SPIXIANA	Supplement 11	149–160	München, 30. Dezember 1985	ISSN 0177-7424

A description of the adult female of Buchonomyia thienemanni Fittkau and a re-assessment of the phylogenetic position of the subfamily Buchonomyiinae

(Diptera, Chironomidae)

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Murray, D. A. & P. Ashe (1985): A description of the adult female of *Buchonomyia thienemanni* Fittkau and a re-assessment of the phylogenetic position of the subfamily Buchonomyiinae (Diptera: Chironomidae). – Spixiana, Suppl. 11: 149–160.

The adult female of *Buchonomyia thienemanni* Fittkau is described and figured. The interpretation of the female genitalia of *B. thienemanni* presented in this paper differs from that given by Brundin and Saether (1978) for *B. burmanica* Brund. et Saeth., the only other species known in the subfamily Buchonomyiinae. The gonapophyses VIII are simple and without evidence of division. An apodeme lobe is absent. Gonocoxite IX is reduced and fused with tergite IX to form a gonotergite. Coxosternapodeme IX is broad. The rami of gonapophyses IX are fused. This, together with supportive evidence from male genitalia and the recently described 1st instar larva suggests that the subfamily Buchonomyiinae belongs with the phylogenetic unit Tanypodinae + Podonominae + Aphroteniinae.

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Introduction

The position of *Buchonomyia* in chironomid phylogeny has been subject to speculation and debate since the adult male of *B. thienemanni* Fitt. was first described by Fittkau (1955) who provisionally assigned the new genus to the Podonominae. Brundin (1966) suggested that the genus could belong to the Orthocladiinae but while dealing with subfamily relationships within the Chironomidae states (op. cit.) "... a considerable hinderance for further progress is lacking information of the larva and pupa of *Buchonomyia* and some other plesiomorph Orthocladiine genera". Brundin and Saether (1978) described the adult male and female of a second species, *B. burmanica* Brund. et Saeth., and assigned the genus to a new subfamily, the Buchonomyiinae. Based on their interpretation of the male and female genitalia of *B. burmanica,* but relying heavily on apparent apomorphic features of the female, Brundin and Saether regard the Buchonomyiinae as the sister group of the phylogenetic unit Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae. This placement was re-affirmed by Saether (1979 a, b, c). The description of the pupa of *B. thienemanni* by Murray and Ashe (1981) from material collected in the River Flesk, Killarney, Ireland, did little to further establish the phylogenetic position of the subfamily because of the general predominance of plesiomorphic and lack of apomorphic features. However, it was suggested, based on an interpretation of the male terminalia of *B. thienemanni* different from that given by Brundin and Saether for *B. burmanica,* that the Buchonomyiinae could equally well be associated with the Tanypodinae + Podonominae + Aphroteniinae. A detailed treatment of the situation was deferred to allow further examination of the female *B. thienemanni* and additional time to search for the larva. Despite intensive efforts, searching in various habitats in the River Flesk, larvae of *B. thienemanni* have eluded capture. However, fertilized adult females were obtained in 1981 which were induced to lay egg masses from which 1st instar larvae were obtained. Descriptions of the egg mass and development of the larva have already been given (Ashe and Murray 1983). A description of the 1st instar larva is given by Ashe (1985).

Evidence now available from a detailed examination of the female *B. thienemanni* and features of the 1st instar larva gives further credence to the previous suggestion by Murray and Ashe (op. cit.) that the Buchonomyiinae is indeed more likely to be associated with the Tanypodinae + Podonominae + Aphroteniinae.

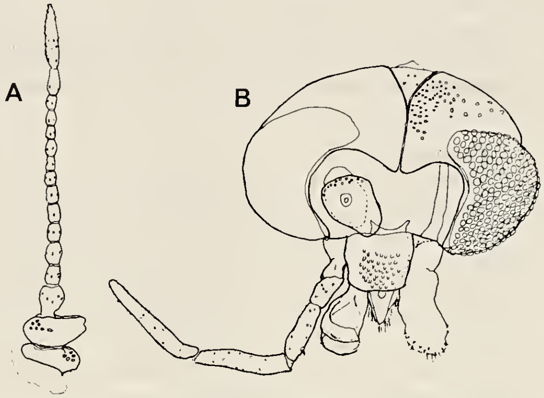


Fig. 1: *B. thienemanni,* female; A) antenna, B) head.

