ERETMOPTERA MURPHYI SCHAEFFER (DIPTERA: CHIRONOMIDAE), AN APPARENTLY PARTHENOGENETIC ANTARCTIC MIDGE

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ABSTRACT. Chironomid midges are amongst the most abundant and diverse holometabolous insects of the Antarctic and sub-Antarctic. *Eretmoptera murphyi* Schaeffer, 1914, has been enigmatic to systematists since the first discovery of adult females on South Georgia. The rediscovery of the species as a suspected introduction to Signy Island (South Orkney Islands) allows the description of the immature stages for the first time and the redescription of the female, the only sex known. *E. murphyi* larvae are terrestrial, living in damp moss and peat, and the brachypterous adult is probably parthenogenetic. *Eretmoptera* appears to have an isolated position amongst the terrestrial Orthocladiinae: the close relationship with the marine *Clunio* group of genera suggested by previous workers is not supported.

INTRODUCTION

In the Antarctic and sub-Antarctic regions, the Chironomidae (non-biting midges) are the commonest, most diverse and most widely distributed group of holometabolous insects. For example, *Belgica antarctica* Jacobs is the most southerly distributed free-living insect (Wirth and Gressitt, 1967; Usher and Edwards, 1984) and the podonomine genus *Parochlus* is found throughout the sub-Antarctic islands. Recently, Sublette and Wirth (1980) reported 22 species in 18 genera belonging to 6 subfamilies of Chironomidae from New Zealand's sub-Antarctic islands.

One sub-Antarctic midge that has remained rather enigmatic since its discovery is *Eretmoptera murphyi*. Two females of this brachypterous chironomid were collected by R. C. Murphy from South Georgia in 1913 and described, together with other insects, by Schaeffer (1914). The generic placement of the species followed Kellogg's (1900) excellent description of the male and female of *Eretmoptera browni*, a brachypterous chironomid collected from the Californian intertidal shore. Schaeffer (1914) listed several characters that his species shared with the then monotypic *Eretmoptera*, but he expressed some reservations about the generic placement, which he believed would be resolved by the discovery of males of *E. murphyi*.

Edwards (1926), relying on Schaeffer's original description, suggested that *E. murphyi* was a synonym of *Belgica antarctica*, but later (1931) retracted this opinion. In a footnote in his 1931 paper, Edwards mentioned that he had seen a female pupa and larvae of *E. murphyi*, but the brief note on the procerci of the larvae indicates that his identification was incorrect and he had larvae of a podonomine, probably *Parochlus steinemi* – the commonest chironomid on South Georgia (Brundin, 1970). The next reference to *E. murphyi* was by Wirth (1949) in a review of all genera of marine Chironomidae, but, like Edwards, Wirth had no material available to him when he considered the generic placement of *murphyi*. Although Wirth retained *murphyi* in *Eretmoptera*, he listed several characters that Schaeffer had not described, examination of which would be necessary to determine the correct generic placement. The only published record on material examined since the original description was from a collection made in South Georgia by the Bishop Museum and sent to Brundin for

identification. The short report mentioned female adults, female pupae and larvae of '*Eretmoptera*' *murphyi* collected from moss at low altitudes on South Georgia, but Brundin (1970) commented that 'the generic assignment seems highly questionable'.

Block, Burn and Richard (1984) report the discovery of a small population of chironomid (identified by the present author as '*Eretmoptera*' *murphyi* from Signy Island, in the South Orkney Islands, maritime Antarctic (60° 42′ S, 45° 38′ W). This site is small, about 1 m^2 in area, 13 m a.s.l. and was the place where plant introduction experiments had taken place in 1967. The authors believe that the species was accidentally introduced with plant material from either South Georgia or the Falklands or both. As in all previous collections of this species, no male was found.

Since lengthy series of larvae, female pupae and female imagines of this enigmatic species are now available, the opportunity is taken to describe the immature stages for the first time, to redescribe the female imago of *Eretmoptera murphyi* and to re-examine the systematic placement of *Eretmoptera*. The life history stages described below are associated through larval exuviae-pupa and pharate pupa. The terminology follows Saether (1980).

Eretmoptera murphyi Schaeffer

Eretmoptera murphyi Schaeffer, 1914: 91; Edwards, 1926: 789; Wirth, 1949:160.

DESCRIPTION. (Measurements in μm, unless stated otherwise; given as mean followed by range)

Female imago ($n = 10$) (Fig. 1).

