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Austrobrillia Freeman: immature stages, and new species from the Neotropics

(Insecta, Diptera, Chironomidae, Orthocladiinae)

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Austrobrillia Freeman is redescribed in the adult stage, and described for the first time as larva and pupa, for the type-species *A. longipes* Freeman from Australia. Two new species based on pupal exuviae are described from Ecuador and Chile, as *Austrobrillia valereissia*, spec. nov. and *A. chilensis*, spec. nov. Phylogenetic analysis links *Austrobrillia* in a clade with *Eurycnemus* and *Euryhopsis*, within a probable monophyletic *Brillia*-group clade at the base of the Orthocladiinae.

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Introduction

Ideas concerning the age of Chironomidae clades derived from their extant distributions (i.e. Brundin 1966, Cranston & Edward 1992, Cranston et al. 1989) conflict with ideas of species formation associated with Pleistocene glaciations. The over-arching effects of range disruption of these glaciations imply that it is in the southern hemisphere, on the land masses that comprised Gondwana in the Jurassic/ Cretaceous, that distributions may retain the signal of deeper history – as understood particularly by Freeman (1961: 613-4) and Brundin (1966: 452).

Brundin (1966) stressed the Gondwanan distributions in the subfamilies Podonominae and Aphroteniinae, and in the tribe Heptagyini of the Diamesinae, but similar patterns in the Tanypodinae, Orthocladiinae and Chironominae increasingly are being revealed. Although Freeman (1961) allocated *Austrobrillia* Freeman to his category “peculiarly Australian genera”, the extensive Neotropical chironomid collections at the Zoologische Staatssammlung Munich (Germany) reveal that this genus joins an expanding list of Gondwanan-connected orthocladiine taxa linking Australia to South America.

In this contribution, in commemoration of Dr Reiss’s global perspective on chironomid studies, the immature stages of *Austrobrillia* are described formally, thereby allowing recognition of two pupal taxa from the Neotropics. That the Neotropical material consists solely of pupal exuviae does not deter description, since the stage is distinctive and creation of synonymy is precluded, because the one putative adult congener described from the region, based on a female, is unlikely (see below).

Methods and morphology

The association between larva, pupa and adult necessary for full taxonomic descriptions was attempted by rearing live larvae individually through to the adult, but as with many other wood-mining taxa, success was elusive. Associations have been made through fortuitous larval head capsules retained attached to pupae, and from pharate adult pupae, recovered predominantly from drift net samples. Morphological terminology and abbreviations follow Sæther (1980) and Cranston (1994) with Langton's (1994) term taenia (adjective taeniate) used for "filamentous" or "lamelliform" (LS) pupal setae. In pupal descriptions the conjunctive is numbered as belonging to the segment anterior to it. Some larval measurements are of exuviae, but length and head capsule measurements are based on complete fourth-instar larvae. Measurements of larval antennal features and subsequent calculations of the antennal ratio are based on sclerotised antennal parts, disregarding the sometimes variably distended membranous intersegmental regions. Unless indicated otherwise, measurements are in μm , rounded to the nearest 5 μm except in cases where measurement at maximum magnification provided accuracy to 1 μm . Material is preserved in the Australian National Insect Collection (ANIC), CSIRO Entomology, Canberra, or Zoologische Staatssammlung, Munich, Germany (ZSM). Abbreviations for geographic features: Ck = Creek, L. = Lake, Mt = Mount(ain), N.P. = National Park, R. = River, S.F. = State Forest.

Austrobrillia Freeman, 1961

Type-species: *A. longipes* Freeman, 1961, by monotypy.

Diagnosis

Adult male, female and larva – see description of *A. longipes*.

Pupa medium-sized, 5.0-7.8 mm long, pale yellow to medium brown with darker dorsal transverse apophyses, lateral apophyses scarcely indicated.

Cephalothorax: frontal setae on weakly crenulate frontal apotome. Ocular field with 1 postorbital, without vertical seta. Thorax with 1-2 median anteprenotals, 1 LAp (may be reduced to peg); 3 precorneals, their thickness and relative lengths variable; 4 stout dorsocentrals, D₃ and D₄ longer and closer together. Thoracic horn elongate cylindrical, may broaden subapically, micro-spinose. Dorsum of thorax smooth. Prealar area triangular, bare. Wing sheath without pearls.

