species *Usumbaromyia nigrala* Andersen & Sæther and placed it in Tanypodoinae as the sister group of the other subfamilies combined.

Brundin (1983) and Andersen & Sæther (1994) placed their new subfamilies in their phylograms with some hesitation because the immature stages were then, and remain, unknown. Chilenomyiinae are strikingly different from other chironomids, and with no obvious phenetic resemblance it is difficult to be comfortable with any placement. However, the problem with Usumbaromyiinae is the opposite: at first glance it would be placed in Orthocladiinae. The combination of characters, however, clearly place it in Tanypodoinae. The question is then, could the similarities with Tanypodoinae all be homoplasious? Although the pupa and the early instar larva of *Buchonomyia* are known, the subfamily poses some of the same problems as with Chilenomyiinae.

Although the phylogeny of the subfamilies of chironomids has been treated several times, it never has been analysed cladistically using parsimony programs. Although I am sceptical of several aspects of such analyses (Sæther, 1983, 1986, 1988, 1990a,b), the 'true' phylogenies probably never are completely unparsimonious. When analysing at the family level it also is possible to be much more 'objective' than when doing parsimony analysis at the generic or specific level (Sæther, 1990a). Reweighting according to the rescaled consistency index reduces or eliminates characters showing extensive homoplasy.

To have a wide scope of outgroup is important in parsimony analyses. Traditionally, Ceratopogonidae has been regarded as the sister group of Chironomidae. However, Pawlowski *et al.* (1996) and Miller *et al.* (1997) recently derived rather different phylogenies, and the morphology of the female genitalia (Sæther, 1977) suggested that both Thaumaleidae and Simuliidae are more closely related. Parsimony analysis of Culicomorpha with other selected dipterous families as outgroup (Sæther, 1999) showed that Culicomorpha was monophyletic with Nymphomyiidae as the sister group, and thus these families were included in the analysis.

Methods

Parsimony analysis was performed using PAUP 3.1.1 (Swofford, 1993) and MacClade 3.06 (Maddison & Maddison, 1996) on a Power Macintosh 8200/120. Cladograms were compared using MacClade 3.06.

The data matrix was analysed using no outgroup, all non-chironomid families, Nymphomyiidae + Thaumaleidae or Thaumaleidae alone. It was also analysed using no outgroup but with different constraints suggested by the results of Sæther (1999). The different constraint cladograms were: (1) Nymphomyiidae or Thaumaleidae or both basal to all other families; (2) the same with Culicoidea monophyletic; (3) the preferred cladogram of Sæther (1999), i.e. (Nymphomyiidae, Thaumaleidae) ((((Ceratopogonidae (Simuliidae, Chironomidae)) (((Dixidae ((Corethrellidae (Chaoboridae, Culicidae))))).

Nymphomyiidae, although forming the plesiomorphic sister group of Culicomorpha, is quite aberrant and may give misleading results when included in the analysis. A data matrix excluding Nymphomyiidae was thus also analysed. Successive approximations character weighting, using the rescaled consistency index, was applied in all analyses. All searches were branch and bound or exhaustive.

Characters and character states

The first sixty-five characters used were listed and discussed in Sæther (1999), and are mostly characters derived from or discussed by Sæther (1977, 1990b), Wood & Borkent (1989), Oosterbroek & Courtney (1995) and Michelsen (1996). The abbreviations WB, OC and S refer to the discussions in the above papers. The number following refers to the character number.

Imagines

1. *Pedicel*: (0) not especially enlarged, and male flagellum not markedly plumose nor noticeably different from that of female; (1) pedicel enlarged, especially in males; (2) enlarged, male flagellum markedly plumose (WB79, OC65, S2).
2. *Setae of flagellomeres*: (0) arranged haphazardly; (1) in encircling whorls (OC64, S3).
3. *Male antenna*: (0) with more than 15 flagellomeres; (1) with 13–15; (2) with 11 or fewer (S4).
4. *Female antenna*: (0) with 13–15 flagellomeres or clearly secondary reduced; (1) with fewer (S5).

The trend differs slightly from that of Sæther (1999), which has female antenna with fewer flagellomeres than male antenna as apomorphous.

5. *Origin of episto-dorsocervical muscle*: (0) not transferred to laterocervical; (1) transferred (Michelsen, 1996; S7).
6. *Frons (vertex)*: (0) without saggital (coronal) suture; (1) with saggital (coronal) suture (Pawlowski *et al.*, 1996; S10).
7. *Costa*: (0) completely surrounds wing but is strongest along anterior margin (or wing reduced); (1) costa fades out and becomes absent beyond insertions of R and M (McAlpine, 1981; OC71, S11).

8. *Posterior veins of wing*: (0) distinct, without marked concentration of anterior veins along costal margin; (1) reduced, anterior veins concentrated along costal margin (OC72, S12).
9. *Pulvilli*: (0) present; (1) absent (OC83).

Where the character alternative of the archetype is clear only this is scored for the subfamily. However, this is not clear for Tanypodinae and Podonominae, and in Buchonomyiinae the pulvilli are vestigial or absent. These subfamilies are thus scored 0 and 1.