Body length 4.3 (3.4–4.9) mm, wing length 807 (747–880), haltere length 126 (99–148). Medium brown with slightly darker vittae. Head: Antenna (Fig. 1b) with 5 flagellomeres, exceptionally with 3, of length: width–pedestal 48 (33–59): 68 (58–76); when five flagellomeres: 82 (72–99):46 (40–53); 55 (48–61):41 (36–49); 48 (41–56):39 (36–46); 48 (40–46):38 (33–43); 125 (105–140):39 (35–45); when 3 flagellomeres ($n = 1$): pedestal 50:59; flagellomeres 102:40; 92:36; 109:36 with some indication of median division of flagellomeres 1 and 2. Flagellomeres 1 to 5 with 2, rarely 3 apical sensilla chaetica, ultimate flagellomere with at least 2 lateral sensilla chaetica. Antennal ratio 0.55 (0.47–0.61). Temporal setae consist of 3–5 inner verticals in a group. Clypeus with 11 (6–16) scattered setae. Eyes rounded, not dorsally extended, with short microtrichia between facets. Palps 3- or 4-segmented, length:width —1st palpomere 24 (20–27):31 (26–33); 2nd palpomere 42 (36–49):40 (33–46); wh[illegible] 4-segmented ($n = 6$), 3rd palpomere 78 (56–89):46 (43–49), 4th palpomere 85 (66–105):38 (36–40); when 3-segmented ($n = 4$), 3rd palpomere 116 (99–129):44 (40–52). Palp apparently without sensilla chaetica. Tentorium weakly sclerotized, especially apically, and length difficult to determine.

Thorax with 3 or 4 strong, decumbent acrostichal setae starting a short distance behind the anterior of the pronotum. Antepronotum broad, lobes completely separated anterior to pronotum, each lobe bearing 2–3 lateral setae. Seventeen (12–24) strong dorsocentral setae arising from paler pits scattered on the mediolateral pronotum, distinct from 2–3 prealars and a single, isolated 'antescutellar' seta. Anapleural suture absent. Postnotum with weaker pigmented median band, but without distinct median furrow. Scutellum very narrow, reduced, bearing 4 (2–6) setae in a single line.

Wing strap-like, without venation, with dense microtrichia and a row of 7–10 setae

