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A description of the pupa of Buchonomyia thienemanni Fittkau, with notes on its ecology and on the phylogenetic position of the subfamily Buchonomyiinae

(Diptera, Chironomidae)

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Abstract

Pupae of *Buchonomyia thienemanni*, recently found in Ireland are described in this paper. The pupae exhibit mainly plesiomorphic features but the nature of the attachment of the pharate adult tracheal system to the pupal integument is, apparently, synapomorphous with the Orthocladiinae and Diamesinae. However, in the adult male abdomen, the laterosternite IX and sternite IX are reduced and a gonotergite is indicated, i. e. synapomorphic with the Tanypodinae + Aphroteniinae + Podonominae. As a result of this conflicting evidence a definitive phylogenetic placement of Buchonomyiinae may have to await discovery of the larva. The genus *Buchonomyia* occurs in lotic waters and exuviae have been examined from England, Iran and Ireland.

Introduction

The occurrence of adult males of *Buchonomyia thienemanni* Fitt. adjacent to the River Flesk, near Killarney, Ireland, was noted by Murray (1976). During further investigations in this region, mature pupae, pupal exuviae and imagines have been obtained and descriptions of the pupa forms part of this paper. The phylogenetic placement of *Buchonomyia* has been problematical since the genus was first described by Fittkau (1955). A second species, *B. burmanica* Brund. et Saeth., has recently been described and a new subfamily erected for the genus (Brundin and Saether 1978). The new subfamily was designated the sister-group of the subfamily-group Chironominae + Orthocladiinae + Prodiamesinae + Diamesinae on the basis of synapomorphies of the female imago (Brundin and Saether 1978; Saether 1979a, b). Examination of the adult male of *B. thienemanni* together with the pupa, suggests, however, that the problem relating to the phylogenetic placement of Buchonomyiinae is not yet fully resolved.

Methods

Adults were mounted on slides according to the methods of SCHLEE (1966). Pupal exuviae, obtained in drift nets from the River Flesk, were preserved in 70% alcohol and slide mounted in Eupa-

ral. The terminology used in the description follows SAETHER (1971) and HIRVENOJA (1973). Voucher specimens are deposited in the Natural History Division, National Museum of Ireland, Dublin, 2.

The pupa of Buchonomyia thienemanni Fittkau

(n = 10). Total length 5.22-6.66 (5.98) mm, exuvium heavily sclerotised and dark brown in colour.

Cephalothorax (Fig. 1a, b, plate 1a). Frontal setae well developed, 331–414, (379) µm long, on tubercles arising from the frontal apotome; vertex seta 1 and one setal scar on dorsal edge of the ocular field; post ocular setae 2 and one setal scar (Sc); sub ocular seta 1 at base of palp sheath adjacent to the pre-frons. Antennal sheath much expanded and projecting anteriorly at base (corresponding to the region of the pedicel which is much

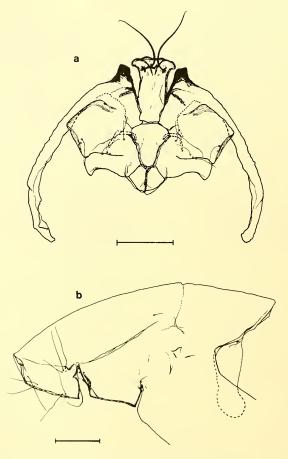


Fig. 1. B. thienemanni, pupa: a) frontal plate, ventral; b) thorax, lateral (Scale: 300 μm).





Plate 1. B. thienemanni pupa: a) anterior part of cephalothorax (lateral), b) anal lobe.

expanded in female *Buchonomyia thienemanni*). The male pupae of *B. thienemanni* also possess this process on the antennal sheath but the pedicel of the male antenna is not expanded. Thoracic horn absent. Pharate adult tracheal tube attached to a sclerotised ridge on the pupal integument at the posterior border of the pre-corneal slit aperture which opens to a thin walled internal chamber. The tracheal tubes apparently end blindly. (Additional pharate adult tracheal attachments to the pupal skin are evident as one pair posterior to the wing sheaths, one pair in each of abdominal segment I-VII attached laterally at the base of the "robust spine" and one pair on the posterior dorsal intersegmental region between segment VIII and IX). Precorneal setae (PcS) 3, lengths in µm, PcS₁, 140–214 (181); PcS₂, 254–291 (277); PcS₃, 254-268 (263). Setal scar present between PcS₁ and PcS₂, 1 dorsocentral seta, 1 supra alar seta with 1 setal scar, 2 metanotal setae with 1 setal scar, 3 median pronotal setae and 2 lateral pronotal setae. "Pearl row" present on posterior margin of wing sheaths.