Abdomen: Tergites I, VIII bare, II-IV may have some pleural shagreen; tergites II-V(-VII) evenly spinose, T II-V(VI) with posterior transverse row of short blunt spines; T II without hook row. Posterior borders of tergites I-III with bands of pigment polygons extending onto conjunctives, conjunctives II-IV spinose, bands can be medially interrupted, notably on IV, and on V-VI(VII) with few very fine spinules laterally. Anterior sternites with shagreen, II with or without multiserial transverse band of long, thin, hyaline spines, II-VII with variably distributed shagreen, IV posteriorly with patch of spinules medial-posteromedial to pedes spurii A, the latter comprising whorl of fine spinules. Pedes spurii B absent. Anal lobe oval, with sparse anterior shagreen and multiserial fringe taeniae, with translucent spines interspersed amongst taeniae, lacking macrosetae. Male genital sac tapering to point, extending beyond anal lobe apex; female sac shorter, rectangular, with postero-lateral tubercle. Setation: 5 D, 4 V; 2 minute L on I, 3 on II-V, 4 on VI-VII, 5 on VIII, becoming increasingly taeniate on posterior segments. 0 dorsal O-setae, 1 ventral pair on conjunctive margin of segments II-VII.

Recognition

Austrobrillia is distinctive in the larva by the mentum construction with large paired median teeth and only two laterals, but otherwise bears a close resemblance to that of *Eurycnemus*. In the pupa the lack of a hook row on tergite II, the transverse bands of posterior tubercles and absence of anal macrosetae on a fringed anal lobe is a distinctive combination. In the adult the bare wing cells and restriction of anteprenotal setae to the lateral area are unusual amongst the *Brillia*-group; in the male genitalia the presence of an anal point and the deeply bifid gonostylus without megaseta or taeniate seta are distinctive, and the narrowed and anteriorly projecting transverse sternapodeme appears to be of some phylogenetic significance, being shared uniquely in the clade with *Euryhopsis* + *Eurycnemus*. The female genitalia provide a combination of features seen in related taxa: 3 seminal capsules, with a reduction in size of the median, each with microtrichia; spermathecal ducts with separate openings; labia microtrichiose.