10. *Sperm*: (0) transferred as liquid or amorphous mass, often by a sperm pump; (1) transferred by a complex, 2-chambered, symmetrical spermatophore formed within male before or during ejaculation (WB83, OC93, S17).
11. *'True' aedeagus (gonapophyses VIII joined medially)*: (0) well developed; (1) gonapophyses VIII separate; (2) gonapophyses VIII strongly reduced (OC87?, S18).
12. *Gonocoxites*: (0) without basal or apical lobes (volsellae) beyond extreme base, parts or appendages or both of gonapophyses (volsellae) placed basally between gonocoxites; (1) with lobes or appendages or both beyond base (S19).
13. *Gonostylus*: (0) double or deeply furcate; (1) simple (S20).
14. *Sternite IX of male*: (0) well developed; (1) reduced to apodemes; (2) apodemes reduced (S21).
15. *Seminal capsules*: (0) 3 subequal; (1) 3 capsules with one reduced; (2) 2 capsules; (3) one capsule; (4) no capsules (Sæther, 1977; OC97, S22).
16. *Spermathecal ducts*: (0) opens separately; (1) with common opening; (2) partly fused (WB85, S23).
17. *Female gonocoxite VIII*: (0) present; (1) reduced to internally thickened ridges; (2) absent (Sæther, 1977; S24).
18. *Female gonapophysis VIII*: (0) well developed, sometimes divided; (1) reduced or fused or both; (2) absent (Sæther, 1977; S25).
19. *Female gonostylus IX*: (0) present; (1) absent (Sæther, 1977; 1990b; S26).
20. *Notum of female gonapophysis IX*: (0) well developed; (1) reduced; (2) absent (Sæther, 1977; S27).
21. *Rami of female gonapophysis IX*: (0) well developed; (1) reduced; (2) absent (Sæther, 1977; S28).
22. *Gonocoxite IX of female*: (0) well developed; (1) fused with tergite IX to form a gonotergite; (2) fused with sternite IX to form a gonosternite (2) (Sæther, 1977; 1990b; S29).
23. *Postgenital plate of female*: (0) well developed; (1) reduced or absent (Sæther, 1977; S31).
24. *Labia of female*: (0) well developed; (1) reduced or absent (Sæther, 1977; S32).

Pupa

25. *Metathoracic leg sheath*: (0) extending beyond wing sheath, parallel to sheaths of other 2 legs; (1) metathoracic leg sheath bent in an S-shape, concealed beneath wing sheath, ending beside apex of mesothoracic leg (WB76, OC60, S33).
26. *Apex of abdomen*: (0) terminating in a pair of immovable lobes or projections or in terminal discs or spines; (1) terminating in paddle-like but not articulated anal lobes; (2) terminating in pair of articulated, membranous paddles, each with supporting midrib (WB77, OC62, S34).

Although several parasitic or semiaquatic orthoclads lack anal lobes, these are interpreted as secondary reductions and the orthoclads are scored as 1.

Larva

27. *Frontoclypeal apotome*: (0) triangularly V-shaped; (1) broadly U-shaped (OC1, S35).
28. *Ventral surface of labrum*: (0) without labral brushes; (1) with pair of labral brushes, each in form of a convex, cushion-like area of cuticle covered with parallel, transverse rows of long setae (WB2, OC4, S36).
29. *Labral brushes*: (0) simple; (1) complex (WB55, OC5, S37).
30. *Premandible*: (0) absent; (1) present (OC7, S38).
31. *Premandible*: (0) when present consisting of a simple sclerite lacking invaginated portion; (1) with invaginated apodeme for insertion of labral retractor muscle (WB3, OC9, S39).
32. *Mandible*: (0) without comb-like or brush-like row of long, curved setae along dorsal surface; (1) with (WB4, OC21, S41).
33. *Mandibular articulations*: (0) located more or less dorsoventral to each other, with mandibles operating in a horizontal plane; (1) mandibular epicondyle displaced medially and hypocondyle displaced laterally, with mandibles operating obliquely or vertically (WB5, OC18, S43).
34. *Torma*: (0) in form of a band-like sclerite, with point of attachment of premandible at surface of cuticle occurring at posteromedial corner of torma; (1) folded on itself, invaginated, with premandible intimately associated with torma and dorsal to body of torma (WB57, OC13, S44).
35. *Premandible*: (0) mainly an external sclerite, with a well developed external comb of setae and a small, invaginated apodeme for insertion of labral retractor muscles or absent; (1) mainly internal as a result of invagination, with only a small remnant of external sclerite; (2) entirely internal (WB58, OC10, S45).
36. *Premandible*: (0) when present mainly an external sclerite, with well developed external comb of setae and with a small, invaginated apodeme for insertion of labral retractor muscles; (1) leverage-like, moveable in an anteroposterior direction as a result of separate insertions of labral compressors pulling intertorma in a dorsal direction (WB59, OC11, S46).
37. *Labiohypopharynx*: (0) not connected to paraclypeal phragma; (1) connected (WB61, S47).
38. *Hypopharyngeal brush of long setae*: (0) absent; (1) present (Sæther, 1990b; S48).
39. *Pharyngeal filter*: (0) present; (1) absent (WB62, OC27, S49).