Materials and methods

The specimens on which this study is based were obtained from two locations in Ireland. The occurence of *B. thienemanni* at one of these locations, the River Flesk, Killarney, has previously been reported (Murray 1976; Murray and Ashe 1981). Recently the species was also noted from the River Nore south of the town of Kilkenny by Hayes (pers. comm) during the course of a continuing study on the use of chironomid pupal exuviae as indicators of water quality. Adult females of *B. thienemanni,* easily recognisable on the wing, were collected by hand-net at both locations during July 1981 (River Flesk) and August 1982 (River Nore) and preserved in 70 % alcohol. Slide preparations were made according to standard procedures. Some specimens were further dissected to reveal details of the genitalia, in particular the elements of gonapophyses IX, which were also mounted on slides. Additionally, a number of specimens were prepared for Scanning Electron Microscopy. In order to reveal the genitalia more clearly some dissection was also necessary on these specimens and the following series of preparations was made: specimens with (I) cerci removed; (II) cerci and sternite X removed; (III) cerci, sternite X and one of the gonapophyses VIII removed. Subsequently these specimens were critical point dried, gold sputter coated and examined in a Joel JSM 35C scanning electron microscope.

The terminology and abbreviations used in the text and descriptions are in accordance with the glossary of Saether (1980).

Description of the female of Buchonomyia thienemanni Fitt.

Adult female (n = 2 unless otherwise stated). Total length 4.0–4.5, 4.3 mm; wing length 2.8–3.34, 2.99 mm.

Head (Fig. 1): Scape of antenna 34–40 µm long, with 8–10 setae. Pedicel 55–60 µm long with 12–13 setae and a distinct ventrolateral projection (Fig. 1A). First flagellomere 60 µm long (n = 1); flagellomeres 1–13 428 µm long; flagellomere 13 50 µm, flagellomere 14 125 µm long. AR 0.26. Temporal setae 65–68, post orbitals 6–8, outer verticals 18, inner verticals 32, preoculars 9–10. Clypeus with 42–46, 44 setae. Tentorium 168–172, 170 µm long. Palp lengths (µm) 38–42, 40; 49–51, 50; 107–112, 110; 234–239, 237.

Thorax (n = 3): Antepronotum with 12–16, 14 setae. Dorsocentrals 98–105, 103; including 11–15, 13 humerals. Acrostichals 125–139, 132; prealars 57–65, 60; parascutellars 10–12, 11. Scutellum with 104–113, 109 setae, postnotum with 14–21, 17 setae.

Wing (n = 6): VR 0.74–0.77, 0.76. First axillary sclerite with 8–12, 11 setae; brachiolum with 8–11, 10; R with 82–106, 91; R1 with 94–123, 110; R2+3 absent; R4+5 with 153–186, 165; M with 91–112, 103; M1 + 2 with 149–167, 158; M3+4 with 76–91, 83; Cu with 54–63, 59; Cu1 with 25–39, 29 setae. Squama with 49–61, 52 setae. Sensilla campaniformes 11–13 at base of brachiolum (Plate 1); 11 at apex of brachiolum; 3–4 on subcosta; 2 on R4+5. Lanceolate setae on veins and wing membrane.

Legs. Spurs of front tibia 70–86, 73 µm long; spurs of middle tibia 82–91, 85 µm long; of hind tibia 85–101, 92 µm long. Pseudospurs: 1 on ti of front leg; 8 on ti of middle leg; 1 on ti of hind leg; 7–8 on ta1 of middle leg; 8–10 on ta1 of hind leg; 2 on ta2 of middle and hind legs; 1 on ta3 of middle leg; 1–2 on ta3 of hind leg; 1 on ta4 of hind leg; lanceolate setae present (Plates 2, 3). Lengths of pseudospurs 68–75 µm. Pulvilli absent. Leg measurements and ratios in Table 1.

Table 1: Leg measurements (µm) and ratios for *B. thienemanni* female.

	Fe	Ti	Ta_1	Ta_2	Ta_3	Ta_4
p_1	966–1132,1049	1113–1279,1119	791– 920, 853	506–601,555	386–460,421	294–350,322
p_2	1150–1380,1265	1168–1325,1247	616– 736, 679	359–414,387	267–304,283	193–230,211
p_3	1003–1196,1100	1389–1619,1504	957–1095,1021	561–644,600	368–432,400	267–304,286

	Ta_5	LR	SV	BV
p_1	212–221,217	0.69–0.71,0.70	2.59–2.67,2.63	2.04–2.06,2.05
p_2	175–198,187	0.52–0.54,0.53	3.64–3.78,3.70	2.96–3.78,3.70
p_3	202–212,207	0.68–0.69,0.69	2.49–2.60,2.54	2.39–2.46,2.42

