A systematic reappraisal of the Australian Aphroteniinae (Diptera: Chironomidae) with dating from vicariance biogeography

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Abstract. The chironomid subfamily Aphroteniinae is revised for the Australian fauna. The larval-based genus Anaphrotenia Brundin is synonymized with Aphroteniella Brundin, and Anaphrotenia lacustris Brundin with Aphroteniella filicornis Brundin, and all stages redescribed and illustrated. A second Australian species, Aphroteniella tenuicornis Brundin, has been reared and the larva is described and the pupa and male redescribed here.

Paraphrotenia fascipennis Brundin, previously known only from the Australian type locality, is reported from a second site. The pupa and previously undescribed female adult are described and figured.

Aphrotenia Brundin, previously known only from Cape Province, South Africa, is recorded from Australia through Aphrotenia australiensis, newly described here and taking the authorship of Hergstrom. An unreeled and unnamed larva of Aphrotenia is described and figured.

Aphrotenia, and thus the subfamily, can be dated through a vicariance paradigm substantiated by a Cretaceous fossil record, to a minimum of 120 m.y.b.p.

Keys are given to larva, pupa and adults of the Australian Aphroteniinae.

Introduction

The significance of non-biting midges (Chironomidae) in interpretation of biogeographic processes has been recognized since Brundin's (1966) pioneering synthesis of Hennigian phylogenetics (cladistics) and biogeographic analysis. Brundin's recognition of multiple congruent vicariant sister groups within the subfamilies Podonominae, Aphroteniinae and Diamesinae (Heptagyiae) allowed him to postulate a congruent geological sequence of Gondwanan fragmentation.

Brundin's (1966) monograph was based almost exclusively on material he collected in running waters, predominantly using drift nets. The technique collects mainly pupal exuviae and pharate adults, as well as some incompletely eclosed adults, thus allowing association of these stages. However, few larval associations are made and, although Brundin made diligent searches, the advantages in having complete associations for the interpretation of phylogeny did not always materialize. Brundin's field studies were geographically wide-ranging, although they were focused on habitats and seasons in which cold stenothermic organisms were to be expected. Collections from montane streams predominated while those from warmer and lentic waters were limited.

Our subsequent studies on Australian Chironomidae generally confirm Brundin's observations on podonomine ecology, although Archaeochlus is a notable exception (Cranston et al., 1987). Two further species of Podonominae with larvae in warm, scarcely flowing waters in South Australia (Hergstrom, 1974) and Podonomopsis from Western Australian warm streams (Storey & Edward, 1989) expand the distributional range and thermal tolerances for some Australian members of the subfamily.

Modifications likewise are required to the geographic and ecological interpretations concerning the subfamily Aphroteniinae in Brundin's (1966) monograph, due to Brundin (1983), Edward (1986) and studies reported in the present paper. The Aphroteniinae was erected by Brundin (1966) for three Recent genera: Aphrotenia, with two species in Cape Province, South Africa, Paraphrotenia with two species in southern Chile and one in southeastern Australia and Aphroteniella, with one species in southern Chile and two in southeastern Australia. Subsequently Kalugina (1980) described an aphrotenine,
Electrodonia brundini, from a fossil in Cretaceous amber from Siberia. The only known aphrotenini larva was presumptively that of Aphrotenia tsiiskiamae Brundin (from South Africa), until the descriptions of a larval Paraphrotenia from Chile and an unreared Australian larva from Lake Booenigen (now spelt Boomanjin), Fraser Island, south Queensland, for which a new genus Anaphrotenia was erected (Brundin, 1983). The discovery of Aphroteniella in Western Australia (Bunn et al., 1986; Edward, 1986) considerably extends the range of the subfamily in Australia.

This study describes the previously unknown larvae of two species of Aphroteniella, correctly places the larval-based genus Anaphrotenia, records Aphrotenia from Australia and documents more extensive geographic distributions and broader ecologies for Australian species of Aphroteniinae than previously recognized.

**Methods and Materials**

Material was collected in western Australia by Surber sampling with a 250 μm mesh as part of extensive stream faunal surveys. In eastern Australia specimens were collected by drift net and Surber sampler, both of mesh size 300 μm. Live larvae from Fraser Island, Queensland, and Lees Creek, Brindabella Ranges, Australian Capital Territory were reared individually in cotton-wool stoppered 12 × 50 mm tubes in small volumes of water from the collecting sites, at ambient temperatures of 21°C to >30°C.

Microscope slide preparation involved clearing where necessary with 10% KOH, neutralization and initiation of dehydration with glacial acetic acid, then mounting from propan-2-ol (isopropanol) into Euparal. Some larvae with detritus entrapped (esp. Aphrotenia) were cleaned by sonication for 2–3 s.

Morphological terminology follows Saether (1980) and Brundin (1983) and differs from that of Brundin (1966).

Abbreviations used in the text are as follows: ANIC: Australian National Insect Collection; BMNH: The Natural History Museum, London; DHDE: D.H.D. Edward collection; I: Larva; Le: Larval exuviae; MDFRC: Murray Darling Freshwater Research Centre; MV: Museum of Victoria Survey Section; P: pupa; Pe: pupal exuviae; Pf: pharate female in pupa; Pm: pharate male in pupa (Le/Pe/im: male reared with associated larval and pupal exuviae, etc.).