40. *Antenna*: (0) slender, tapering apically, and usually short; (1) large and stout, and one-segmented (WB64, OC14, S50).
41. *Antenna*: (0) slender or stout; (1) markedly reduced (OC15, S51).
42. *Antenna*: (0) capable of relatively little movement, terminating in several straight setae; (1) prehensile, terminating in claw-like setae, capable of holding prey captured by mandibles as well as of grasping substrate (WB65, OC16, S52).
43. *Mentum (postmentum, hypostomium)*: (0) a separate plate; (1) with posterior/lateral margins fused to postgenae (OC31, S53).
44. *Mentum (postmentum, hypostomium)*: (0) with numerous teeth; (1) with few teeth; (2) without teeth (OC30, S54).
45. *Mentum*: (0) simple or absent; (1) a double-walled plate (ventromentum and dorsomentum) (Sæther, 1971; S55).
46. *Mentum*: (0) well developed; (1) reduced; (2) absent (S56).
47. *Ventromental plates*: (0) without setae (beard) underneath; (1) with setae underneath (S57).
48. *Labiopharynx*: (0) not connected to pharyngeal phragma; (1) dorsolateral corner of labiopharynx connected via cibarial bar to paraclypeal phragma (OC34, S59).
49. *Abdominal segments*: (0) 9 or 10; (1) 8 or fewer (OC35, S60).
50. *Prothoracic parapods*: (0) absent; (1) present in first-instar larva; (2) present in all instars, crowned apically with rows of hooklets (WB66, OC38, S61).
51. *Last abdominal segment*: (0) without parapods; (1) with crochet-tipped, anal parapods (OC40, S63).
52. *Anterior thoracic spiracle*: (0) present; (1) absent (WB67, OC49 in part, S64).
53. *Thoracic segments*: (0) distinct, not appreciably wider than first abdominal segment; (1) enlarged and fused (WB68, OC37, S65).
54. *Abdominal spiracles*: (0) absent or when present flush with surface; (1) on elevated siphon (WB69, OC51, S66).
55. *Posterior abdominal spiracle*: (0) situated laterally on abdominal segment; (1) situated dorsally on segment, or at end of siphon; (2) situated at end of last abdomen segment (OC50, S67).
56. *Posterior abdominal spiracles*: (0) absent, or when present surrounded by 2 pairs of flaps; (1) posterior pair of flaps reduced, elevated to apex of siphon (WB70, OC52, S68).
57. *Procerci*: (0) absent; (1) present (WB71, S69).
58. *Lobes surrounding abdominal spiracles*: (0) immovable or absent; (1) movable (WB72, OC48, S70).
59. *Anal papillae*: (0) retractable; (1) non-retractable (WB73, OC43, S71).
60. *Last abdominal segment*: (0) without fan-like row of long setae; (1) with (WB74, OC41, S72).
61. *Pigment of adult eye*: (0) appearing in pupa, after larval stage; (1) developed precociously, becoming conspicuous as early as second instar (WB75, OC28, S73).
62. *Gastric caeca*: (0) absent; (1) 4 or 8 short and small caecae arranged around circumference of anterior end of midgut; (2) 2 or 3 large caecae present at anterior end of midgut; (3) 4 usually large caecae at the anterior end of midgut (OC46, S75).
63. *Anastomoses*: (0) 10 or 11 anastomoses present; (1) at least dorsal anastomoses 1–3 and usually 1–9 absent, anastomose and 10 present; (2); dorsal anastomoses 4–10, 3–10 or 2–10 absent (OC53, S76).
64. *Lateral longitudinal trunk*: (0) complete; (1) reduced beyond region of first or second transverse connective (OC55, S78).
65. *Sex chromosomes*: (0) distinguishable; (1) not distinguishable (White, 1949; Hackman & Väisänen, 1982; S81).

The following characters were added to help resolve relationships within Chironomidae. For most characters, state 0 is found in other families. However, several of the characters are based on characters not applicable to groups outside the chironomids. Giving outgroup families the plesiomorphous character alternative should not influence the inside topology of Chironomidae as long as the relationships between the related families and the monophyly of Chironomidae is judged by other characters.

Imagines

66. *Scape and/or pedicel*: (0) with setae, at least in female; (1) bare.
67. *Crossvein MCu*: (0) absent; (1) present.

Lindeberg (1964) suggested that MCu is a secondarily acquired crossvein. The distribution of the character indicates that it has either been lost several times or developed in parallel. It is, however, constantly present or absent within each subfamily except in Harrisonini of Diamesinae.

68. R_{2+3}: (0) present; (1) absent.
69. *Fork of Cu*: (0) below, proximal or rarely slightly distal to RM; (1) distinctly distal to RM.
70. *Postnotum*: (0) with setae; (1) without setae.
71. *Tibial spurs*: (0) without lateral teeth, not comb-like; (1) with lateral teeth, comb-like or lyrate.

The lack of lateral teeth on the tibial spurs in *Anatopynia* Johannsen of Tanypodinae is here regarded as a reversal.

72. *Hind tibial comb*: (0) well developed, occupying full width of tibia or secondarily with setae fused or reduced; (1) weak, not occupying full width of tibia at least in some taxa.

The character is scored as 1 for Tanypodinae to stress the similarity with Usumbaromyiinae, although many genera have a well developed comb. The comb is reduced also in several orthoclads, but these do not appear to be of the same type.

73. *Male tergite IX*: (0) with setae not arranged in transverse row; (1) setae in transverse row at least in some taxa.

As with the two preceding characters, this character is scored as 1 for Tanypodinae although most taxa do not have a transverse row of setae on tergite IX. If the characters are scored 0 and 1, the apomorphous character alternative will appear as an autapomorphy for Usumbaromyiinae in the parsimony analysis.

74. *Male laterosternite IX and/or sternite IX*: (0) separate; (1) tergite IX fused with laterosternite IX (and sternite IX) forming a gonotergite; (2) laterosternites fused with sternite IX forming a gonosternite.

The male laterosternite IX is fused with tergite IX in Tanypodoinae. However, in males of Podonominae genera *Lasiodiamesa* Kieffer and *Trichotanypus* Kieffer, vestiges of a laterosternite still are indicated. In Buchonomyiinae, the laterosternites IX are fused with a distinct sternite IX (Sæther, 1990b).

75. *Male gonocoxite*: (0) without conspicuous arrangement of spines and lobes; (1) at least some taxa with such arrangement.

The peculiar armament of the gonocoxites in *Paraphrotenia* Brundin and *Aphroteniella* Brundin of Aphroteniinae is mentioned by Brundin (1966) as having their only counterpart in Boreochlini of Podonominae. The character is scored as 1 for both subfamilies, although not all members have similar armament.

76. *Sternapodeme*: (0) absent; (1) present.
77. *Apical megaseta of gonostylus*: (0) absent; (1) present or clearly secondary reduced.
78. *Female gonapophyses VIII*: (0) very large, elongate; (1) short.
79. *Female gonapophysis VIII*: (0) simple, undivided; (1) with at least some indication of division or clearly divided.
80. *Female tergite IX*: (0) undivided; (1) more or less divided by notch or into 2 setigerous protrusions.
81. *Apodeme lobe*: (0) not apparent; (1) well developed.
82. *Notum of female*: (0) relatively short; (1) long.

Pupa

83. *Thoracic horn*: (0) present; (1) absent.