Genitalia (Fig.2, A, B; Plates 4–8): Tergite VIII normal. Sternite VIII with mid ventral caudal projection, partially composed of reduced setae particularly obvious in lateral view, under the vagina. Gonocoxapodeme VIII expressed caudoventrally, extending to the base of gonapophyses VIII and reaching caudolaterally to terminate in a knob articulating against gonotergite IX. Gonapophyses VIII simple, well developed, broadly tongue shaped, partially covered with microtrichia which are for the most part mesally directed, posterior third devoid of microtrichia. Entire mesal margin of gonapophyses VIII fringed with microtrichia. In the natural, i. e. undissected, specimen the posterior third traverses a dorsal path anterior to the cerci while in dissected specimens this microtrichia free area is clearly evident projecting caudally (Plates 5, 6). Membrane evident, in SEM (Plates 7, 8) and some slide preparations, anterior to the spermathecal eminence. Tergite IX large, hood-shaped, with 95–130 setae, without evidence of division in two lobes and over-reaching the cerci caudally. Two seminal capsules, 160 µm long and 90 µm wide (Fig 2C). A distinct hyaline neck and annulated collar on the spermathecal duct at its junction with the seminal capsule. Gonocoxite IX reduced and fused with tergite IX to form a gonotergite IX. Gonapophyses IX well developed (Fig. 3). Notum arched and joined into the fused plate-like

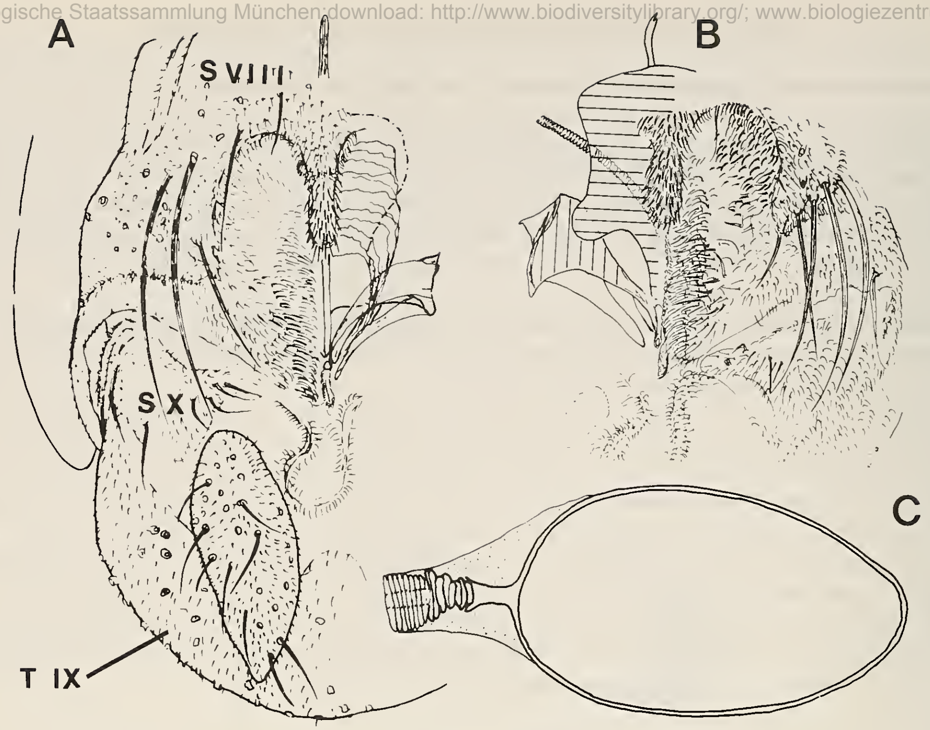
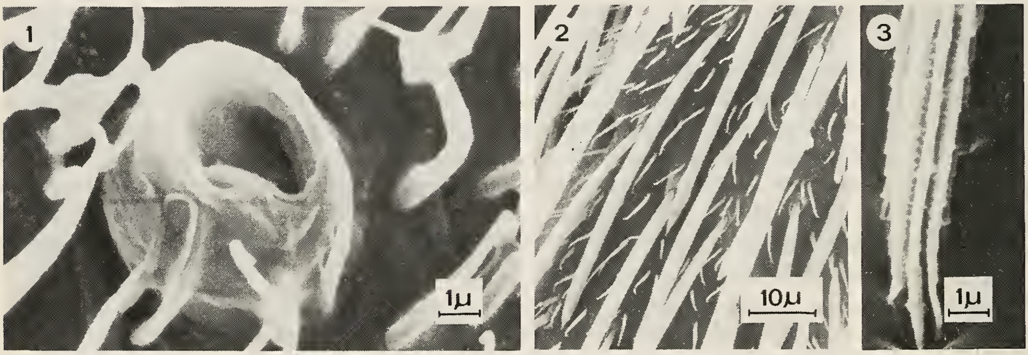