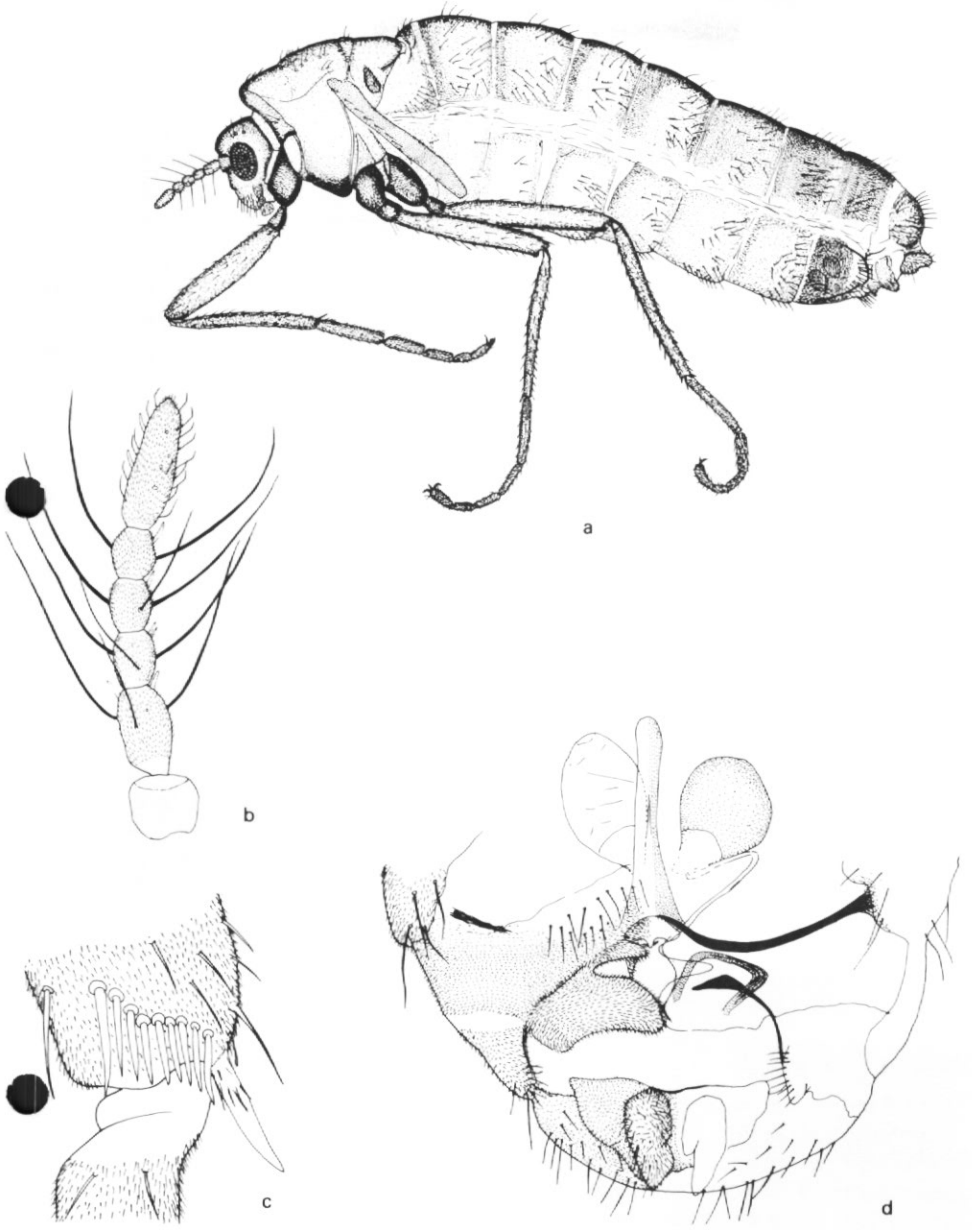

Fig. 1. *Eretmoptera murphyi*, adult female. a: Lateral view; b: antenna; c, comb on apex of tibia of hind leg (P3); d, genitalia, ventral view.

in a median line. Squama bare. Haltere quite strongly developed but without distinct neck region.

Legs strongly developed, lacking pseudospurs, sensilla chaetica and pulvilli. Empodium as long as the simple claws. P1 with single spur 33 (21–43) long, P2 usually with two spurs 30 (26–49) and 24 (10–33) long but inner, shorter spur sometimes

absent, P3 with two spurs 50 (42–59) and 20 (16–23) long. Comb on P3 (Fig. 1c) with 7–9 strong setae of maximum length 33 (30–40). Beard ratio less than 1 on all legs.

Leg lengths:

	Fe	Ti	Ta1	Ta2
P1	698 (630–778)	715 (606–813)	335 (261–381)	194 (141–216)
P2	763 (705–854)	743 (585–854)	329 (249–373)	186 (149–203)
P3	810 (705–929)	820 (697–954)	354 (290–440)	186 (166–216)

	Ta3	Ta4	Ta5	LR
P1	136 (112–150)	100 (79–116)	117 (99–133)	0.47 (0.43–0.49)
P2	131 (116–149)	89 (79–104)	115 (99–125)	0.44 (0.40–0.50)
P3	135 (116–154)	92 (83–108)	117 (104–136)	0.43 (0.38–0.46)

	BV	SV
P1	3.20 (3.03–3.47)	4.25 (4.00–4.74)
P2	3.54 (3.31–3.71)	4.60 (4.20–5.18)
P3	3.74 (3.61–3.86)	4.63 (4.28–5.21)

Abdomen. Tergites bare anteriorly, with uneven pattern of setae posteriorly, partially divided into median and lateral groups. Sternites also bare anteriorly, but more densely setose medially and laterally.

Genitalia (Fig, 1d). Tergite IX large, visible in ventral view, undivided but with setae arranged into two lateral groups with 25–38 setae in each group. Cerci 128 (100–161) long by 89 (69–105) wide. Gonocoxite IX poorly developed, bearing 3–6 long setae and a larger number of finer, shorter setae. Gonapophysis VIII divided into three distinct lobes; the ventrolateral lobe tongue-shaped, not covering either of the other two lobes or the vagina and labia; the dorsomesal lobe of rather similar shape to the ventrolateral lobe but smaller, with a dorso-basal extension linking to the well-sclerotized apodeme lobe. Gonocoxapodeme VIII evenly curved. Membrane round vagina and labia present but weakly sclerotized. Tergite X scarcely delimited. Two darkened oval seminal capsules, without microtrichia, with short, translucent neck region; of length 160 (158–198) and width 114 (92–132). Spermathecal ducts translucent, very difficult to see but with at least one convolution and ending separately, without bulbs, at the vagina. Notum distinctive, broad, bluntly rounded anteriorly, 246 (224–300) long.

Pupa ($n = 8$) (Fig. 2)

Total length 4.6 (4.0–5.0) mm, scarcely pigmented.