The thoracic horn is absent only within the Chironomoinae. Brundin (1966), however, mentioned a species of *Podochlus* Brundin of Podonominae that apparently lacks a thoracic horn.

84. *Thoracic horn*: (0) with direct tracheal connection and respiratory atrium; (1) direct tracheal connection and respiratory atrium lost.

Coffman (1979) examined several hundred chironomid species belonging to 123 genera and found that there was no direct tracheal connection in any Chironomoinae, whereas there always was in the other subfamilies. This is one of the few uniquely derived synapomorphies of the semifamily (Sæther, 1983).

85. *Anal lobe of pupa*: (0) without lateral fringe of setae; (1) with fringe of short setae; (2) with fringe of long setae.

This was one of the main characters used by Sæther (1976) for separating Prodiamesinae + Orthocladiinae + Chironominae from Diamesinae. The character should not be ordered as a fringe with short setae appear to be secondary reductions from a fringe with long setae and occurs independently. The character is scored as polymorphic for orthoclads and chironomines. However, it may be more correct to give them the apomorphous character alternative 2 as short fringe or absence are probably always secondary reductions.

Larva

86. *Maxillary palp*: (0) without a distinct bisensillum sitting at a lower level; (1) with such a bisensillum (Strenzke, 1960: Figs 35–40; Ashe, 1985: Fig. 8).

The maxillary palp in Aphroteniinae is interpreted as being of the simple type. Although the palp is extraordinarily elongated the apparent bisensillum is not sitting at a lower level (Brundin, 1983).

87. *Glossae*: (0) small, inconspicuous, not forming large, sclerotized ligula; (1) glossae fused to large, sclerotized ligula.

Cranston *et al.* (1987: Fig. 36) pointed out and illustrated the presence of a ligula and paraligula in the podonomine genus *Archaeochlus* Brundin. Cranston & Edward (1998) recently described the immature stages and the male imago of *Afrochlus harrisoni* Freeman illustrating and discussing the prementohypopharyngeal complex of the larva (Cranston & Edward, 1998: Figs 17, 18) and performing a revised cladistic analysis of the genera of Podonominae. A larva of *Afrochlus harrisoni* was borrowed to examine more closely the prementohypopharyngeal complex. A well developed, dark, bifid ligula (Fig. 1A) is flanked by serrate paraligula resembling that in Tanypodinae (Fig. 1B). Comparison with the second-instar larvula illustrated by Mozley (1979; Fig. 1C) makes the similarities even more striking. A similar formation, but not as dark, is present at least in *Parochlus kiefferi* (Garrett) (Fig. 1D), to some extent in *Lasiodiamesa* (Fig. 1E) and probably in all Podonominae.

88. *Ventromentum*: (0) not to slightly extending lateral of mentum; (1) extending distinctly lateral of mentum.
89. *Procerci*: (0) more than 2.5 times as long as wide; (1) less than 2.5 times as long as wide.

Cranston *et al.* (1987) doubted several of the synapomorphies given by Brundin (1966, 1976), especially those asserting the monophyly of Boreochlini. They mention among other features the characteristic bicoloured procercus of Boreochlini and state that the same type occurs elsewhere. This character thus could have been included in the character matrix. However, Sæther (1990b) regarded the coloration of the procercus of Boreochlini as not strictly homologous with that of other groups.

Results

In the analyses, the multistate characters 11, 16, 22, 26, 44, 46, 55, 62, 74 and 85 were unordered, the other characters ordered. The characters were given equal weight in most analyses. However, some characters are clearly more significant and deserve higher weight than others and characters 5, 8, 10, 21, 32, 33, 36, 43, 67, 71, 79, 80, 84, 85 and 87 were thus given a weight of 10. The first eight are discussed in Sæther (1999), whereas the last seven are diagnostic for chironomid semifamilies and subfamilies (Sæther, 1977, 1990b). Another data matrix was analysed, differing only in scoring character 85, presence of fringe of long setae on the pupal anal lobe, as apomorphous (2)

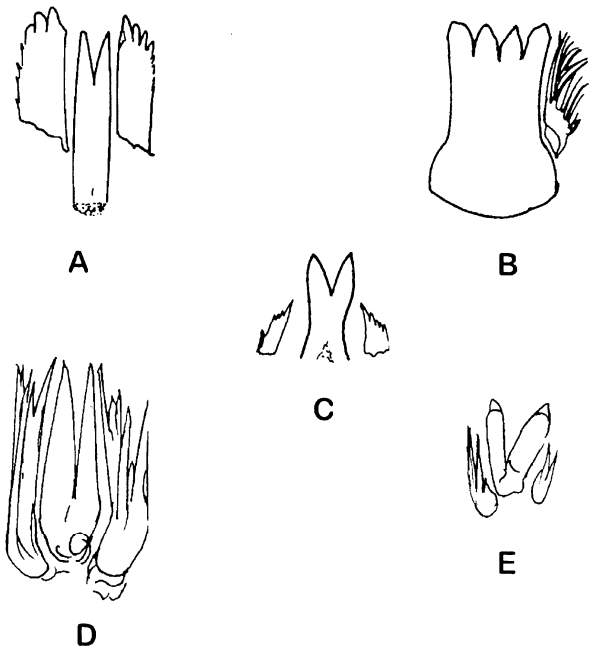


Fig. 1. A, Ligula and paraligula of *Afrochlus harrisoni* Freeman; B, Tanypodinae, fourth instar; C, Tanypodinae, second-instar larvula; D, *Parochlus kiefferi* (Garrett); E, *Lasiodiamesa* sp.

instead of polymorphous (0 and 1 and 2) for all Orthocladiinae and Chironominae. This may be more correct since short setae or absence of fringe seem to be secondary reductions. Character 74, the fusion of laterosternites with tergite IX in male, is highly significant but not weighted at first because in several taxa it is somewhat unclear when there is a gonotergite. Character 74 was given the weight of 10 when some characters were weighted in the second data matrix.