**Aphroteniella Brundin**


Syn.n.

Generic diagnosis: as given by Brundin (1966) for adult and pupa and Brundin (1983) for larva (under *Anaphrotenia*), differing in the male adult antennal segments. Brundin stated that *Aphrotenia* had 15 segments, as did *Paraphrotenia*, but *Aphroteniella* had 14, counting the pedicel as first antennal segment. In current terminology the antenna comprises scape, pedicel and a variable number of flagellomeres, thus flagellomeres are n–1 of Brundin’s ‘segments’ and *Aphrotenia* and *Paraphrotenia* have 14 flagellomeres, in contrast to the 13 ascribed to *Aphroteniella*. However, all male *Aphroteniinae* have 14 flagellomeres, there being an obscure delimitation of the apical from subapical flagellomere in *Aphroteniella* when examined unmounted.

**Remarks**

The genus *Aphroteniella* is based upon *A. filicornis* Brundin described from a male and pupae plus pupal exuviae from Cedar Creek, Tamborine Mountain, southeast Queensland (Brundin, 1966). The species was known from elsewhere in south Queensland and from Rutherford Creek, Brown Mountain, New South Wales.

A second Australian species, *A. tenocornis* Brundin, was described from Rutherford Creek and was reported also from streams in the Australian Capital Territory (Brundin, 1966). The presence of the genus in the neotropics was established by the discovery of pupal exuviae in southern Chile (Brundin, 1966).

In May 1975, I. A. E. Bayl collected hundreds of larvae of an extremely small insect from the sand sediments of Lake Boomanjin on Fraser Island, south Queensland. Following difficulties in obtaining an identification, they were recognized by Brundin (1983) as belonging to the *Aphroteniinae*. Although acknowledging the dangers inherent in describing new taxa on unrecorded larvae alone, Brundin erected the genus *Anaphrotenia* for the distinctive taxon and named the species *lacustris*.

The larva of *Aphroteniella* was unknown until a Western Australian larva with distinctive body sculpturing was reared to a pupa (by D.H.D.E.) that was identical to *A. filicornis*. This larva appeared to be close, if not identical, to that described and profusely illustrated by Brundin (1983) for *Anaphrotenia lacustris*. A less sculptured but clearly congeneric larva is partially sympatric in Western Australia. In eastern Australia this latter larval type had been reared to pupae and pharate adults of *Aphroteniella tenuicornis* (by P.S.C.).

The close resemblance of the larvae of *Anaphrotenia lacustris* and *Aphroteniella filicornis* required establishment of the true identity, preferably by rearing of the Fraser Island species. Despite scientific visits to Lake Boomanjin, *Anaphrotenia* was not rediscovered until our visit in September 1989, when pupal exuviae were found in Lake Boomanjin, in its stream inflows and at Lake Mackenzie. Diligent searching of the sandy substrates, particularly where fine particulate organic matter was deposited, revealed a single live larva from Lake Boomanjin and three from Lake Mackenzie. Subsequently, the
larva from Lake Boomanjin pupated and died as a pharate adult. Close examination shows that this larva is identical to those described by Brundin as *Anaphrotenia*. Furthermore, the associated pupa, pharate male and unassociated pupal exuviae are identical with *A. filicornis*.

**Aphroteniella filicornis** Brundin

*Aphroteniella filicornis* Brundin 1966: 348.

*Anaphrotenia lacustris* Brundin 1983: 423. **Syn.a.**

Description: as Brundin (1966) for adult, pupa; as Brundin (1983) for larva, except for the following additions, emendations and mensural characters.

**Imago male** (*n = 4*)

Small, with body length 0.89–1.1 mm, wing length 607–675 μm. Brown, with vittae scarcely darker.


Head usually bare, with at most 1 frontal seta, clypeus bare. Eye rounded, without dorsomedian extension, with fine short microtrichia between ommatids. Palp 5 segmented, 1 not measurable, 2–5 respectively 18–23, 16–17, 29–32, 87–93 μm long; without pit or sensilla basiconica.

Thorax with narrow anterpronotum; each lobe bearing 1–2 lateral antepnoitals. Dorsocentrals uniseral, totaling 6–7 setae; 6–7 biserial acrostichals ending in midscutum; 4–5 prealars; 2 scutellars.

Wing (Fig. 1a) basally tapered without anal lobe, densely microtrichose and with macrotrichia apically in most cells and along most veins. Squama with 2–4 setae.

Legs. Unicoloured, lacking sensilla chaetica, with pulvilli approximately 75% of claw length, claws with small inner hook. Leg segment lengths and ratios as in Table 1.

Abdomen. Tergites weakly banded, with darker anterior half, bearing medial transverse row of 6 evenly-spaced setae; sternites with only 2 closely-approximated median setae.

Genitalia (Fig. 2b). Tergite IX characteristically large, covered with very elongate stout setae (easily abraded to leave large pits). Gonocoxite stout, 36 μm long, bearing weak volsella at about mid-point comprising fused bases of stout setae; gonostylus 27 μm long, boat-shaped, without megaseta.