Cephalothorax (Figs 2a, b). Frontal setae weak, 34 (26–42) long, situated on frons. Ocular and postorbital setae absent. Antennal sheaths without pearl row. Cephalic area smooth. Thoracic horn absent. Antepronotum with 2 lateral setae 41 (33–49) long, reduced to a single seta in 1 specimen. Only 2 precorneal setae present, arising separately on a slightly elevated tubercle. Most anterior precorneal seta 40 (25–56) long, posterior precorneal seta 36 (25–59) long (another specimen has only 1 precorneal seta). Always only 3 dorsocentrals, although the distribution is very variable. The most anterior dc (1) is 25 (23–33) long and 82 (75–92), exceptionally only 46, from dc2. Posterior two dorsocentrals are both 21 (17–26) long and are usually separated from each other by 7–10 although exceptionally up to 49 apart. There is no trace of dc4. Suture weakly rugulose; antepronotal sheath rugose; wing sheath smooth, without pearl row. Leg sheaths arranged as usual in Orthocladiinae,

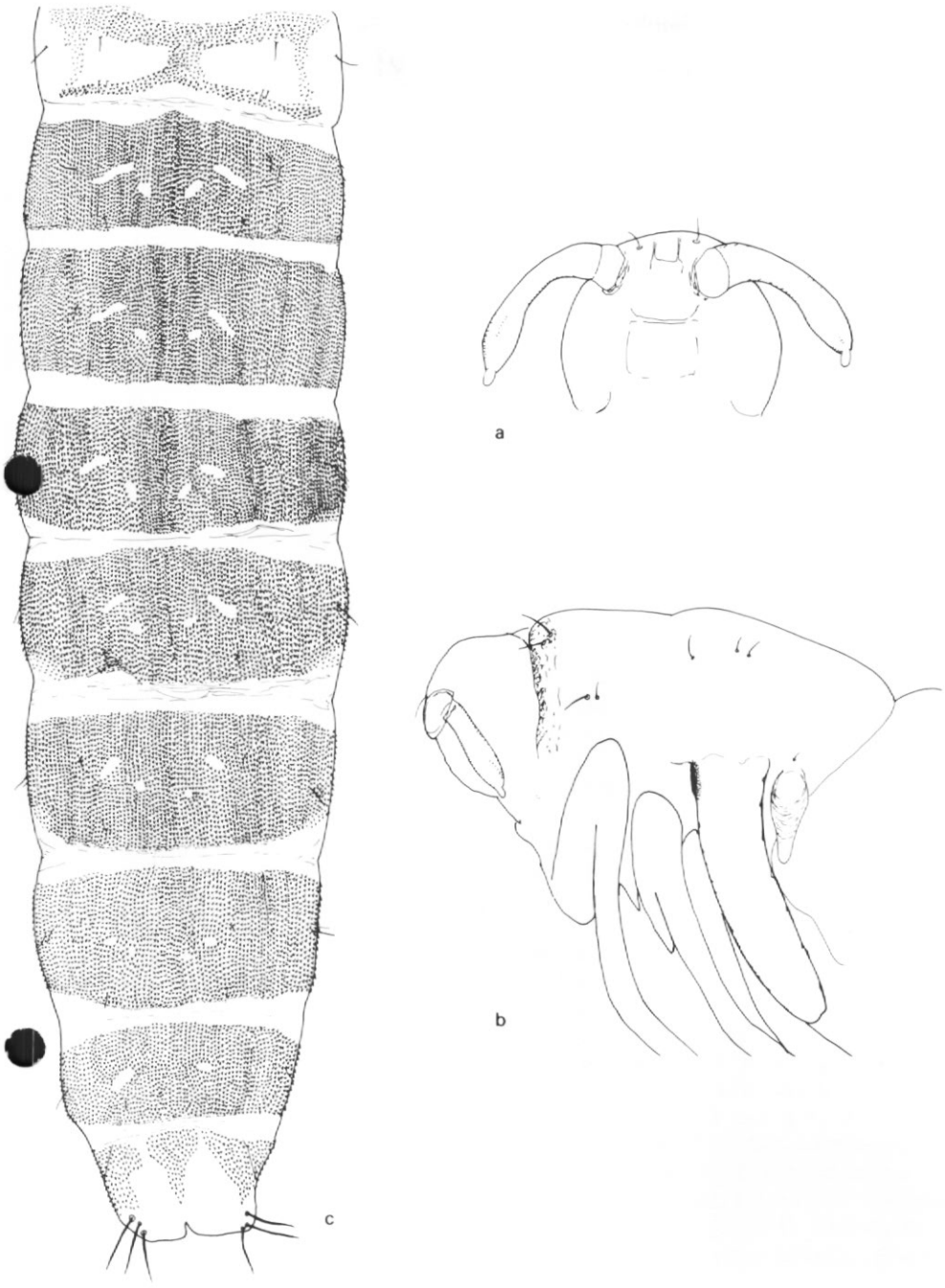

Fig. 2. *Eretmoptera murphyi*, pupa. a: cephalic area; b: cephalothorax, lateral view; c: abdominal tergites.

with all sheaths continguous and recurved beneath the thorax, extending to abdominal segment 3 or 4.