For the first data matrix (Table 1), there were no differences in any of the cladograms in using all non-chironomid families outgroup, default outgroup or Nymphomyiidae + Thaumaleidae as outgroup; or, when Nymphomyiidae was excluded with Thaumaleidae as outgroup.

When no outgroup (or default outgroup) is used, and Nymphomyiidae included, there are twenty cladograms each with 310 steps, a consistency index (CI) of 0.72, a retention index (RI) of 0.67 and a rescaled consistency index (RC) of 0.48 (Fig. 2A). Thaumaleidae form the sister group of Chironomidae. Reweighting these cladograms according to the rescaled consistency index gives a single cladogram identical to the majority rule cladogram of Fig. 2A, except that Simuliidae now forms the sister group of Thaumaleidae and Chironomidae combined. Giving a weight of 10 to the characters mentioned above makes Aphroteniinae part of the semifamily Tanypodoinae and Orthocladiinae + Chironominae the sister group of Chilenomyiinae, Buchonomyiinae and Diamesinae + Prodiamesinae. Reweighting these weighted cladograms according to RC gives two cladograms with either Podonominae or Aphroteniinae as the sister group of Usumbaromyiinae + Tanypodinae. Orthocladiinae plus Chironominae now form the sister group of Diamesinae + Prodiamesinae only.

Aphroteniinae forms the sister group to the other subfamilies except Telmatogetoninae when all other included subfamilies combined are used as outgroup, and when no outgroup is used, whether the results are reweighted or not, and when constraint 2 (Nymphomyiidae and Thaumaleidae basal in Culicomorpha, Culicoidea monophyletic) with Nymphomyiidae excluded is used. However, with all other constraints, and when some characters are weighted, Aphroteniinae is a part of the semifamily Tanypodoinae otherwise consisting of Tanypodinae, Usumbaromyiinae and Podonominae. Either Aphroteniinae or Podonominae may be the sister group of the other two subfamilies.

Chilenomyiinae is placed basally in Tanypodoinae when any of the constraints and Nymphomyiidae included are used, and when using the preferred cladogram from Sæther (1999; constraint 3) as constraint and Nymphomyiidae excluded; also when the results are successively reweighted according to the rescaled consistency index. However, in all other cladograms, regardless of outgroup, constraints, weighting or reweighting, Chilenomyiinae is part of semifamily Chironomoinae otherwise consisting of Buchonomyiinae, Diamesinae, Prodiamesinae, Orthocladiinae and Chironominae. Chilenomyiinae forms the basal subfamily of Chironomoinae when no characters are given extra weight, and when constraints 1 or 2 are used, whether Nymphomyiidae is included or excluded. For all cladograms with some characters given extra weight, Chironominae + Orthocladiinae combined form the sister group of the remaining subfamilies of Chironomoinae. When these cladograms are reweighted according to RC, Chilenomyiinae becomes the basal subfamily.

The relative positions of Diamesinae, Prodiamesinae, Orthocladiinae and Chironominae are highly variable between different cladograms. Only when the results are reweighted, and no constraint or constraints 1 or 2 used, is the above phyletic sequence obtained. Without reweighting or weighting, Chironominae form the sister group of the other three subfamilies combined, regardless of outgroup or constraints used. As mentioned above, Chironominae + Orthocladiinae combined form the sister group of the remaining subfamilies of Chironomoinae when some characters are given extra weight. When these cladograms are reweighted according to RC, Diamesinae + Prodiamesinae become the sister group of Orthocladiinae + Chironominae. Prodiamesinae + Chironominae form the sister group of Orthocladiinae when Nymphomyiidae is included in the data matrix, constraints used and the results reweighted; and when Nymphomyiidae is excluded, constraint 3 used and the results reweighted.

With the second data matrix there is just one inside topology of the relationships between subfamilies of Chironomidae regardless of the choice of sister groups, or constraints (Fig. 2B). The shortest cladograms with Nymphomyiidae included are 306 steps long with CI of 0.72, RI of 0.67 and RC of 0.48; with Nymphomyiidae excluded the shortest

Table 1. Characters and states for Chironomidae subfamilies and outgroup taxa. Polymorphies: A = 0 & 1, B = 1 & 2, C = 0 & 2, D = 0 & 1 & 2, E = 0 & 1 & 2 & 3, F = 0 & 1 & 2 & 3 & 4, G = 0 & 4.

Character states	1111111111222222222233333333334444444444555555555566666666667777777777888888888
Taxa	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789
Culicidae	2110110000011AFB211221AA12A11111112010110010000110011111011111001000000000000000000000000
Chaoboridae	2110?100002A120B2212211112A0000110000001011C0A0000?11111011110??10000000000000000000000000
Corethrellidae	2110?1000020120022122111101000011000100101100101 0A?1111101100?0010000000000000000000000000
Dixidae	1010?0000001103022122111101111111111010110012 00A1000100100000?0010000000000000000000000000
Thaumaleidae	0020?0000101A0402010000010000100100001101010A0000110001010100?0000000000000000000000000000
Simuliidae	002000110100A03A2010010110111111112000000001D10A0111100?0000001211000000000000000000000000
Ceratopogonidae	211A1011010010E1201211011010011010 0A0A00001D0D000AA100?0000000011000000000000000000000000
Telmatogetoninae	1120011101111141200001001000011010010100101010000111100?0101001211001110000010100000000001
Chilenomyiinae	2110011111211 10?2110000??1??10110100000000000???????
Usumbaromyiinae	21110111111111301010000??1??10001111110101000???????
Tanypodinae	211A0111A1A011C0B01001001100001010010000000A0000011100?0101001211A1AAA1111011100000000100
Podonominae	211A0111A1AAA1CD20100A00110000101001000000101000011100101010012 11AA1AA00011111000000 0A100
Aphroteniinae	11110111111111C12010010010000010100100001 00C1000011100?0101001211A0111000111000000000000
Buchonomyiinae	21100111A1010121201002001100001010010000 00?0?0000111100?0101001211A1000000200011A101100001
Diamesinae	B1110111A11AA1C010100000A100011010010A00001D1000011100?0A01001211AA00100000111AA1AA1A1001
Prodiamesinae	211101110111A1001010000011000110100100000010100001 1100?0101001211110A1000001111111010121011
Orthocladiinae	B1B10111A11AA1DDA0100000AA0001101001000 0A01D10A00AA100?0A0100121110AAA00000111AA11A1D10A1
Chironominae	B1B10111A1111121101000001100011A1001000000111000011100?0101001211100A100000101AA11A1DA011
Nymphomyiidae	002010011?01024?20A001??000000000000000?000100000001100?000000????000000000000000000000000