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**Fig. 1.** Aphroteniinae adults. **a–c**, wings; **a**, *Aphroteniella filicornis* ♂; **b**, *Aphrotenia australiensis* ♂; **c**, *Paraphrotenia fascipennis* ♀; **d–g**, antennae. **d**, *A. filicornis* ♂; **e**, *A. filicornis* ♀; **f**, *A. australiensis* ♂ (denuded); **g**, *P. fascipennis* ♀ (denuded).
Table 1. Lengths and ratios of leg segments. Measurements in µm to nearest 5 µm, ratios to second place. Abbreviations: A. fil. m: Aphronella filamentosa m; A. fil. l: A. filamentosa l; A. australiensis male; P. fasc: Paraphronella fasciopennis female, P.I—III: fore-, mid and hind leg; fc: femur; ti: tibia; ta: tarsomere 1–5; L: ratio of ta length: ti length; BV: ratio of combined lengths of fc + ti + ta1; combined lengths of ta2–5; SV: ratio of combined lengths of fc + ti : ta1 length.

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Pupa (n = 20)

Total length 1.0–1.4 mm. Exuviae evenly distributed grey to mid- to dark brown with dark setation. Cephalic area (Fig. 4d) weakly wrinkled and with one pair of cephalic setae without tubercle. Thorax (Fig. 4a) length 365–355 µm, dorsally rugulose. Thoracic horn elongate, tapering, with felt chamber visible within, often apically broken off, up to 1037 µm. Ratio of thoracic horn length to thorax length 1.24–2.25, mean 1.8. Anterior dorso-central seta (dc1) developed as stout, apically rounded rod, dc2 a short peg-like seta close to dc1, dc3 displaced to above wing sheath base, dc4 a fine seta. Wing sheath with distinct pearl extending from apex to middle of posterior margin. Abdominal tergites as in Fig. 3(a). On the anal lobe, the longest of the 3 well-developed setae is about 2.5 times the length of the middle seta.

Pupa (n = 33)

Less tubular, more dorso-ventrally flattened than is usual for Chironomidae (Fig. 5a), 1.3–2.2 mm long, cream-coloured, often enmeshed in fine particulate material. Head capsule pale, 137–164 µm, long, comprising 9–13%, mean 10.2% of body length. Labrum (Fig. 5d) with SH seta very strongly developed, about 65 µm long. Antenna with four segments, lengths 5–6, 6–7, 8–9, 7–8 µm. Mandible (Fig. 5f) about 65 µm long, teeth golden. Prementum, genae and maxillary palp as in Fig. 5(e). Body covered with papillae, some of which (especially in some Western Australian specimens) may bear apical hooklets and with frequently darkened body setae (Fig. 5j). Proccerus bare, 133–203 µm long, 20–29 µm wide at base, 9–12 µm wide at apex, bearing median seta 4–10 µm long, sited at 0.35–0.45 of proccercial length from apex, subapical seta 41–73 µm long, sited at 0.11–0.17 of proccercial length from apex, and 5 or apical setae of lengths 261–345, 49–116, 14–38, 12–23 and fifth, if present, 14–17 µm. Posterior parapods with small papillae basally.

Variation

There is quite substantial variation amongst and between the larvae, particularly between Lake Boomanjin (LB) and more extreme examples from Western Australia (WA). Variation occurs in the length of proccercus (133–148 µm in LB, 174–203 µm in WA.), proccercal apical setal number (5 in LB, the fifth missing in WA), length of second proccercal apical seta (81–116 µm in LB, 49–75 µm in WA) and elaboration of body sculpturing and depth of pigmentation of body setae (weaker and paler in LB, sometimes stronger and darker in WA). This variation might warrant recognition of specific identity for the WA specimens, but we resist this in view of (a) the variation seen within the WA material, some of which closely approaches LB specimens, (b) our inability to find comparable morphological differences in the usually diagnostic

Imago female (n = 3)

As male except (Fig. 1e) with 8 flagellomeres, lengths 22–25, 18–22, 18–22, 18–32, 22–29, 8–14, 11, 18–20 µm. Antennal ratio 0.12–0.14, with 5 setae on scape; thorax with 1 antecornit, 10–13 biserial acrostichals, 5–6 dorsocentrals, 1–4 prealars, 2–4 scutellars. Palp 5-segmented, 1 not measurable, 2–5 respectively 18–22, 14–18, 30–34, 36–72 µm long. Leg segment lengths and ratios as in Table 1. Genitalia as Figs 2 (d, f), similar to Saether (1977: fig. 125A, B), except neither collar of seminal capsule nor common opening onto spermathecal eminence visible.
Fig. 2. Aphroteniinae adult genitalia. a–c, male (left side, dorsal; right side, ventral): a. Aphroteniella tenuicornis; b. Aphroteniella filicornis; c. Aphrotenia australiensis; d–g, females; d, f. Aphroteniella filicornis (d, ventral; f, dorsal); e, g. Paraphrotenia fascipennis (e, ventral; g, dorsal).
Fig. 3. Aphroteniinae pupal tergites. a. Aphroteniella filicornis; b. Paraphrotenia fascipennis.

pupal exuviae and the adult male, (c) the unknown significance of allometry, and (d) the possibility that the observed variation arises from ecophenotypic effects associated with specimens from lotic (LB) and lentic (WA) environments.