Abdomen (Fig. 2c). Tergite I with anterior and posterior bands of spinules, meeting medially. Tergites II to VIII covered with spinules except for paired muscle marks. Tergite IX and anal lobe with covering of spinules except for the posterior margin. Sternite I with only fine shagreen. Sternite II–VIII with finer spinules than on tergites but similarly arranged. Sternite IX with fine shagreen except on genital sacs. Conjunctives bare. All segments with 1 strong and 1 fine L setae, except for I and VIII which have only 1 strong L seta. Tergites with 3 very weak D setae except VII and VIII, which appear to have only 1 seta. Sternites I–VIII apparently with 2 fine V setae. O setae absent. Apophyses absent. Pedes spurii A and B absent. Sternite VIII with unusual paired ventral bulges, perhaps sheaths of protruding gonapophysis VIII. Genital sacs not overreaching anal lobe. Anal lobes heavily sclerotized, rugulose, squared off, with 3 macrosetae, lengths 145 (116–191), arising apicolaterally from separate tubercles. Macrosetae easily damaged but apparently with swollen apices.

Fourth instar larva ($n = 1$) (Fig. 3).

Body length 4.4 mm, preserved body colour yellow. Head capsule 514 μm, yellow, with slightly darker occipital margin, and dark brown mentum and apical half of mandible.

Antenna (Fig. 3a), five-segmented, less than half the mandible length, segment lengths 21, 11, 2, 2, 3.5. Antennal ratio 1.13. Antennal blade 25, overreaching flagellum; subsidiary style on subapex of segment 2, 3–4 long. Basal ring organ 12, proximal ring organ 17 respectively from base of segment 1. Lauterborn organs absent but two fine setae inserted (?) on apex of segment 2.

Labrum (Fig. 3b) with all S setae simple. S I, II and III lanceolate. S IV a small bisensillum. Two pectinate labral chaetae present. Labral lamellae absent. Pecten epipharyngis of three subequal rounded scales. Two or 3 chaetulae laterales, 2 chaetulae basales close to inner margin of ungula. Premandible 77 long, with 5 teeth, the innermost a distinct rounded bulge, without a brush.

Mandible (Fig. 3f). 165 long, apical tooth slightly longer than innermost of four inner teeth. Mola extended, bigger than innermost lateral teeth. Seta subdentalis absent, seta interna located on inner surface of mandible, with 3 or 4 simple branches. Inner and outer margin of mandible without crenulations or spines.

Mentum (Figs. 3c, d). 174 wide between bases of outermost of 5 pairs of lateral teeth. In unworn mentum (Fig. 3d) the paired median teeth can be seen to consist of a smaller lateral tooth adpressed to each median tooth, but in all other specimens wear has obscured this feature.

Maxilla (Fig. 3e). Palpiger short, clearly consisting of two parts, all sensillae short. Palpiger base and galea without chaetae or lamellae. Lacinia with a broad bulbous extension at base of 1 broad, triangular and 3 finer lacinial chaetae. Weak membranous appendix present. Pecten galearis absent.

Abdomen (Fig. 3g). Anterior and posterior parapods absent, without claws. Procerci absent, with no setae at the site. Anal tubules absent. Body setation minute.

Third instar larva ($n = 8$).

As fourth instar larva, except for the following measurements: Body length 4.2 (3.4–4.7) mm, head capsule 380 (340–412) ($n = 4$). Antennal lengths: 16.2 (14–18); 8.9 (7–10); 1.3 (1–1.5); 1.2 (1–1.5); 2.2 (1.5–3). Antennal ratio 1.2 (1.0–1.33). Blade