cladograms are 295 steps long. When some characters, including character 74, are weighted, Aphroteniinae is placed in Tanypodoinae in all cladograms (Fig. 2C).

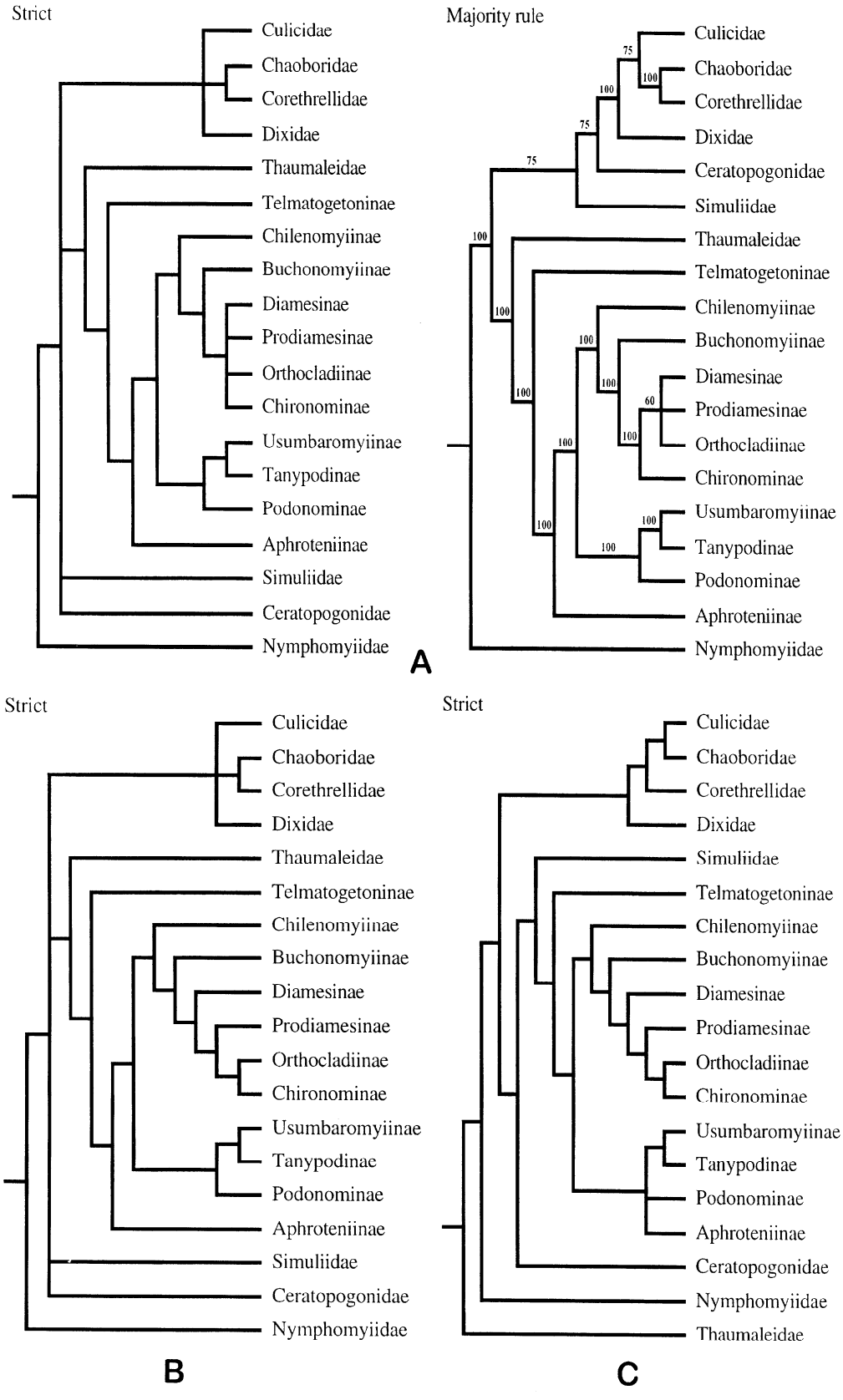
Discussion

The relationships between the different families of Culicomorpha were analysed by Sæther (1999). When Chironomidae is treated as a unit and not divided into subfamilies, and characters are unordered and reweighted, or some characters ordered and some unordered and then reweighted, Chironomidae, Simuliidae and Ceratopogonidae form a monophyletic sister group of Culicoidea with Simuliidae as the sister group of Chironomidae regardless of outgroup chosen. The same configuration is found when the characters are ordered or ordered and reweighted and all nonculicomorph families, Tipuloidea (as suggested by the cladogram in Wood & Borkent, 1989), Psychodidae + Trichoceridae + Tipuloidea + Neodiptera (as suggested by the result in Oosterbroek & Courtney, 1995) or Trichoceridae + Tipuloidea + Tanyderidae + Ptychopteridae (as suggested by the cladogram of Michelsen, 1996) chosen as outgroup, or by using Lundberg rooting (i.e. a theoretical archetype with character alternative 0 for all characters, which essentially equals the outgroup of Mecoptera, Nannochoristidae and Siphonaptera used by Oosterbroek & Courtney, 1995).