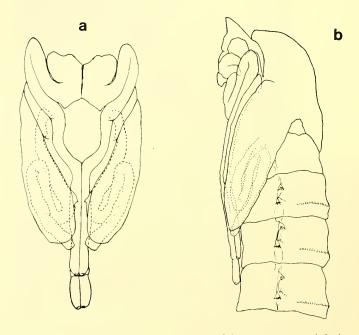


Fig. 2. B. thienemanni, leg sheath arrangement of the pupa; a) ventral, b) lateral.

Leg sheath arrangement (Fig. 2a, b). Fore and mid sheath directed backwards, sheath of the fore leg reaching the anterior border of abdominal segment IV, and lying directly ventral to the sheaths of the mid-legs which reach to the middle of segment III. Tarsal portion of hind leg sheath recurved and bent in S-like fashion beneath the distal half of the wing sheath and terminally medially directed.

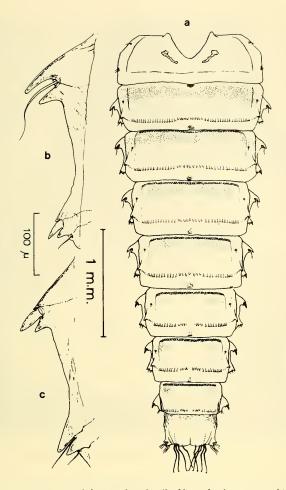
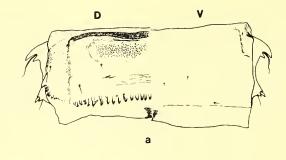


Fig. 3. B. thienemanni, pupa: a) abdomen; b-c detail of lateral spine groups, b) seg. V, c) seg. VI.

Abdomen (Fig. 3a-c; 4a, b, plate 1b). Segment I devoid of shagreen. A continuous transverse band of shagreen extends over to the anterior third of tergite II. A slightly narrower band on tergites III and IV in association with a progressive reduction in the median field. On tergites V to VII shagreen is present in two areas only, i. e. the lateral fields. Posterior margins of tergites II to VIII with well developed single row of spines extending to the lateral borders. All sternites are devoid of shagreen. Lateral regions provided with characteristic robust spines and setae. On each of segments II to VII the anterior spines are more robust, while on segment VIII the posterior spine group is absent. The detailed structure of these processes varies in association with the arrangement of lateral setae (LS) as follows: Sg I with 3 LS, Sg II to VII with one dorsally situated on the anterior fourth (i. e. LS₁). Sg II with one anterior and one posterior couplet of robust



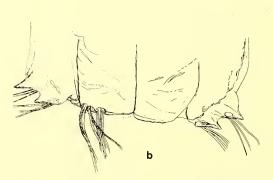


Fig. 4. B. thienemanni, pupa: a) chaetotaxy on seg. IV, (D = dorsal, V = ventral); b) anal lobe.

spines, between the anterior couplet one seta – (LS_2) , between the posterior couplet 1 seta (LS_3) and an additional seta (LS_4) immediately posterior to the spines. On segment III-V the posterior spine couplet differs and LS_3 is apparent as an articulating spine (Fig 3 b). Evidence that this articulating spine is LS_3 is seen by the presence of a "dendrite" running to the base of the spine, a similar "dendrite" runs to the base of all LS setae of B. thienemanni whether normal or modified. On segments VI and VII the anterior spine couplet is modified, i. e. LS_2 is spine like and articulates, while in the posterior couplet LS_3 and LS_4 are normal and have an arrangement similar to that on segment II (Fig. 3 c). On segment VIII the anterior, dorsally situated LS_1 is apparently absent, the anterior spine couplet resembles that on segments VI and VII. The posterior couplet, present on segments II to VII is reduced to a chitinised protruberance on Sg VIII from which LS_3 arises, while LS_4 occupies a slightly dorsal position.