Types. Holotype male of Aphroteniella filicornis, Eunalus slide (from poor preservation in alcohol/glycerol): AUSTRALIA: south-east Queensland, Tamborine Mountain, Cedar Creek, 14.xi.1961 (Brundin) (ANIC); Holotype larva of Anaphrotenia lacustris, slide (unknown.
Fig. 4. Aphroteniinae pupae. a–c, thorax in lateral view; a, Aphroteniella filicornis; b, Aphroteniella tenuicornis; c, Paraphrotenia fascipennis; d, cephalic area of A. filicornis; e, posterior of tergite VI, A. tenuicornis.


Other material examined (all slides mounted in Euparal). 1L, Northern Territory: South Alligator River, Coronation Hill, site 1, xii.1989 (Dostin) (ARRRI #34); riffle 1, 21.vii.1987 (McKeagh) (Dames & Moore); 1 Le/Pm, 15Pe, Queensland, Fraser Island, Lake Boomanjin, 25°33' S, 153°05' E, 23/4.ix.1989 (Craston & Edward) (ANIC); 8Pe, same data except inflow stream to Lake Boomanjin; 3Pe, Fraser Island, Lake MacKenzie, 25°33' S, 153°03' E, 24.ix.1989 (Craston & Edward) (ANIC); 1Pe, Bundaroo Creek, 27.ix.1989 (Craston & Edward) (ANIC); 1L, Stony Creek site 1, 19.iii.1990 (Bunn); 1L, Victoria, Upper Tambo River, downstream of S. branch, 37°03' S, 147°52' E, 8.iii.1990 (Hortle), L, Acheron River, 37°30' S, 145°41' E, 9.iv.1987 (MV voucher 18E); L, upstream bridge, 37°34' S, 145°45' E, 16.ii.1989 (MV voucher 18E); L, same data, 19.ii.1989 (MV voucher 18E); 1 Le/Pe/m, Western Australia, North Dandalup, Cronin Brook, 32°31' S, 116°03' E, 30.xi.1989, emergence 21.xii (Edward) (DHDE); 1 Le/Pe/m, 1 Pe/m, 3 Pe/f, 1 Le/P, 11e, same data, variably later emergence up to 28.xii; 11e/P, North Dandalup, Foster Brook, 32°30' S, 116°02' E, 2.xi.1989 (Edward) (DHDE); 5L, Wungong Catchment, Waterfall Gully, 32°14' S, 116°04' E, 31.iii.1983 (Edward) (DHDE); 1 Le/P, 7L, Wungong Catchment, Seldom Seen Brook, 32°15' S, 116°04' E, 6.x.1983 (Edward) (DHDE); 1 Le/Pf, same data except 17.x; 1L, Deep River, 34°48' S, 116°37' E, 13.x.1983 (Edward) (DHDE); 3L, Carey Brook, 34°24' S, 115°50' E, 20.x.1989 (Edward) (DHDE); Brunswick River below confluence with Ernest River, 33°14' S, 115°55' E, 30.x.1983 (Edward) (DHDE).

Aphroteniella tenuicornis Brundin


Description as Brundin (1966) for adult, pupa, except for the following additions, emendations and mensural characters.

Imago male (n = 3, teneral and many features unmeasurable)

Small, with body length 1.2–1.5 mm. Brown, with vittae scarcely darker.
Fig. 5. Aphroeninae larvae. a. Aphroenella filicornis; b–c, antenna. b. Atenicornis; c. Aphroenella larval sp.; d–g, A. filicornis: d, labrum; e, prementum, gills and maxillary palp; f, mandible. Aphroenella larval sp.; g, prementum and galea; h, abdominal cuticle; i, processae apicae setae and adjacent cuticular setae; j, A. filicornis abdominal cuticle, k. A. tenuicornis abdominal cuticle.

Thorax with narrow antepronotum; each lobe bearing 3 lateral antepronotals. Dorsoventrals uniserial, totalling 7–8 setae; 8 biserial acrostichals ending in mid-scutum; 4 prealars; 6–8 scutellars.

Wings and legs retained in sheaths, only one foreleg measurable: fe: 209 μm, ta: 245 μm, tα: 91 μm, tα: 45 μm, tα: 40 μm, tα: 36 μm, LR: 0.37, BV: 5.0, SV: 2.9.

Abdomen. Tergetes banded, with darker anterior half, bearing medial transverse row of 10–12 basically uniserial transverse setae, except tergite IX with 4 setae; sternites with 4 closely approximated median setae.

Genitalia (Fig. 2a). Tergite IX characteristically large, covered with very elongate stout setae up to 120 μm long (easily abraded to large pits). Gonocoxite stout, 40–45 μm long, bearing dorsally raised moderately-developed volsella at about mid-point with medio-lateral band of stout setae; gonostylus 34 μm long, boat-shaped, without megaseta.