When Chironomidae is divided into subfamilies and characters unordered and reweighted or some ordered and others unordered and reweighted, the families are related in the phyletic sequence Chironomidae, Simuliidae, Ceratopogonidae. The same configuration is found when Chironomidae is divided, and characters unordered and reweighted with Lundberg rooting.

When Chironomidae is treated as a unit and characters either unordered or ordered, the families follow the phyletic sequence Chironomidae, Ceratopogonidae, Simuliidae. The same configuration is obtained when the subfamilies of the chironomids are included separately and the characters are unordered or unordered and reweighted, and when all non-culicomorph families is used as outgroup and the characters ordered.

Ashe *et al.* (1987) used two arguments for reconsidering the position of the marine Telmatogetoninae as the sister group of all other chironomids, one ecological and one morphological: (1) their ecology does not agree with the presumed habitat of the ancestral chironomid in cool, well oxygenated, mountain water as suggested by Brundin (1966); (2) the gonostylus IX of female Telmatogetoninae is not homologous with the gonostyli of Nymphomyiidae and Sciaridae and not a plesiomorphous feature. Their arguments were countered by Sæther (1990b). Telmatogetoninae breed in mountain torrents on Hawaii and marine species can actually be reared in freshwater. Although it is apparent that the subfamily is pre-Jurassic and did not originate in Hawaii, this shows that it could well have originated in freshwater. The female genitalia of *Thalassomya cocosensis* Hashimoto have now also been examined. Although of a different type, with better developed gonocoxite and both gonocoxite and gonostylus covered by microtrichiae, the gonostylus is evident. Furthermore, P. S. Cranston (personal communication) and colleagues at CSIRO, Canberra, are presently undertaking gene sequencing of the different subfamilies of Chironomidae. Their results are not yet finalized.


Strict
Culicidae
Chaoboridae
Corethrellidae
Dixidae
Thaumaleidae
Telmatogetoninae
Chilenomyiinae
Buchonomyiinae
Diamesinae
Prodiamesinae
Orthocladiinae
Chironominae
Usumbaromyiinae
Tanypodinae
Podonominae
Aphroteniinae
Simuliidae
Ceratopogonidae
Nymphomyiidae
A
Majority rule
Culicidae
Chaoboridae
Corethrellidae
Dixidae
Ceratopogonidae
Simuliidae
Thaumaleidae
Telmatogetoninae
Chilenomyiinae
Buchonomyiinae
Diamesinae
Prodiamesinae
Orthocladiinae
Chironominae
Usumbaromyiinae
Tanypodinae
Podonominae
Aphroteniinae
Nymphomyiidae
Strict
Culicidae
Chaoboridae
Corethrellidae
Dixidae
Thaumaleidae
Telmatogetoninae
Chilenomyiinae
Buchonomyiinae
Diamesinae
Prodiamesinae
Orthocladiinae
Chironominae
Usumbaromyiinae
Tanypodinae
Podonominae
Aphroteniinae
Simuliidae
Ceratopogonidae
Nymphomyiidae
B
Strict
Culicidae
Chaoboridae
Corethrellidae
Dixidae
Simuliidae
Telmatogetoninae
Chilenomyiinae
Buchonomyiinae
Diamesinae
Prodiamesinae
Orthocladiinae
Chironominae
Usumbaromyiinae
Tanypodinae
Podonominae
Aphroteniinae
Ceratopogonidae
Nymphomyiidae
Thaumaleidae
C

However, based on molecular evidence, Telmatogetoninae form the sister group of all the remaining chironomids.

Brundin (1966) placed Aphroteniinae as the sister group of Podonominae. There is, however, only one character that may be a synapomorphy for the two subfamilies, and then with secondary reductions in Podonominae, the peculiar armament of the male gonocoxite. Among chironomid subfamilies, a fully isolated mentum not fused to the genae (ch. 43) is found only in Aphroteniinae and Tanypodinae (see Sæther, 1999). Although this character is most likely a plesiomorphy for Diptera as a whole, it is almost certainly a secondarily derived feature in chironomids and a strong potential synapomorphy for the two subfamilies.

The possession of large sclerotized ligula (ch. 87) discussed above is a strong potential synapomorphy for Tanypodinae + Podonominae. Analyses of the data in Table 1 do not resolve the question whether Aphroteniinae + Podonominae form the sister group of Tanypodinae + Usumbaromyiinae, or if Aphroteniinae or Podonominae alone is the sister group. All cladograms resulting from scoring character 85 as 2 for Orthocladiinae and Chironominae have Aphroteniinae as the sister group of all other subfamilies except Telmatogetoninae. Nevertheless, I consider Aphroteniinae is an integral part of Tanypodoinae as exemplified by the above-mentioned potential synapomorphies.

The different cladograms obtained all have Usumbaromyiinae as the sister group of Tanypodinae. This, however, is more a result of how characters 71–73 are scored than a result of non-ambiguous synapomorphies. As the immatures are unknown the placement is highly tentative.

Brundin (1983) gave two characters as synapomorphies for Chironomoinae + Tanypodoinae relative to Chilenomyiinae. Both concern the peculiar genitalia of the male and female, and the plesiomorphous character alternatives appear more as autapomorphies for Chilenomyiinae. Chilenomyiinae do not possess the important synapomorphy of Tanypodoinae that tergite IX is fused with laterosternite IX forming a gonotergite (ch. 74). On the contrary, the laterosternites (regarded as gonocoxites IX by Brundin, 1983) are extremely well developed. Furthermore, the female gonocoxites of certain orthoclads are approaching the size of those found in Chilenomyiinae. The anteriorly tapered tergite VIII is other-