Fig. 2: *B. thienemanni,* female; A, B) ventral aspect of genitalia, C) Spermatheca.

rami which extend caudally, dorsal to coxosternapodeme IX. Coxosternapodeme IX broad, attached to gonapophysis IX at the spermathecal eminence and laterally articulating with gonotergite IX. A single accessory gland evident ventral to the rami of gonapophyses IX. Ducts from this gland pass ventral to coxosternapodeme IX and terminate caudal of the spermathecal eminence surrounded by the labia (PAcc, Fig. 3). Labia fused at base and provided with numerous microtrichia. Intergonocoxal connective evident, connected to the caudal end of coxosternapodeme IX. Cercus 153–196, 162 µm (6) long. Sternite X with 7–11, 9 setae.



Plates 1–3: *Buchonomyia thienemanni,* adult female. 1. Campaniform sensillum at base of brachiolum. 2. Lanceolate setae on femur of mid-leg. 3. Lanceolate seta, detail of apex showing serrated borders of ridges.

Discussion

Previous phylogenetic position of Buchonomyiinae

Brundin and Saether (1978) and Saether (1979a, b, c) regard the subfamily Buchonomyiinae as the sister group of the Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae based upon their interpretation of the genitalia and other features in the male and female *B. burmanica.* Foremost in the arguments put forward to support this placing was the mistaken concept that the adult male showed no apparent apomorphies and the consequent reliance on supposed "underlying synapomorphic" features in the female genitalia. Murray and Ashe (1981), deferring comment on the female genitalia pending more detailed study, suggested that the Buchonomyiinae could be placed with the monophyletic unit Tanypodinae + Podonominae + Aphroteniinae with an interpretation, principally based on the male genitalia, different from that of Brundin and Saether (op. cit.). The apparent conflict of evidence regarding the phylogenetic position of the Buchonomyiinae can now be resolved with the new information available from the description of the 1st instar larvae of *B. thienemanni* (Ashe, 1985) and an interpretation of the female genitalia different to that proposed by Brundin and Saether (1978) and Saether (1979a, b).

Features of the adult

Most of the discussion and comparison of plesiomorphic and apomorphic features of the adult Buchonomyiinae in relation to the other chironomid subfamilies treated by Brundin and Saether (1978: 273–274), except their interpretation of certain features of the male and female genitalia, is valid and need not be repeated here. Brundin (1983a), however, has revised the previous plesiomorphic interpretation of the lanceolate setae present on the legs and wings of *B. burmanica* and now considers the development of these setae as an apomorphic trend with parallel development in different subfamilies among the Chironomidae. The mid ventral caudal projection on the female sternite VIII was regarded as an autapomorphy but attention must be drawn to a somewhat similar structure present in some members of the Telmatogetoniinae where a setose "anal point" occurs. Additionally, the presence of an annulated neck and collar on the spermathecal duct – perhaps having a pumping action is reminiscent of the structure in *Aphroteniella filicornis* Brundin (Saether 1977, fig. 25). Brundin and Saether (op. cit.) contend that there are no apparent apomorphies in the male genitalia of *B. burmanica.* However, Murray and Ashe (op. cit.) indicate that a real apomorphy is present and the description of the male genitalia of *B. burmanica* is in error in the reference to the presence of sternite IX, laterosternite IX and the composition of tergite IX. Apparently the abdominal segments were miscounted in the description of *B. burmanica* and the parts referred to as sternite IX and laterosternite IX are, in fact, parts of sternite VIII. Tergite IX was stated to be divided in a caudal area, a median membranous area and a basal part. It is quite clear from examination of male *B. thienemanni* that the caudal area is tergite IX while the basal part is tergite VIII and the membranous part is a much enlarged intertergal connective. The gonocoxite IX is apparently reduced and fused to form a gonotergite IX. This fusion of the tergal and sternal elements of segment IX thus gives rise to a simple ring-shaped segment which is a good apomorphic trend to aid in the phylogenetic placement of the subfamily.

At least seven apomorphies were identified by Brundin and Saether (op. cit.) in the female *B. burmanica* some of which, because of their susceptibility to convergence and parallelism, could not be used in the formulation of the phylogenetic diagram for the chironomid subfamilies and use was made instead of underlying synapomorphies.