Imago female: Not available

Pupa (n = 3), as A. filicornis except:

Total length 1.5–1.7 mm. Exuviae pale yellow with golden setation. Thorax (Fig. 4b) length 500–580 μm, rugulose or with polygonal sculpturing throughout. Thoracic horn elongate, tapering, with felt chamber visible within, often apically broken off and therefore at least 455–638 μm long. Ratio of thoracic horn length to thorax length 0.9–1.28. Anterior dorsoventral seta (de) developed as a stout, apically pointed rod. Wing sheath without pearl row. Abdomen very similar to filicornis but with spines of posterior transverse rows smaller and contiguous across segment (Fig. 4c). On the anal lobe, the longest of the 3 well-developed setae is about 3 times the length of the middle seta.

Larva (Fig. 6a) (n = 4) as A. filicornis except:

1.5–1.7 mm long, head capsule 159–168 μm long, comprising 9–11% of body length. Labrum and epipharynx as in Fig. 6(e); mandibles, maxillae and prementum as in Fig. 6(f); antenna as in Fig. 5(b). Body with minute papillae never developed as hooklets (Figs 5k, 6a). Pro cercus 157–197 μm long, 26–29 μm wide at base, 12–15 μm wide at apex, bearing median seta 17–35 μm long, sited at 0.35–0.41 of pro cercal length from apex, and 4 apical setae of lengths, 276–487, 128–157, 26–52, 17–26 μm.

Types. Holotype male (alcohol preserved): AUS TRALIA; New South Wales, Brown Mountain, tributary of Rutherford Creek, 4.xi.1961 (Brundin) (ANIC); Other material examined (all slide mounted in Euparal): 2 Le/Pm, AUSTRALIA: Australian Capital Territory, Brindabella Ranges, Lees Creek, 35°21′S, 148°52′E, 2.x.1989, pupation 22.xi (Cranston & Edward) (ANIC); 2Pm, 1Pm, Brindabella Ranges, Condor Creek, drift net, 35°22′S, 148°51′E, 7–8.xi.1987 (Cranston) (ANIC); 1L, Brindabella Ranges, Blundell's Creek, 35°22′S, 148°50′E, iv.1988 (Cranston) (ANIC); 2L, 1Pm, New South Wales, stream by Bujong Road to Kangaroo Valley, 34°47′S, 150°28′E, xi.1990 (Edward) (ANIC); 1L, Blue Mountains, Cedar Creek, 15.i.1989 (Sydney Water Board); 1LP, Brown Mountain, Rutherford Creek, 36°36′S, 149°47′E, 16.x.1990 (Cranston & Edward) (ANIC); 4Pe, 17.xii.1990 (Cranston); 4Pe, 1Pm, Victoria, Buckland River, panning site, 36°48′S, 146°51′E, 6.xi.1990 (Cook) (MDFRC, ANIC); 1Pm, Snowy Creek at Mitta Township, 36°33′S, 147°23′E, 10.xi.1989 (MDFRC); 3L, Western Australia, Wungong Brook, 32°17′S, 116°08′E, 2.vi.1982 (Edward) (DHDE); 1L, Canning River East, 32°11′S, 116°11′E, 2.x.1985 (Bunn) (DHDE).

**Aphrotenia Brundin**


Generic diagnosis: as given by Brundin (1966) with the following modifications for the adult: 8 acrostichal setae, staggered biserial, ending at mid-scutum; cubitus forked well beyond the level of R-M in the distal half of the wing; larva: abdominal plates strongly to weakly developed, abdominal cuticular extrusions strongly to weakly developed.

**Remarks**

The genus *Aphrotenia* was described by Brundin (1966) for the type species *A.tisitsikamai* from Cape Province, South Africa. The species was known in all life cycle stages though the larval association was uncertain. A second South African species, *A.barnardi*, was described from pupal exuviae and a partial exuviae taken further west in Cape Province.

Hergstrom (1974), in an unpublished thesis, recognized the genus to be Australian, based upon two male adults collected in South Australia. Subsequently *Aphrotenia* larvae have been collected from streams in the Brindabella Ranges in the Australian Capital Territory, but rearing has not been successful.
**Aphrotenia australiensis Hergstrom**

*Aphrotenia australiensis* Hergstrom 1974: 68 [Invalid, ICZN, 1985: Article 8a]

*Aphrotenia australiensis* Hergstrom in Cranston & Edward, sp.n.

Description: as Brundin’s (1966) generic diagnosis, except for the following additions, emendations and mensural characters.

*Imago male (n = 2)*

Small, with body length 1.3 mm, wing length 0.9–1.0 mm. Brown, with dark vittae.

Antenna (Fig. 1f) with 14 flagellomeres, lengths 43–49, 29–32, 29–32, 32–34, 35–38, 35–38, 38, 38–41, 41, 41–43, 41–43, 46, 49–58, 26 μm. Antennal ratio 0.16–0.18. Flagellomeres apparently lacking sensilla trichoidea. Head bare, clypeus bare. Eye small, rounded, with slight dorsomedian extension, with no microtrichia between ommatids. Palp 5 segmented, 1 not measurable, 2–5 respectively 32, 29, 49–55, 177–179 μm long.

Thorax with basally broad, apically abruptly tapered anterpronotum; each lobe bearing 5 lateral anterpronotals. Dorsoceerals uniserial, totalling 8 setae; 8 staggered biserial acrostichals ending in mid-scutum; 4–5 prealars; 2 pairs of strong setae on lateral scutellum.