Setae of the anal segment arranged in two groups. Posterior lateral corner with two chitinised spurs and at the base of each a group of 2–3 setae i. e. 4–6 setae on either side. On the posterior border 8 macrosetae in the arrangement 2+3+3 in progression from the



Plate 2. B. thienemanni: male hypopygium, lateral.

lateral to the median area. The setae are characteristically bent (wavy?, sensu Brundin 1966) in the basal half and distally are hook shaped. A summary of the chaetotaxy of abdominal tergites is given - Table 1. Sexual dimorphism present, $\mathcal Q$ sternite VIII with two ventral caudally projecting lobes, such lobes absent in the $\mathcal O$.

Lateral

Seg.	Dorsal	Normal	"Spine"	Ventral	Total
I	5 + 2Sc	3	0	1	9
II	5 + 2Sc	4	0	3 + Sc	12
III	4 + 2Sc	3	1 Posterior	3 + Sc	11
IA	4 + 2Sc	3	1 Posterior	3 + Sc	11
Λ	4 + 2Sc	3	1 Posterior	3	11
VI	4 + 2Sc	3	1 Anterior	3	11
VII	4 + 2Sc	3	1 Anterior	2 + Sc	10
VIII	2	2	1 Anterior	1	6

Table 1 -

Summary of pupal abdominal chaetotaxy, B. thienemanni. Sc: Setal scar.

B. thienemanni male

The new material of *B. thienemanni* allows the following additional comments to be given to the original description by FITTKAU (1955) – median furrow is indicated on the postnotum. The legs were incomplete on the type specimen and the measurements and ratios of the legs from the Irish material are given in Table II.

Hypopygium: Sternite IX and laterosternite IX reduced and fused. In dorsal view a simple posterior contour is evident as in the Podonominae, a consequence of the formation of a gonotergite IX. (Tergite IX is not divided in a basal, median and caudal part as indicated by Brundin and Saether for *B. burmanica*, the basal part referred to in *B. burmanica* is tergite VIII). Dorsal portion of the gonostylus with 4 apical setae and 3 distal setae (Plate 2).

Ecology

In the absence of the larva it is not possible to give the full ecology of *B. thienemanni*. Pupal exuviae have been obtained regularly from the River Flesk during the months July to September; maximun occurrence is in late July and early August. It appears to be a univoltine summer-emerging species. During a 24 hours period on 27/28 July, 1976,

Table II: Leg measurements (µm) and ratios of male B. thienemanni (range and mean values).

	221	188	215				
Tm5	212-235, 221	188	211-224,				
	344	233	300				
Tm4	329-353,	224-247, 233	294-306,				
	438	306	406		89	89	17
Tm ₅	-447,	-318,	.412,	~	3.20-4.05, 3.68	5.83-6.05, 5.89	4.49-7.85, 6.17
	435	294	, 400	BR	20-4.0	33-6.0	3-7-61
	, 597	, 421	, 597		3.5	5.8	4.4
Tm ₂	576-612	400-447, 421 294-318, 306	576-612		2.05-2.09, 2.07	2.90-2.92, 2.91	2.50-2.57, 2.53
	924	718	1068	BV	-2.09,	-2.92,	-2.57
Tm ₁	871-976,	682-753, 718	035-1106,				
	356		647 1		2.58	3.65	2.59
Тi	1313-1388, 1356 871-976, 924 576-612, 597 435-447, 438 329-353, 344	1282-1388, 1332	1576-1718, 1647 1035-1106,1068 576-612, 597 400-412, 406 294-306, 300 211-224, 215	SV	2.52-2.66, 2.58	3.59-3.74, 3.65	2.57-2.60, 2.59
			6 15			4	
	, 1030	, 1292	, 1126		, 0.68	, 0.5	, 0.6
E4 O	P ₁ 1000-1078,	1270-1318,	1094-1163,	LR	0.66-0.70,	P ₂ 0.53-0.55, 0.54	P ₃ 0.64-0.66, 0.65
	F L	P ₂	Б3		ъ Т	P ₂	P 3

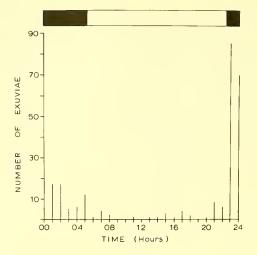


Fig. 5. Numbers of *B. thienemanni* pupal exuviae obtained in 24 successive hour long driftnet collections from the R. Flesk, 27-28/VII/'76. Shading on horizontal bar indicates hours of darkness.