Acceptance of the use of underlying synapomorphic features is central to the ideas put forward by Saether (1977) for elucidation of subfamily relationships within the Chironomidae. Three underlying synapomorphic features of the female chironomid genitalia i. e. the capacity for a division to arise in Gp VIII, the capacity for the development of an apodeme lobe from Gp VIII and the capacity for the division of T IX into two setigerous protrusions, are used extensively by Saether (1977; 1979a, b) for the

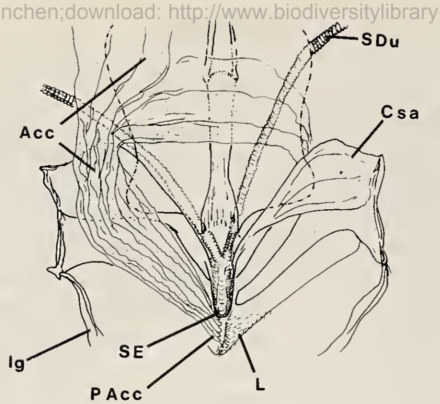


Fig. 3: *B. thienemanni,* female; Gonapophyses IX and coxosternapodeme IX. Abbreviations – Acc, Accessory gland; PAcc, Papillae of accessory gland; Csa, Coxosternapodeme IX; Ig, Intergonocoxal connective; L, Labia; SE, Spermathecal eminence; SDu, Spermathecal duct.

Plates 4–8: *Buchonomyia thienemanni,* female genitalia. 4. Ventral aspect of terminal abdominal segments, cerci removed. 5. Ventral aspect of terminal abdominal segments with cerci and segment IX removed, note the microtrichia-free area on Gp VIII. 6. Lateral aspect of Gp. VIII and mid-ventral "anal point" (A). 7. Ventral aspect of vaginal region. 8. Oblique latero-ventral aspect of vaginal region; Mb = membrane, S = Spermathecal eminence, L = labia.

establishment, within the family Chironomidae, of two monophyletic units: (1) the Tanypodinae + Aphroteniinae + Podonominae and (2) the Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae. The same three features are used by BRUNDIN and SAETHER (op. cit.) to provide evidence for the inclusion of the Buchonomyiinae with the latter of the above mentioned units. Since the placement of Buchonomyiinae has been based to a large extent on these three underlying features it is necessary to elaborate on some aspects of the description of the female genitalia of *B. thienemanni* before considering the phylogenetic position of the Buchonomyiinae.

Gonapophysis VIII: Referring to the use of the underlying trend for a division to arise in Gp VIII and at the same time putting forward supportive ideas for the earlier placement of Buchonomyiinae, SAETHER (1979 a: p 20) regards all gonapophyses VIII which indicate an oromesal lobe, even if this is not distinctly set off from the remainder, as "divided" and thus considers the gonapophyses VIII of *B. burmanica* to be "divided" (SAETHER's parentheses). This statement refers to the dorsomesal lobe indicated by a weak line in fig. 3 C in BRUNDIN and SAETHER (1978). Whether or not a dorsomesal lobe is present in *B. burmanica* is a matter of opinion. It is quite evident that there is no indication of a dorsomesal lobe in *B. thienemanni* (Plate 4).

Apodeme-lobe: An apodeme lobe (a secondary development of Gp VIII) was stated to be present, bearing microtrichia and partially covered by the ventrolateral lobe, in *B. burmanica* (BRUNDIN and SAETHER, 1978). The structure described as an apodeme lobe in *B. burmanica* is also clearly evident in *B. thienemanni.* However, microdissection of the genitalia and removal of Gp VIII has revealed the facts that Gp VIII is simple in nature as already indicated and also that the so-called apodeme lobe of Brundin and Saether is intimately connected with Gp IX and thus can not be considered an apodeme lobe since, by definition, the apodeme lobe is a secondary development of Gp VIII. Examination of specimens dissected for SEM has shown that the so-called apodeme lobes of Brundin and Saether are, at least in *B. thienemanni,* the labia which project mesally, are covered with microtrichia and perhaps fused basally, are situated just caudal of the spermathecal eminence and surround papillary components of the accessory gland.

Tergite IX: According to BRUNDIN and SAETHER (1978) an incomplete division is indicated in the female tergite IX of *B. burmanica.* In all specimens of *B. thienemanni* examined in this study the posterior contour of T IX is without any evidence of emargination. There is, thus, conflict in this character between the two species and obviously the posterior emargination can not be used as a diagnostic character for *Buchonomyia.* It could be argued that since an incomplete emargination is indicated at least in *B. burmanica* then the subfamily has the capacity for emargination. However it is worth noting that even in the Aphroteniinae a slight posterior emargination may occur as is the case with *Paraphrotenia excellens* Brundin (SAETHER 1977: p 54, Fig. 25 D).