Wing (Fig. 1b) basally tapered without anal lobe, densely microtrichose and with macrotrichia from near base to...
more dense at apex in most cells and along most veins. Squama with 4–5 setae.

Legs. Unicoloured, lacking sensilla chaetica, with pulvilli approximately 75% of claw length, claws with small inner hook. Leg lengths and ratios as in Table 1.

Abdomen with 6–10 setae on each tergite arranged in an irregular transverse row; sternites with fewer setae, sited more towards lateral margin.

Genitalia (Fig. 2c). Tergite IX posteriorly rounded, bearing long setae (abraded in both specimens). Gonocoxite 51–54 μm, broad, bearing small volsella formed from fused bases of stout setae, directed medially. Gonostylus 36–39 μm long, broadened apically.

Female imago, pupa and larva: unknown.


**Aphrotenia larval species indet.**

Description: as generic diagnosis of Brundin (1966) with the following modifications and emendations:

**Larva** (Fig. 6b) (n = 3)

1.4–1.6 mm long, cream-coloured with fine particulate matter entrapped on cuticle. Head capsule pale, rugose, 159–168 μm long, comprising 9–10% of body length. Antenna unclearly 3-segmented, possibly with segments 2 and 3 fused (Fig. 5c); prementum and hypopharynx as Fig. 5(g). Mandible 65 μm long. Body segments with multiple fringed extensions and complexly divided setae with strongly developed tubercular bases (Figs 5h, 6c).

Posterior parapods without papillae, hooks or spines; Procorpus (Figs 5i, 6d) spinose, 188–209 μm long, 29 μm wide at base, 14–15 μm wide at apex, bearing compound median seta 41–49 μm long, sited at 0.44–0.50 of length of procorpus from apex, subapical seta 102 μm long, sited at 0.11–0.12 of length of procorpus from apex, and 4 apical setae of lengths, 157–174, 87–96, 35–43, 23–26 μm.

**Remarks**

The larva described above is congeneric with those of *Aphrotenia* from South Africa, but lack of rearing has prevented association with pupa or adult and we refrain from naming this taxon. The Australian larva more closely resembles *A. barnardi* Brundin of the two previously known Afro tropical larvae, in possessing feathered abdominal setae (Fig. 5h, compare Brundin, 1966: fig. 485), but differs from larvae of both species in the poorly defined dorsal abdominal plates and in the extraordinary development of the cuticular expansions (Figs 5i, 6b).


**Paraphrotenia Brundin**


Generic diagnosis: as Brundin (1966), and Saether (1977: 54) for female, except female imago may have 9, 10 *fascipennis* (Brundin) or 12 flagellomeres and the apical (fifth) palp segment is approximately 3 × as long as the penultimate (i.e. not distinguishable from *Aphrotenia*, contra Brundin, 1966).

**Remarks**

*Paraphrotenia* was described for two Neotropical species, *excellens* and *multispinosa*, and the Australian *fascipennis*, all described by Brundin (1966). The female was known for *excellens*, the species whose putative larva subsequently was described by Brundin (1983). *P. fascipennis*, known from pharate material from the type locality in southern New South Wales, has not been found in numerous visits to the site. However, pupae with associated reared females have been discovered in a new site in northern Victoria, but no larvae have been found.

**Paraphrotenia fascipennis Brundin**

*Paraphrotenia fascipennis* Brundin 1966: 358.

Description: as Brundin (1966) for pupa and pharate male. Larva unknown, female as Saether (1977: 54) with mensural features described below.

**Imago female** (n = 6)

Moderately small, with body length to 1.40–1.48 mm, wing length 845–950 μm. Brown, dorsum darker than pleurae, vittae not distinct, thoracic setal pits pale; wing with transverse dark band.

Antenna (Fig. 1g) with 9 or 10 (n = 1) flagellomeres, lengths (9 flagellomeres) 31–38, 28–30, 28–32, 17–23, 26–29, 17–23, 24–29, 35–43, 26–35 μm. Antennal ratio 0.12–0.15. Scape with 8–12 setae; flagellomeres 2–3 with subapical sensilla trichoida 0.3 length of flagellomere. Head and elypeus bare. Eye rounded, without dorso-median extension, with fine short microtrichia between ommatids. Paip 5-segmented, 1 not measurable, 2–5 respectively 29–35, 32–40, 40–49, 116–127 μm long. Thorax with 3–4 anteprontals, 22–27 biseri al acrostichals ceasing anterior to prescutellar area, 16–20 anterior-
ly biserial dorsocentrals, 12–15 prealars, 13–16 uniserial scutellars and 3 postalars.

Wing without anal lobe, densely microtrichose and macrotrichose. Macrotrochria somewhat scale-like in basal 0.75 of wing, dark brown, c. 50 μm long and 2 μm wide, with 3–5 parallel longitudinal ridges: macrotrichria pale in apical 0.25 of wing, also c. 50 μm long but narrow (<1 μm), with 0–1 longitudinal ridge. Squama bare.

Legs. Unicoloured mid-brown, lacking sensilla chaetica and pulvilli. Claws simple. Lengths and ratios of segments as in Table 1.