Fig. 6. Known geographical distribution of Buchonomyiinae.

twenty-four successive collections of surface drift, each lasting one hour, were made in the River Flesk. A total of 247 exuviae of *B. thienemanni* was obtained for the diel. The greatest number was obtained in the two hour period after dusk and few exuviae were obtained in daylight hours (Fig. 5). The overall percentage number of male and female exuviae obtained was 51% and 49% respectively. However, within the two hour period of maximum emergence (from 22.00 hours to 24.00 hours) a greater number of females emerged during the first hour (58% $\mathbb Q$ and 42% $\mathbb C^3$), whereas males predominated during the second hour (67% $\mathbb C^3$ and 33% $\mathbb Q$). Adult males form small composite swarms under overhanging branches adjacent to and over the river. Swarms have been obeserved at heights varying form 1.0 to 5.0 metres above the ground.

The geology of the area is Lower Carboniferous Limestone and Old Red Sandstone. Rainfall is relatively high varying with altitude in the catchment from 1263 mm yr⁻¹ at 60 m.a.s.1. to 3000 mm yr⁻¹ at 700 ma.s.1. Mean winter and summer air temperatures in the area are 6.0°C and 14.0°C respectively. In the period April, 1978 to March, 1979, minimum and maximum water temperatures recorded at the site where *B. thienemanni* occurs, at 120 m.a.s.l., were 5.5°C and 16.0°C respectively.

Distribution

Two species of the genus *Buchonomyia* occur in the northern hemisphere (Fig. 6). *B. thienemanni*, first recorded by FITTKAU (1955) from the Wasserkuppe region of the Fulda at 800 m.a.s.l. has subsequently been recorded from the River Flesk, Ireland (Murray 1976), between 20–120 m.a.s.l. and the River Exe, England (Wilson, pers. comm.). Pupal exuviae exhibiting slight morphological differences from *B. thienemanni*, have been taken from the River Zyanderhud, Central Iran (Dowling, 1980). *B. burmanica* is recorded, as adults only, from the Kambaiti region (2380 m.a.s.l.) Northern Burma (Brundin and Saether l.c.).

Phylogenetic placement of Buchonomyiinae

The genus *Buchonomyia* was first placed by FITTKAU (1955) within the Podonominae. Brundin (1966) suggested it may belong to the Orthocladiinae, a placing also adopted by FITTKAU, Schlee and Reiss (1967), and tentatively indicated by FITTKAU and Reiss (1978). Saether (1977, 1979 a) associated *Buchonomyia* with the monophyletic group Chironominae + Orthocladiinae + Diamesinae + Prodiamesinae. In a recent description of male and female of a new species of *Buchonomyia*, *B. burmanica* Brund. et Saeth, Brundin and Saether (1978) erect a new subfamily Buchonomyiinae. That *Buchonomyia* warrants the status of subfamily is beyond question, however, the position of this subfamily forming the sister group of Chironominae + Orthocladiinae + Diamesinae + Prodiamesinae, as suggested by Brundin and Saether (l. c.), is less clear.

An account of the apomorph and plesiomorph features in Buchonomyiinae has been given by Brundin and Saether (l. c. p. 273). Some of the points trated by these authors, however, require modification, and evidence form the examination of *B. thienemanni* could suggest an alternative phylogenetic placement. The general morphology of *Bu*-

chonomyia in both pupa and adult is plesiomorph. Such plesiomorph characters as the leg sheath arrangement of the pupa; male and female antennae with 14 flagellomeres; setae on the scape, pedicel and postnotum; and persistence of open spiracles on five abdominal segments are of little help phylogenetically. Brundin and Saether state (l. c. page 273) "the male imago, however, shows no apparent apomorphies of the hypopygium" and cite the presence of sternite IX and laterosternite IX in B. burmanica as plesiomorph features. Although the presence of such structures would indicate plesiomorphy, in B. thienemanni both sternite IX and laterosternite IX are clearly reduced and fused. This apparent conflict in the two species is due to a misinterpretation of the posterior abdominal segments in B. burmanica. It now appears that the structure referred to as sternite IX in the male B. burmanica is not sternite IX but is sternite VIII, and that both sternite IX and laterosternite IX are reduced and fused in B. burmanica as is the case in B. thienemanni.