Features of the pupa

The pupa of *B. thienemanni* has many plesiomorphic features but MURRAY and ASHE (op. cit.) drew attention to the nature of the pharate adult tracheal connection to the pupal integument. In *B. thienemanni* the pharate adult tracheal tubes end blindly on a sclerotised ridge posterior to the pre-corneal slit. COFFMAN (1979) has indicated the presumed plesiomorphic condition where the pupal respiratory organ is attached directly to the pharate adult tracheal system. This type of connection is found in the subfamilies Tanypodinae, Aphroteniinae and Podonominae. The apomorphic alternative is seen in the remaining subfamilies where the pupal respiratory organ is indirectly attached to the pharate adult tracheal system. It was suggested by MURRAY and ASHE (op. cit.) that the situation in *B. thienemanni* was similar to that in the Orthocladiinae and Diamesinae and thus could be interpreted as an apomorphic state. However the absence of a respiratiory organ in *Buchonomyia* detracts from the arguments put forward previously and from the use of this character in this case. The general plesiomorphic nature of the pupa is thus of little help in the formulation of the phylogenetic relationships of *Buchonomyia.*

Features of the larva

Although as yet only the 1st instar larva is known (Ashe, 1985) sufficient information is available to aid determination of the phylogenetic position of Buchonomyiinae. Apomorphic characters of the larva relevant to the present discussion are (1) absence of the premandible, (2) form of the labral SII on well developed pedestals (sensu Brundin 1983 b = socles sensu Brundin 1966) and (3) the presence of a labral rod. The reduction and loss of the larval premandible is firmly established as a synapomorphic feature of the monophyletic group Tanypodinae + Podonominae + Aphroteniinae. Absence of the premandible in *Buchonomyia* is a clear indication that this subfamily should also belong to this group. Further evidence in the larva of *Buchonomyia* linking the subfamily with the Podonominae + Aphroteniinae is the presence of a labral rod and long stout curved SII setae on well developed pedestals. Saether (1980) considers a peg-like structure on the larval labrum of some Orthocladiinae as a labral rod. It is not clear if this structure is homologous with the elongated and usually apically rounded labral rod present in the Podonominae and Aphroteniinae. The labral rod in *B. thienemanni* is strikingly similar to that seen in the Podonominae and Aphroteniinae and is quite unlike the structure which occurs in some Orthocladiinae. The presence of two chaetulae laterales, one simple and one trifid, is very reminiscent of the situation in *Podochlus* and *Parochlus* as indicated by Brundin (1966; figs. 32, 33). These features indicate a relationship with the Podonominae + Aphroteniinae and the characteristic development of the SII setae in particular (which has reached its greatest expression in the Aphroteniinae) is synapomorphic for the Buchonomyiinae + Podonominae + Aphroteniinae. A plesiomorphic feature of the larva of *Buchonomyia* is seen in the retention of a large number of setae on the procercus, a character which the Buchonomyiinae shares with the Podonominae and Tanypodinae although the procercus in Aphroteniinae is greatly modified with a secondary reduction in the number of procercal setae.

Revised phylogenetic position of Buchonomyiinae

Brundin (1966, 1976) has given ample evidence to show the monophyly of the Tanypodinae + Podonominae + Aphroteniinae. The principal synapomorphic features identified by Brundin (op. cit.) are (1) the presence in the male of a ring-shaped ninth tergite resulting from the fusion of tergal and sternal elements and (2) the loss of the larval premandible. Saether (1977) gives further related evidence in females of these subfamilies where fusion of tergal and sternal elements of T IX has resulted in the formation of a gonotergite. It is apparent from the foregoing discussion of adult and larval characters of *B. thienemanni* that the Buchonomyiinae should also be included with this group of subfamilies. The only disadvantage of this placing is the fact that the presence of the anal point on the female S VIII, which is also indicated in some Telmatogetoniinae, is ignored. However the weight of evidence would suggest a relationship closer to the Podonominae + Aphroteniinae + Tanypodinae rather than to the Telmatogetoniinae. It seems that the development of the anal point might best be considered a parallel or convergent trend.

The question now arises as to the position of Buchonomyiinae within this enlarged monophyletic unit. Brundin (1966, 1976) has shown that the Aphroteniinae is the apomorph sister group of the Podonominae and that the Tanypodinae is the sister group of the Podonominae + Aphroteniinae. Saether (1977) provides supportive evidence. The large number of plesiomorphic features in *Buchonomyia* suggests that it occupies a plesiomorphic position within this phylogenetic unit. Autplesiomorphies within Buchonomyiinae are: double gonostyli articulating separately with the gonocoxite, setae present on first axillary sclerite and the pupal abdominal chaetotaxy.