Abdomen. Tergites uniform brown, bearing median transverse band of 14–18 setae, sternites with median cluster of 5–6 setae flanked by 2 medio-lateral setae.

Genitalia as in Figs. 2c, g, very similar to P. excellens Brundin (Saether. 1977: figs 25C, D) except seminal capsules virtually spherical, about 60 μm in diameter, brown pigmented, as is the neck.

Pupa (n = 6)

Total length 1.8–2.3 mm. Exuviae golden brown. Thorax (Fig. 4c) length 695–750 μm, with polygonal sculpturing and rugosity throughout. Thoracic horn narrow, untapered, apically bluntly rounded, with felt chamber visible in basal half, 255–275 μm long, 0.4–0.5 thorax length. Anterior dorsocentral seta (de4) developed as stout, apically rounded rod, 70–85 μm long. Wing sheath without pearl row. Abdomen with posterior transverse spine rows contiguous across segment; anal lobe with longest of 3 well-developed setae twice as long as subapical apical and middle seta (Fig. 3b).

Larva: unknown.

Types. Holotype male and pupa (alcohol), AUSTRALIA: New South Wales, Brown Mountain, Rutherford Creek, 11.xi.1961 (Brundin) (ANIC).

Other material examined. 5 females with associated pupal exuviae, Victoria, Buckland River, 36°48'5" S, 146°51'5" E, 25.1.1991 (Cook) (ANIC: 1 to BMNH).

Key to Australian Aphroteniinae

(Taxon marked * is keyed from a Neotropical congener (Brundin 1983). † is keyed from an Afrotropical congener (Brundin 1966)).

Imagines (male hypopygial features in parentheses):

1. Wing vein R-M angled relative to continued direction of R4+5; free end of costa shorter than R4 (Fig. 1b). (Posterior margin of tergite IX rounded (Fig. 2c)). ....................................... Aphrotenia australiensis Herbstrom

2. Wing vein R-M continued in direction of R4+5; costa longer (Figs 1a, c). (Posterior margin of tergite IX straight or emarginate) ....................................... 2

 nightlife unmarked; costa only slightly longer than R1 (Fig. 1a). Pulvilli present. (Posterior margin of tergite IX straight (Figs 2a, b)). ......................... Aphrotenia: 3

- Wing with dark band in basal 0.75; costa much longer than R1 (Fig. 1c). Pulvilli absent. (Posterior margin of tergite IX emarginate*) .................................. Paraphrotenia fascipennis Brundin

3. (Volvella medially formed from fused bases of 3 aligned stout setae; volvella well-developed as an upright lobe (Fig. 2a)) ......................... Aphroteniella tenuicornis Brundin

- (Stout setae of volvella unaligned; volvella small, transversely orientated (Fig. 2b)) ......................... Aphroteniella filicornis Brundin

Pupa:

1. Posterior margin of each segment bearing uneven multiple rows of small spines; pupal abdomen flattened ... Aphrotenia*

- Posterior margin of each segment bearing even uniserial row (sometimes interrupted) of stronger spines (Figs 3a, b); pupal abdomen arched ........................................ 2

2. All lateral setae on segments VI and VII fine (Fig. 3b) ............... Paraphrotenia fascipennis Brundin

- One lateral seta on segments VI and VII stout (Figs 3a, 4e) ... ... Aphrotenia : 3

3. Thorax completely rugulose; thoracic horn subequal to thorax length; wing sheath without pearl row (Fig. 4b). Transverse posterior row of tergal spines continuous (Fig. 4e) ............... Aphroteniella tenuicornis Brundin

- Thorax with rugulosity confined to dorsal area; thoracic horn half as long again as thorax length; wing sheath with pearl row (Fig. 4a). Transverse posterior row of tergal spines medially interrupted (Fig. 3a) ......................... Aphroteniella filicornis Brundin

Larva:

1. Body with plumose extensions to cuticle; body setae featherted (Fig. 5b). Antenna 3-segmented (Fig. 5c). Procercus spinose (Fig. 5i) ......................... Aphrotenia sp.

- Body smooth, or at most with papillae and hooklets; body setae simple (Figs 5j, k). Antenna 4-segmented (Fig. 5b), Procercus smooth (Fig. 5a) ........................................ 2

2. Body smooth. Head notably large (>15% body length). Antenna as long as mandible ............... Paraphrotenia*

- Body with papillae and hooklets (Figs 5j, k). Head smaller (c 10% body length). Antenna minute, much shorter than mandible (Fig. 5b) ....................... Aphrotenia : 3

3. Body with small papillae, without hooklets (Fig. 5k). Second longest apical seta of procercus long, >130 μm ........................................ Aphroteniella tenuicornis Brundin

- Body with larger papillae, some hooklets (Fig. 5j). Second longest apical seta of procercus shorter, <120 μm (Fig. 5a) ...................... Aphroteniella filicornis Brundin

Ecology of Aphroteniinae

In his original description of the Aphroteniinae, Brundin (1966) states that members of the subfamily are strictly
rheobiotic and confined to ‘more or less swift mountain streams’. Larvae of the South African species of *Aphrotenia* were found in thin algal layers on the surface of stones and blocks fully exposed to the current and never in mosses. Brundin observed that aphroteniines in general avoid very low water temperatures, with pupae occurring in water of 8.8–20.4°C, indicating a preference for warm temperate conditions.