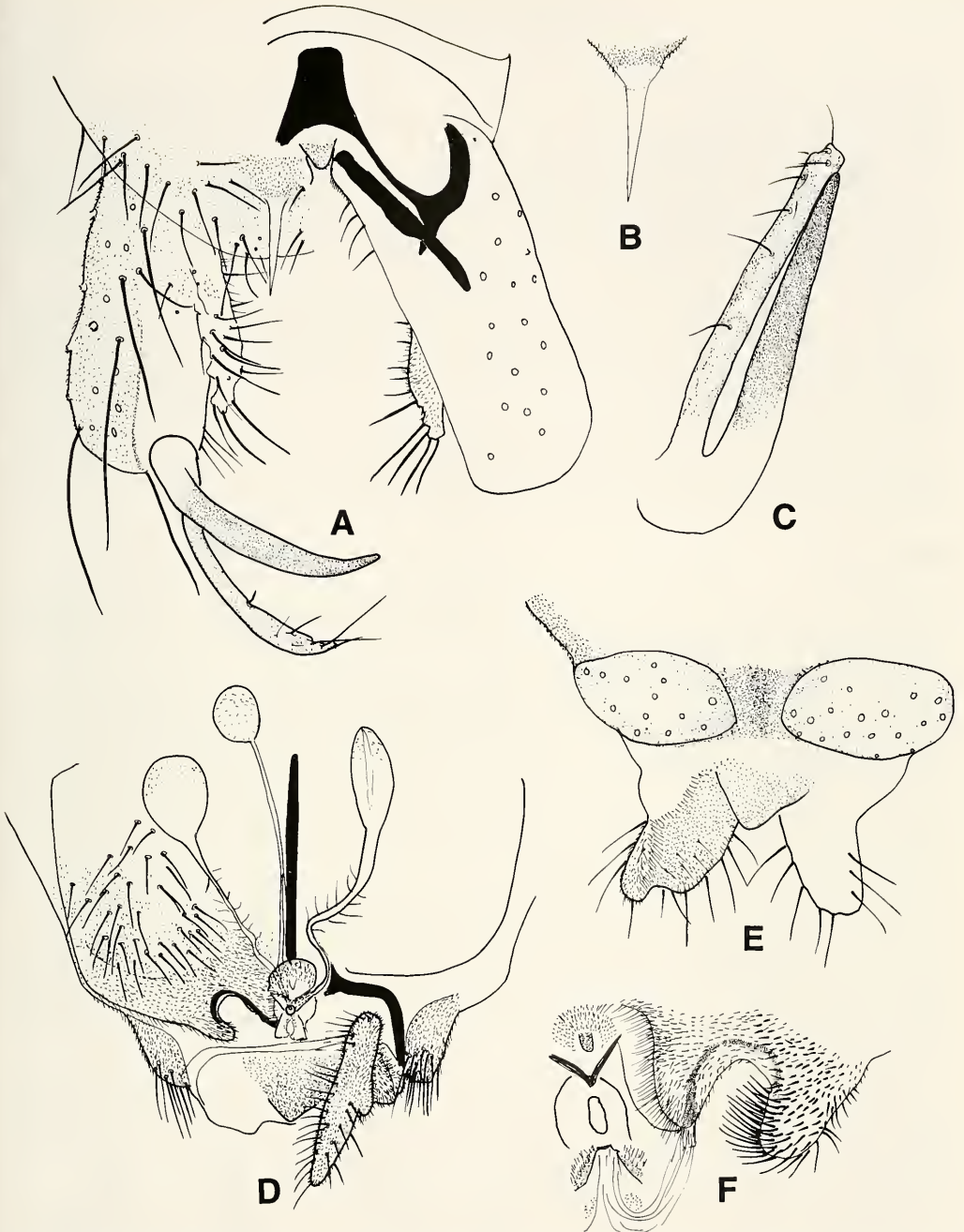


Fig. 1. *Austrobrillia longipes* Freeman: adults. **A-C.** Male. **A.** Hypopygium, left: dorsal, right: ventral. **B.** Anal point. **C.** Gonostylus. **D-F.** Female. **D.** Genitalia, ventral. **E.** Genitalia, dorsal. **F.** Gonapophysis VIII, vagina, and labia.

Austrobrillia longipes Freeman

Figs 1, 2A, 3B-I

A. longipes Freeman, 1961: 640.

Material. Holotype: Adult ♂, pinned, genitalia on celluloid mount, AUSTRALIA, Tasmania, Harz Mts, xii.1922, leg. A. L. Tonnoir (ANIC).

Other (all slide mounted; AUSTRALIA, leg. P. S. Cranston unless stated): New South Wales: Pe, nr Dorrigo, Eve Ck, 30°16'S 152°50'E, 9.X.1996; 3L, Le/P, Barrington Tops, Manning R., 31°53'S 151°29'E, ex-wood, 8.X.1996; Pe, Belmore Falls, Barrengarry R., 34°38'S 150°33'E, 3.IV.1991; 2 Pe, Mongarlowe R., Monga S.F., 35°23'S 149°55'E, 2.II.1991; 4 Pe, Rutherford Ck, Brown Mountain, 36°36'S 149°47'E, 16.X.1990; 2 Pe, Albury Wodonga, Murray R., Union Bridge, 12.XI.1990 (R. Cook).

Australian Capital Territory: 2♂♂, 1♀, Brindabellas, Blundells Ck, 35°22'S 148°50'E, IX.1988.

Victoria: Pe, Mitta Mitta, Snowy Ck, 36°33'S 147°23'E, 3.XII.1991 (MDFRC); Pe, Pigs Point, XII.1991 (MDFRC); 2 Pe, 1♂, Buckland R., 36°48'S 146°51'E, 1.VII.1991 (Cook); Pe, Buckland R., 36°48'S 146°51'E, 6.V.1991 (Cook); 1♂ ("holotype" of *Austrobrillia collessi* of Hergstrom, 1974, see "Comments" below), Mt Beauty, 21.X.1961 (Colless); Le/P ♂, 2 L, Tambo R., Bindi, 37°08'S 147°51'E, 23.III.1991 (Hortle); Le/P ♂, Woori Yallock, Yarra R., 37°48'S 145°32'E, 21.II.1978 (Glaister).