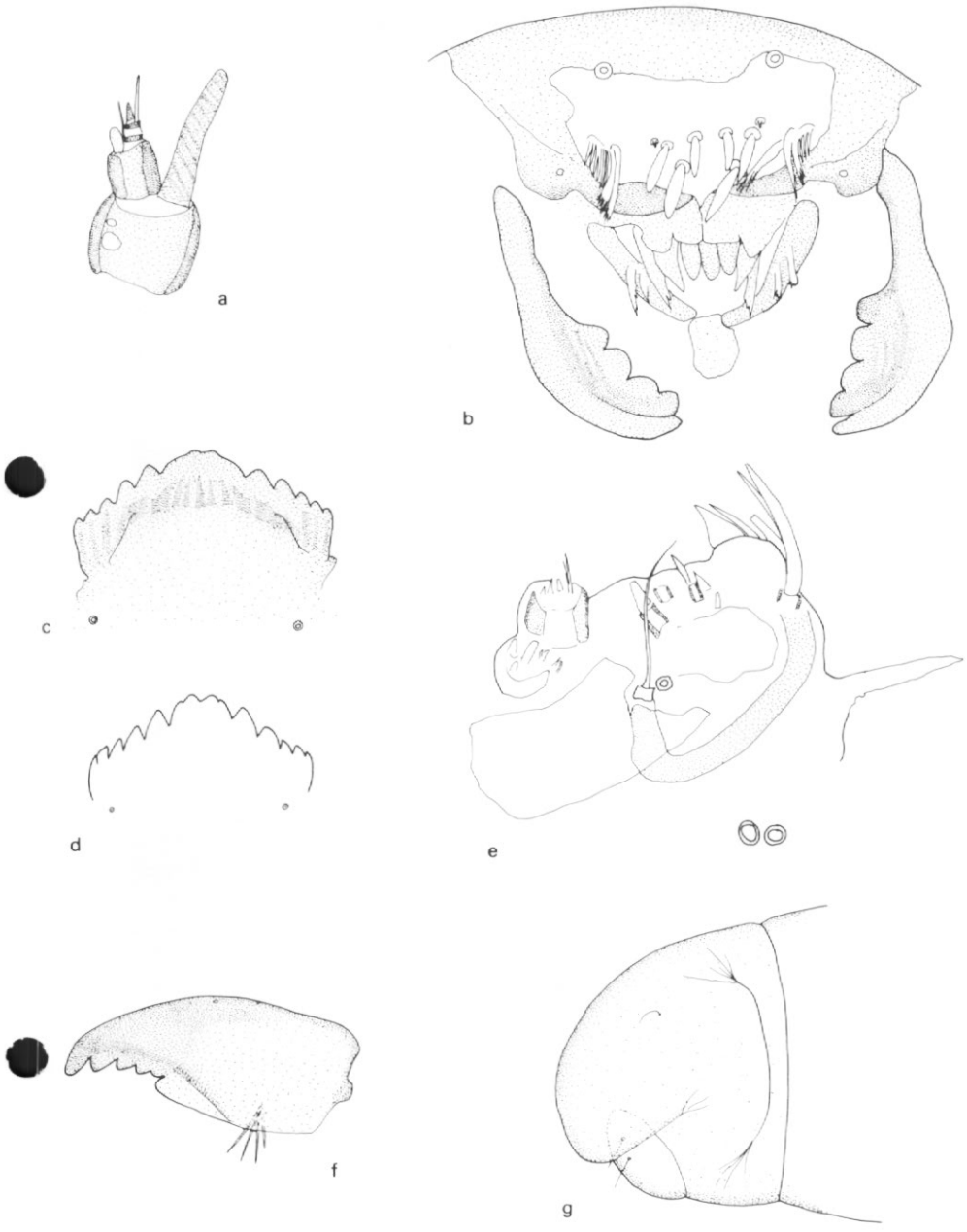

Fig. 3. *Eretmoptera murphyi*, larva. a: antenna; b: labrum; c, d: mentum (c, worn; d, unworn); e: maxilla; f: mandible; g: posterior abdominal segments.

19.8 (18–21), subsidiary style 2–3 long. Basal ring organ 5 (4–6), proximal ring organ 8 (6–10) respectively from base of first antennal segment. Labral SI, SII and SIII 12–14 long. Premandible 63 (60–65) long. Mandible 114 (106–120) long. Mentum 98 (90–109) wide.

Material Examined

Antarctica: South Orkney Islands, Signy Island, Factory Bluffs, near British Antarctic Survey station, 'austral winter 1980', A. J. Burn, and December 1981–January 1982, W. Block (British Antarctic Survey). Numerous larvae, pupae and female imagines collected in 80% ethanol and slide mounted in Berlese or Euparal. Deposited in British Museum (Natural History).

Antarctica: South Georgia Island, near Grytviken, January 1982, L. Sømme (British Antarctic Survey). Deposited in BMNH. Two female imagines slide mounted in Euparal.

Generic Placement

Both Schaeffer (1914) and Wirth (1949) believed that examination of the males of *Eretmoptera murphyi* would be necessary to place the species correctly. However, since all imagines discovered have been female (and pharate females within pupae), it is very likely that the species is parthenogenetic and males may never be found. The unavailability of males, however, does not prevent an assessment of the generic position of *murphyi*.