When discussing the ‘elevated’ surface water temperatures (averaging 25°C) of Lake Boeiminggen (sic), the site of *Anaphrotenia lacustris*, Brundin (1983) suggested that the body papilae of the larva functioned in oxygen uptake in this ‘rather extreme’ environment for an aphroteniine. However, in the light of studies reported here, this elevated temperature is unexceptional. *A. filicornis* larvae were found in water at temperatures of 24°C (August) and 29°C (December) in the Upper South Alligator River, and at 24°C in Lakes Boomanjin and MacKenzie. Streams in which *Aphrotenia* larvae live in Western Australia range in temperature from a winter minimum of 9–10°C to a summer maximum of 23°C.

Larvae of Western Australian *Aphrotenia* have been collected from first to third order streams in forested (jarrah and karri) catchments. Although the collections have been concentrated on riffle areas, subjective observations suggest that the larvae are generally confined to sections in which fine organic matter overlies sand substrates within the riffles.

In Eastern Australia, larvae of *Aphrotenia* are found in routine sampling of riffles in most low order sections of surveyed rivers (Marchant, pers. comm.). However, as in the west, our eastern studies have revealed highest densities where fine organic matter overlies sandy deposits. Larvae of *Aphrotenia* have been found in similar microhabitats in two first/second order lower montane streams.

Brundin (1983) expressed great surprise at the occurrence of an aphrotenine (*A. lacustris*) in Lake Boomanjin, a perched lake on Fraser Island, the world’s largest sand island. Clearly this low pH (3.5–3.6), humid, sandy benthos, low conductivity (95 microSiemens) and, above all, lentic habitat was very different from those recorded previously for the subfamily. Our collections confirm the occurrence (as *A. filicornis*) in Lake Boomanjin, in Lake Mackenzie (pH 3.9, conductivity 85 microSiemens, non-humic, benthos of fine organic detritus over sand) and also in the sandy-bedded inflow streams to Lake Boomanjin. Furthermore, *A. filicornis* has been recorded in Deep River, an acidic and humic stream in Western Australia (Edward, unpubl. data). Thus the ecological disparity stressed by Brundin (1983) in describing *A. lacustris* stems from an assumption of stenotopy that now appears unlikely.

*A. filicornis* is a univoltine species in Western Australia, emerging in late spring and early summer (Edward, 1986). Evidence from the eastern states does not contradict this. A remarkable feature of the life cycle is the length of time spent as a pupa, up to 12 days at 10°C. *A. tenuicornis* appears to have an equally protracted pupal development at ambient (21°C) and cooled incubator (10°C) temperatures. Oliver (1971) reported that the pupal stage in chironomids is very brief, ranging from a few hours to a few days. Our own observations on Chironomidae support this.

### Distribution and historical biogeography

In this section we consider the present-day distribution of Aphroteniinae and follow with an interpretation of the historical biogeography. Brundin (1966) believed *Aphrotenia* to be exclusively South African, and *Aphrotenia*, within Australia, to be restricted to the cooler streams of the south-east of the continent. More recent studies, including this, show that *Aphrotenia* occurs in South Australia and south-east Australia, and *Aphroteniella* is more widespread within the continent. The range of *Aphroteniella filicornis* is recognized now to include Western Australia (south of Perth) and the Northern Territory. *A. tenuicornis* occurs in south-western Australia. Both *Aphroteniella* species are widespread in the eastern half of Australia. These range extensions in no way refute the view that the Aphroteniinae are a group of gondwanan origin, but reinforce the idea that such taxa need not be cool stenotherms restricted to the elevated areas of the south-east of the continent.

Brundin's (1966) monograph was a seminal study of how historical biogeography could be reconstructed through phylogeny. His conclusions of a congruent geological sequence of Gondwanan fragmentation have been confirmed by many subsequent studies (reviewed for Australian insects by Cranston & Naumann, 1991). The use of a vicariance paradigm to explain continental faunal disjunctions allows the estimation of divergence times of lineages. Brundin (1966) had few examples of South African/Australian generic or species group disjunctions, most of his examples coming from Australian/New Zealand/South American cases. However, Cranston et al. (1987), in reviewing the podonomine genus *Archaeoecus*, asserted that newly documented southern African/Australian connections dated this clade to at least 120 m.y.b.p. This present study documents an analogous case of intrageneric South African/Australian disjunction in a second subfamily. This vicariance-based proposal, that a constituent genus of the Aphroteniinae dates from at least the Jurassic, can be substantiated with fossil evidence. Kalugina (1980) described an amber fossil, *Electrotraenia brundini*, from the Siberian Upper Cretaceous, that clearly possesses all the synapomorphies defining Aphroteniinae. The fossil evidence confirms that Aphroteniinae had already shown morphological radiation in the Pangaeic.

Thus, following the same rationale as Cranston et al. (1987), we infer the fragmentation of a continuously distributed aphrotenine clade at Pangean break-up and of *Aphrotenia* by Jurassic rifting of Gondwana.

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