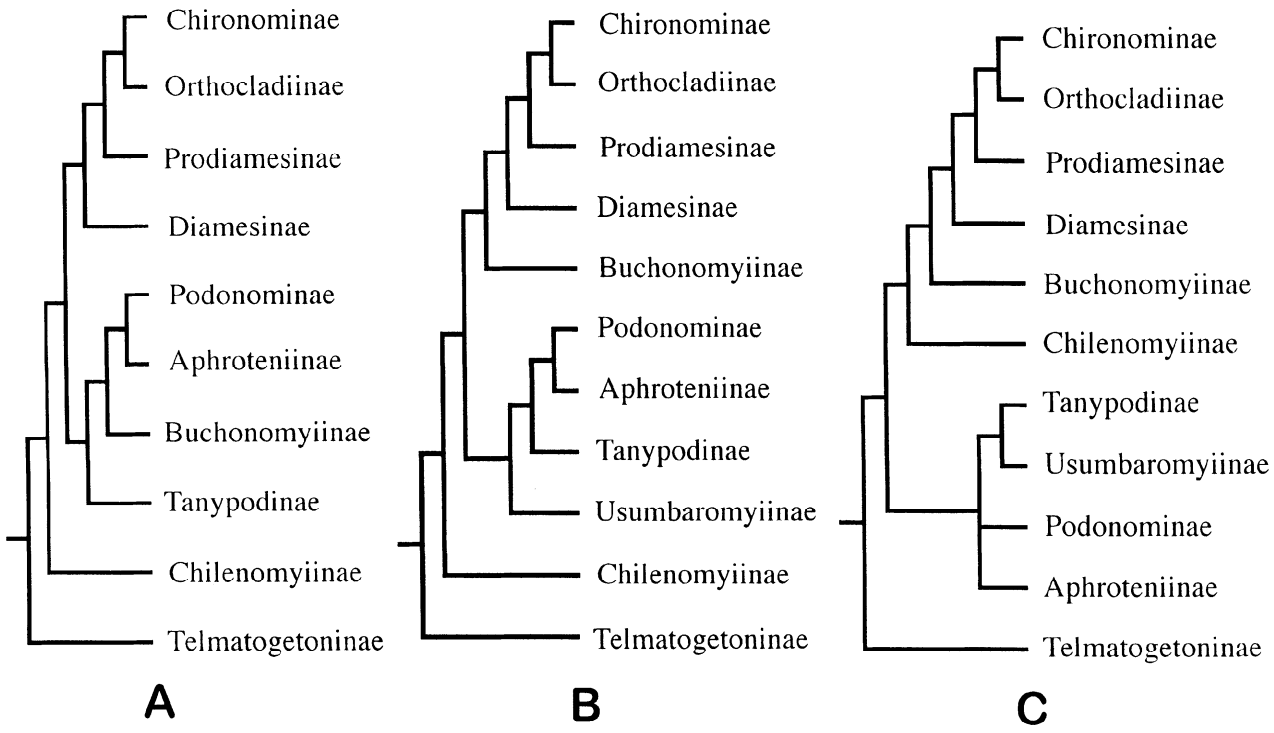


Fig. 3. A, Phylogenetic relationships between chironomid subfamilies suggested by Murray & Ashe (1981, 1985); B, phylogenetic relationships suggested by Sæther (1977), Brundin & Sæther (1978), Brundin (1983) and Andersen & Sæther (1994); C, preferred cladogram and the only one obtained when character 85 is scored as 2 for Orthocladiinae and Chironominae and some characters, including 74, are weighted.

Fig. 2. A, Strict consensus and majority rule cladograms obtained with the data in Table 1 and all families except Chironomidae as outgroup; B, strict consensus cladogram with character 85 scored as 2 for Orthocladiinae and Chironominae and default outgroup; C, strict consensus cladogram obtained with character 85 scored as 2 for Orthocladiinae and Chironominae, some characters including character 74 weighted, and the preferred cladogram from Sæther (1999) used as constraint.

wise found only in Tanytarsini and the chironomine genus *Polypedilum* Kieffer and some related genera. Until the immatures are found, this subfamily should be placed basally in Chironomoinae as suggested by nearly all cladograms when Nymphomyiidae is excluded from the analysis, rather than basally in Tanypodoinae. All cladograms with character 85 scored as 2 for Orthocladiinae and Chironomidae have Chilenomyiinae basally in Chironomoinae.

Three different mutual relationships of Diamesinae, Prodiamesinae, Orthocladiinae and Chironominae are equally short in the different cladograms based on the data in Table 1. Chironominae may form the sister group of the three others forming a trichotomy, Prodiamesinae + Diamesinae may be the sister group of Orthocladiinae + Chironominae and the subfamilies may come in the phyletic sequence Diamesinae, Prodiamesinae, Orthocladiinae, Chironominae, as generally accepted. Finally, in some cladograms, Orthocladiinae + Chironominae form the sister group of all other Chironomoinae, including Chilenomyiinae. However, when character 85 is scored as 2 for Orthocladiinae and Chironominae, all cladograms have the subfamilies in the traditional sequence and position, and the cladograms becomes considerably shorter.

The cladogram of the chironomid subfamilies as suggested by Sæther (1977), Brundin & Sæther (1978), Brundin (1983) and Andersen & Sæther (1994) is shown in Fig. 3B, whereas the phylogeny as suggested by Murray & Ashe (1981, 1985) with Chilenomyiinae tentatively added is shown in Fig. 3A. The preferred cladogram resulting from the above discussion is shown in Fig. 3C and was compared with the other two using MacClade 3.06. When Usumbaromyiinae is excluded from the cladograms in Fig. 3B,C, the cladogram in Fig. 3A is five steps longer than the preferred cladogram, twenty-three steps when some characters are weighted. The cladogram in Fig. 3B is two steps longer; eleven steps longer when some characters are weighted.

Most likely all chironomid subfamilies can be placed in one of three semifamilies: Telmatogetonoinae, Tanypodoinae or Chironomoinae. The placements of both Chilenomyiinae and Usumbaromyiinae, however, are highly tentative and need confirmation by the morphology of the immature stages.

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