Wirth (1949) mentioned two characters of generic importance in which *murphyi* differed from *browni*, namely the bare eyes and six-segmented (five flagellomeres) female antenna, and two further characters that Schaeffer had not mentioned, namely the presence or absence of a tibial comb and the condition of the fifth tarsal segment. Examination of these characters reveals that Schaeffer was in error in describing the eyes as bare when they are pubescent with microtrichia between the ommatids. Although there are 'six antennal segments' in most specimens of *murphyi*, one example from South Georgia has only 'four segments' (three flagellomeres). Furthermore, examination of the legs of *murphyi* reveals that there is a hind tibial comb and that tarsomere 5 is longer than the preceding tarsomere on all legs, as in *browni*. Conclusive evidence that these species are congeneric should come from comparison of the female genitalia of the two species, but unfortunately the single syntypic female of *browni*, the only female of this species known, is in very poor condition. However, it can be seen that gonapophysis VIII is divided into lobes very similar to those of *murphyi*, and tergite IX is similarly constructed.

Although the information detailed above tends to confirm that the two species are congeneric, there remains a doubt. All information on the ecology of *E. murphyi* indicates that the larvae are terrestrial, living in damp moss and peat, yet, in contrast, *E. browni* has only been recorded from the intertidal zone. This latter observation needs to be confirmed, since no larva of *browni* has been found. Kellogg (1900) recorded that Brown, the collector of the type material, found a single pupa along with numerous adults on the surface of a tide pool, but the identity of this pupa has never been confirmed. Wirth (1949) found *E. browni* adults at the type-locality on only one occasion, and found no immature stage despite diligent searching. It remains a possibility that *E. browni*, like *E. murphyi*, is a terrestrial species living in habitats close to exposed marine shores.

It is ironic that re-examination of the adults and the discovery of the immature stages

of *E. murphyi* still does not allow decisive confirmation of the generic placement of the species, but must await similarly detailed study of all stages of *E. browni*. Notwithstanding the remaining doubt about the placement of *murphyi* in *Eretmoptera*, it is possible to discuss the phylogeny of the genus based upon *E. murphyi*.

Phylogeny

Apterous or brachypterous Diptera have often proved difficult to place systematically, and *Eretmoptera* is no exception. When first described, the genus was placed in a family of its own – the Eretmopteridae, of uncertain affinities within the Nematocera. By 1914, when Schaeffer described *E. murphyi*, *Eretmoptera* was recognized as belonging to the Chironomidae.

Wirth (1949), in a major work on the marine Chironomidae, considered *Eretmoptera* to belong to his tribe Clunionini within the subfamily Clunioninae. Then, in one of the first uses of Hennig's (1957) phylogenetic approach to systematics, Strenzke (1960) recognized Wirth's 'Clunionini' as a monophyletic unit exactly equivalent to the *Smittia* group within the subfamily Orthocladiinae and therefore warranting neither subfamily (Clunioninae) nor tribal (Clunionini) status. Strenzke (1960) considered *Eretmoptera* to be the sister-group of *Belgica* combined with *Clunio* and *Tethymyia* and, in turn, these four genera formed the sister group of *Thalassosmittia*. The grouping of these five genera was a monophyletic unit referred to as the *Clunio* group.

The next, and most recent, consideration of the systematic position of *Eretmoptera* was that of Saether (1977) in a study of the value of the female genitalia in identification and phylogeny of the Chironomidae. Saether relied on the establishment of the phyletic relationship of the *Smittia–Clunio* grouping by Strenzke (1960) and, although he included some further trends (derived solely from information in the literature), the basis for the inclusion of *Eretmoptera* (and *Belgica*) in the *Clunio* group is not made clear. Examination of the cladogram (Saether, 1977: p. 86) shows that of 35 apomorphic character states used to place *Eretmoptera* in the *Clunio* group, twelve trends refer to the then unknown larva and pupa, four refer to wing features, which cannot be considered in a brachypterous species, and two further trends are doubtfully apomorphic. Within the *Clunio* group, Saether elucidated the precise relationships of *Eretmoptera* by characters of the then unknown immature stages, and most of the remaining features related to reductions in wing and halteres, notoriously subject to homoplasy wherever adult chironomids occur in conditions of environmental extremes. Furthermore, examination of Strenzke and Saether's cladograms reveals that they placed undue emphasis on the supposedly marine larval habitats of the *Clunio* group, including both *Eretmoptera* and *Belgica*. However, Wirth and Gesssitt (1967) and Sugg and others (1983) found *Belgica antarctica* larvae in abundance in damp moss, grass roots, detritus around penguin rookeries and seabird nests and also in meltwater pools and small ponds with algae. Similarly, *E. murphyi* larvae have been found in damp moss and peat (Block and others, 1984). Neither species has been found in marine or intertidal habitats, although, as noted above, *Eretmoptera browni* might live in the intertidal zone.