According to Brundin and Saether (1978: 274) vein R2+3 is absent in the Telmatogetoniinae, Buchonomyiinae, Podonominae and Aphroteniinae and several small Tanypodinae, Orthocladiinae and Chironominae. The loss of R2+3 in small Tanypodinae, Orthocladiinae and Chironominae is probably due to their small size as a consequence of which less wing area and wing support (i. e. wing veins) are necessary for normal flight. In the Telmatogetoniinae, which are relatively large species, the loss of R2+3 is apparently due to the extreme harshness of their environment where, in the male, the wings are rarely used and the legs are strongly developed for walking but in the female, the wings and legs may be so reduced that they are incapable of flight or walking. Brundin and Saether (1978: 274) state that there is good reason for regarding the loss of R2+3 as synapomorphic for the Podonominae + Aphroteniinae with outside parallelism for the other groups. In *B. thienemanni* R2+3 is absent but in *B. burmanica* a vestige is said to be present although Brundin and Saether (1978: 273) regard this vein as absent in the diagnosis for Buchonomyiinae. Since both species of *Buchonomyia* are relatively large with well developed wings there are valid grounds for considering the loss of R2+3 as synapomorphic for the Buchonomyiinae+ Podonominae + Aphroteniinae. The Tanypodinae, because of the presence of R2+3 and other evidence in the trends, would then be the apomorphic sister group of the Buchonomyiinae + Podonominae + Aphroteniinae.

Cladogram of chironomid subfamilies

Incorporation of the existing knowledge on trends within the Chironomidae with the new interpretation given in this paper allows the construction of a cladogram of phylogenetic relationships of the chironomid subfamilies (Fig. 4). Most of the trends which are used here are taken from Saether (1977), Brundin and Saether (1978) and Brundin (1983a) although some are used for the first time (a = apomorphic; p = plesiomorphic).

Trends 1.

Gonapophysis VIII of female shows capacity for division into two principal lobes (a); never shows such a capacity (p). Capacity for development of an apodeme lobe (a); apodeme lobe never present (p). Male antenna with less than 14 flagellomeres (a); with 14 or more flagellomeres (p). Male antenna with apical flagellomere very elongated (a); apical flagellomere short (p).

Trends 2.

Male tergite IX fused with laterosternite IX (and sternite IX) (a); laterosternites IX and/or sternite IX separate (p). Female gonocoxite IX reduced and fused with tergite IX to form a gonotergite IX (a); gonocoxite IX not reduced or if reduced not fused with tergite IX (p). Larval premandible absent or strongly reduced (a); always present and well developed (p).

Trends 3.

Labia of female genitalia fused (a); separate (p). Body of larvae without sclerotised plates bearing setae (a); with such plates (p).

Trends 4.

Segment X of female reduced (a); well developed (p). Common opening of spermathecal duct conspicuously wide (a); openings separate or, if common, opening narrow (p). Crossvein MCu absent (a); present (p).

Trends 5.

Female sternite VIII with caudal projection (a); without (p). Crossveins close to base (a); more distal (p).

Trends 6.

First axillary sclerite without setae (a); with setae (p). Wings with lanceolate setae (a); without lanceolate setae (p).

Trends 7.

Gonotergite IX reduced to a narrow strap without or with very few setae (a); well developed, hood-shaped, with numerous setae (p). Glossae of larva fused, forming a large, sclerotised ligula which is more conspicuous than the mentum (a); glossae small, inconspicuous, not forming a large sclerotised ligula (p). Larval antennae retractile (a); non-retractile (p).

Trends 8.

Larval labral rod present (a); labral rod absent (p). SII of larval labrum developed as simple, long stout and curved sensillae arising from well developed erect pedestals (a): SII otherwise (p). (Parallel development seen in some *Harnischia*-complex, Chironominae, genera). R2+3 absent (a); present (p).