In the female *B. burmanica* gonocoxite IX was regarded as separate from and not fused with tergite IX, but, as indicated by Brundin and Saether (l. c. p. 273), "the division line between the two is very faint". From observation of the female *B. thienemanni* it appears that gonocoxite IX may be reduced and fused with tergite IX to form a gonotergite IX, but further study is required to clarify this viewpoint. This interpretation of the arrangement of the posterior abdominal segments in both male and female *Buchonomyia* would confer apomorph rather than plesiomorph status on the characters and consequently would indicate an approach to chironomid phylogeny at the subfamily level differing from that suggested by Brundin and Saether.

A unifying apomorphic feature in the Tanypodinae + Aphroteniinae + Podonominae is the presence in the adult male of a simple ring-shaped ninth abdominal segment which is a consequence of the fusion of tergal and sternal elements (Brundin, 1966, 1976). It is evident from the above discussion that a ring-shaped ninth abdominal segment is also present in Buchonomyiinae, thus indicating it may form part of the monophyletic group Tanypodinae + Aphroteniinae + Podonominae on the basis of this common apomorphic condition of the ninth segment. Conflicting evidence is apparent in the nature of the pharate adult tracheal connection to the pupal integument. Coffman (1979) has drawn attention to the potential use of this character in chironomid phylogeny. The presumed plesiomorph condition is to be found in the Tanypodinae + Aphroteniinae + Podonominae (and Telmatogetoninae?) where the pupal respiratory organ is attached directly to the pharate adult tracheal system. In the remaining subfamilies the apomorph alternative of either an indirect connection or no connection between the two structures is apparent. Buchonomyia does not have a respiratory organ but the pharate adult tracheal tubes end blindly on a sclerotised ridge posterior to the pre-corneal slit. This arrangement is similar to that in the subfamilies Orthocladiinae and Diamesinae where no connection is evident and is also quite similar to the situation seen in Cardiocladius (Irish material) which also lacks a respiratory organ.

Thus, conflicting evidence of apomorph characters are seen in *Buchonomyia*. The results presented by Brundin and Saether (1978) suggests placement of Buchonomyiinae with Chironominae + Orthocladiinae + Prodiamesinae + Diamesinae as does the new evidence from the pupal tracheal connection. In contrast, the revised interpretation of the terminal segments of the male abdomen discussed above shows the apomorph reduction of sternite IX and laterosternite IX as a character pointing towards affiliation with Tanypodinae + Aphroteniinae + Podonominae. Such incongruities of opposing apo-

morph trends are known to occur in the Chironomidae (SAETHER 1979b) and a final solution to the phylogenetic placement of Buchonomyiinae may have to await determining the presence or absence of the pre-mandible in the as yet unknown larva.

Zusammenfassung

Die Beschreibung der Puppe von Buchonomyia thienemannni Fittkau mit Anmerkungen zu ihrer Ökologie und zur phylogenetischen Stellung der Unterfamilie Buchonomyiinae.

(Diptera, Chironomidae)

Die Puppe von Buchonomyia thienemanni, die kürzlich in Irland gefunden wurde, wird hier beschrieben. Die Puppe zeigt hauptsächlich plesiomorphe Merkmale, jedoch ist die Befestigungsart des pharaten adulten Tracheensystems mit dem Puppenintegument offenbar synapomorph mit den Orthocladiinae und Diamesinae. Im adulten männlichen Abdomen sind die Laterosternite IX und die Sternite IX reduziert und ein Gonotergite deutet auf die Synapomorphie mit den Tanypodinae + Aphroteniinae + Podonominae hin. Eine Lösung dieses Konfliktes zur gesicherten phylogenetischen Stellung von den Buchonomyiinae mag man von der Entdeckung der Larve erwarten. Die Gattung Buchonomyia tritt in lotischen Gewässern auf und Exuvien sind aus England, dem Iran und Irland untersucht worden.

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