Knowledge of the immature stages and female of *E. murphyi* now allows detailed comparisons to be made with the *Clunio* group (here understood to comprise *Clunio*, *Tethymyia* and *Thalassosmittia*). Character states believed to be important, probably synapomorphous, for the *Clunio* group include: larva with labral lamellae, 4 pairs of lateral mental teeth and stout, anteriorly placed setae submenti; pupa with some tergal and sternal conjunctives bearing a transverse band of anteriorly directed spinules or hooklets, strongly reduced anal lobes lacking macrosetae and a small, more or less

rectangular tergite IX; female with large tergite IX and small cerci. *E. murphyi* shows none of these character states. Furthermore, those adult characters presumed to be apomorphies in which *E. murphyi* resembles *Clunio* and *Tethymyia*, such as reduction in wing, haltere, palp and antennal flagellomeres, occur in parallel in several unrelated lineages, and are probably related to adverse environmental conditions and loss of aerial swarming habit. Therefore, there is little evidence for a close relationship between *Eretmoptera murphyi* and the *Clunio* group of genera.

In assessing the possible systematic placement of *E. murphyi* and, by implication, *E. browni* the following characters, which I believe to be apomorphies, are of significance: the absence of all larval thoracic and abdominal appendages (parapods, claws, procerci and anal tubules); all larval labral S-setae stout and simple; pupa with tergal and sternal shagreen evenly distributed, without differentiation into spines or tubercles and with bare conjunctives; female imago with a tongue-shaped ventro-lateral lobe, which covers neither the well-developed dorsomesal lobe nor the apodeme lobe, and an undivided tergite IX. Important plesiomorphic characters include the presence of a well-developed anal lobe with 3 anal macrosetae and the imago with acrostichals and numerous scattered dorsocentral setae. This combination of characters is unique to *E. murphyi* and a somewhat isolated position amongst the more apomorphic Orthocladiinae is indicated. The female genitalia show some resemblance to those of *Smittia*, although the dorsomesal lobe is less strongly developed in the latter. The immature stages, especially the pupal shagreen, tend to confirm this relationship.

However, it is unwise to seek close relationships amongst the Holarctic genera simply because they are better known in all stages, when there are so many prospective relatives amongst the Orthocladiinae of the southern hemisphere. For example, Sublette and Wirth (1980), in describing midges from the sub-Antarctic New Zealand islands, erected nine new genera of Orthocladiinae, most of which appear to belong to the terrestrial and semi-terrestrial part of the Orthocladiinae. However, I concur with Saether (1982), who believed that many of these showed relationships with the *Parakiefferiella* group of genera. Only *Maryella* Sublette and Wirth (1980) appears to be a possible close relative of *Eretmoptera*, but this monotypic genus is known only from the male, and the authors' reasons for erecting a new genus appear valid, in the absence of the immature stages.

In conclusion, I believe *Eretmoptera murphyi* stands in an isolated position amongst the terrestrial Orthocladiinae centred on *Smittia*, but bears no close relationship to the *Clunio* group.

Distribution and Ecology

Eretmoptera murphyi was described from near the Bay of Isles, Island of South Georgia (Schaeffer, 1914), and Brundin (1970) reported the species from moss at low altitude on this island. A few further representatives have been collected from damp moss near Grytviken by members of the British Antarctic Survey, and it is clear that the species is well established in this area.

Block and others (1984) suggest that *E. murphyi* found on Signy Island had been accidentally introduced with plant material from either or both the Falkland Islands or South Georgia. Since *E. murphyi* is not recorded by Robinson (in press) from the Falklands, nor was the species present in a chironomid larval collection made there by the British Antarctic Survey, it seems likely that South Georgia was the source of the presumed introduction.

The immature stages of *E. murphyi* are known only from Signy Island. Here the

larvae are terrestrial, living in peat and moss on a small (1 m^2) sloping site where a plant introduction experiment had taken place some 17 years previously. Larval densities were about 7500 m^{-2}, but distribution of instars and life history data are not available at present.

The species is presumed to be parthenogenetic – no male has been observed, and females lay gelatinous egg masses from which larvae emerge. Active adults were seen crawling on the ground laying eggs over a 4-day period in early January 1982 during a mild (4 °C), calm, sunny period (Block and others, 1984) and similar conditions were associated with adult emergence in January 1984 (W. Block, *pers. comm.*).

Acknowledgements

I am grateful to the British Antarctic Survey (BAS) for supplying the specimens for this study and particularly to Dr W. Block (BAS) for allowing me to see an unpublished manuscript, for discussion and for reviewing this manuscript.

Received 7 September 1984; accepted 15 October 1984

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