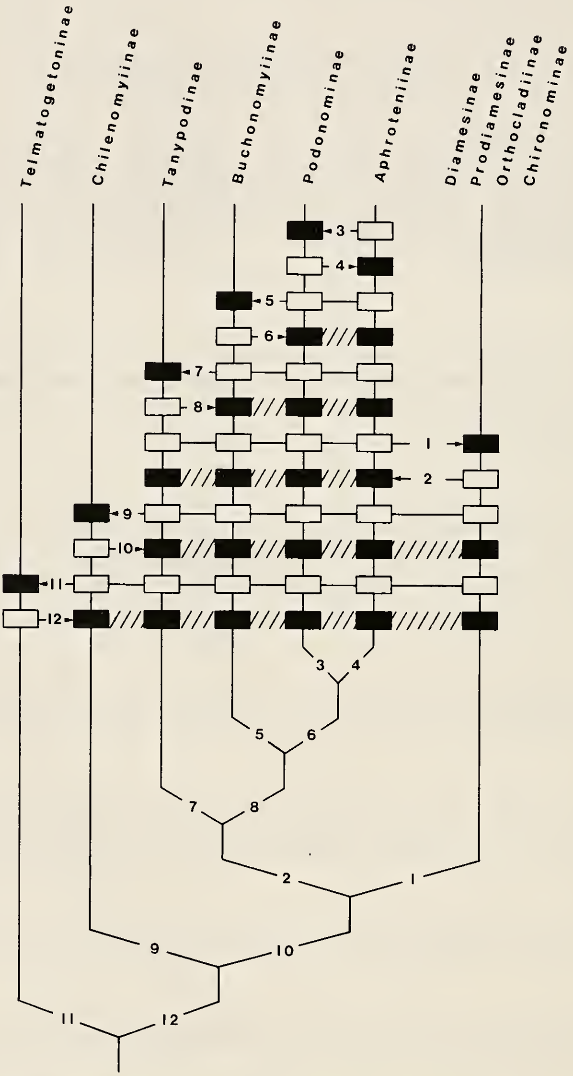


Fig. 4: Revised cladogram of Chironomid phylogeny.

Trends 9.

Male gonostylus rotated through 90° (a); gonostylus in normal position (p). Male gonostylus forms a clasper together with apical end of the gonocoxite (a); gonostylus forms a clasper against the middle or basal part of the gonocoxite (p).

Trends 10.

On each side of male tergite IX a simple sclerite (laterosternite) that is sometimes fused with the tergite and rarely carries a membranous rudiment of a non-clasper gonocoxite (a); on each side of male tergite IX a separate, very large, lobe-shaped non-clasper gonocoxite (p). Female gonocoxite IX of small to moderate size, not reaching tip of cercus, or reduced and fused with tergite IX to form a gonotergite IX that rarely carries a small membranous lobe as a rudiment of the gonocoxite (a); gonocoxite IX very large reaching tip of cercus and carrying numerous strong setae (p).

Trends 11.

Tergite VIII and gonocoxite IX of female reduced (a); well developed (p). Seminal capsules reduced, spermathecal ducts serve as seminal storage organs (a); seminal capsules present and well developed (p).

Trends 12.

Gonapophysis VIII relatively short, single or divided (a); very large, elongate (p). Gonosternite IX absent (a); present (p).

General conclusions

In the foregoing sections the Buchonomyiinae has been considered the plesiomorphic sister group of the Podonominae + Aphroteniinae thus removing it from its previous position, indicated by Brundin and Saether (op. cit.), as the plesiomorphic sister group of the monophyletic unit Diamesinae + Prodiamesinae + Orthocladiinae + Chironominae. The Tanypodinae now forms the apomorph sister group of the Buchonomyiinae + Podonominae + Aphroteniinae. Brundin (1983 a) indicated that the Chilenomyiinae forms the sister group of the eight above mentioned subfamilies. The Telmatogetoniinae is regarded as the sister group of all the other chironomid subfamilies (Saether 1977). This revised interpretation of chironomid phylogeny returns the Buchonomyiinae to a position indicating a close relationship with the Podonominae, a view first suggested by Fittkau (op. cit.) in the initial description of the genus.

Acknowledgements

We wish to express our thanks to: Dr. P. S. Cranston, British Museum (Natural History), London for discussion on aspects of this paper; Mr. B. Cregg, SEM Unit, Department of Agricultural Zoology, University College Dublin for advice in preparation of specimens for scanning and Mr. R. French, Senior Technician, Department of Zoology, University College Dublin who carried out the scanning electron microscopy and prepared the photographic plates. A Praeger Grant awarded to P. Ashe to defray field expenses during July and August 1981 in the Killarney region is gratefully acknowledged.

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Zeitschrift/Journal: Spixiana, Zeitschrift für Zoologie, Supplement

Jahr/Year: 1984

Band/Volume: 011

Autor(en)/Author(s): Murray Declan A., Ashe Patrick

Artikel/Article: A description of the adult female of Buchonomyia thienemanni Fittkau and a re-assessment of the phylogenetic position of the subfamily Buchonomyiinae (Diptera, Chironomidae) 149-160