Tasmania: 2♂♂ (one paratype *A. longipes*), Burnie, 20.X.1922 (Tonnoir); 1♀, Burnie, 1 Feb 1923, (Tonnoir); Pe, Gladstone, Ringarooma R., 40°56'S 148°00'E, 21.II.1993; 2 Pe, Peters Link Ck, 41°09'S 148°07'E, 24.II.1993; 2 Pe, Cradle Mt - L. St Clair N.P., Douglas Ck, Ranger Hut, 41°50'S 146°02'E, 25.I.1990; Pe, Lyall Highway Crossing, Franklin R., 42°12'S 146°02'E, 17.I.1990; 1♂, Bothwell, Clyde R., 13.II.1964 (Dyce & Murray).

Redescription

Adult male (n=5).

Thorax yellow-brown, with indistinct vittae and postnotum darker brown, scutellum paler; legs yellow, unbanded; abdomen yellow, each anterior half of tergites and sternites II-VI with dark transverse band, T VII, VIII and hypopygium all dark.

Body length 4.7-5.2 mm; wing length 2.6-3.1 mm, width 720-750, ratio length/width 3.5-4.1. Antenna with 13 cylindrical, densely microtrichiose flagellomeres; well-developed plume extending to apex lacking strong subapical seta; groove extending from Fm 3 to 13; sensilla chaetica on Fm 2-4, 13; Fm 1-12: 425-505, 13: 740-905, AR 1.66-2.12. Eye bare, with long parallel-sided extension. Temporal setation: 5-8 inner verticals amongst 14-16 continuous temporals, double medially, uniserial otherwise; Tentorium parallel-sided apically, broad basally, without sieve plate, cibarial pump dilate with short cornua. Clypeus small, with 9-12 setae. Palp long, with 5 segments, 4th and 5th elongate, 2nd short, 3rd with 4 subapical sensilla chaetica, without pit.

Thoracic setation: 6-13 lateral anteprenotals; acrostichals absent, 17-20 biserial dorsocentrals, 5-7 uniserial prealars, 0 supraalars, 13-15 biserial scutellars. Pleurae bare.

Wing membrane bare, with coarse punctuation. R_{4+5} ending far distal to M_{3+4} ; costa extended toward wing apex; R_{2+3} running and ending about midway between R_1 and R_{4+5} . RM long, gently curved at obtuse angle to direction of R. 19-20 R setae, 11-21 R_1 , 0-20 R_{4+5} ; Squama with 12-30 uniserial setae. Anal lobe gently rounded. FCu distal to RM (VR 1.14-1.28). Cu_1 straight, with slight curve near wing margin. Vannal fold, An_1 and An_2 strong.

Leg ratios: LR_1 1.04-1.08, LR_2 0.51-0.59, LR_3 0.53-0.56. Fore tibial spur length subequal to tibial apex width; mid tibia with two spurs subequal in length to tibial apex width; hind tibia with one spur longer than, the other subequal to tibial apex width; spur lengths: p_1 63-87, p_2 52-60, 40-49, p_3 53-60, 66-94. Comb present; pseudospurs on mid tarsomeres 1 and 2, and hind ta_1 . Sensilla chaetica absent. Pulvilli very short, not extending to claw base; empodium trifid; all claws toothed apically.

Tergites brown anteriorly, paler caudally with dense, rather evenly distributed setae.

Hypopygium (Figs 1A-C). Tergite IX with dense marginal and submarginal long setae. Anal point 56-66 long, inserted subapically, narrow, with needle-like pointed apex, without microtrichia, projecting beyond apex of tergite. Anteromedian part of sternapodeme elongate, parallel-sided, without oral projections; phallapodeme well developed. Virga absent. Superior volsella absent; inferior volsella a posteriorly-directed, elongate lobe. Gonocoxite 245-650 long, gonostylus double, inner branch 133-160, outer branch 150-160, with slender megaseta on inner branch.

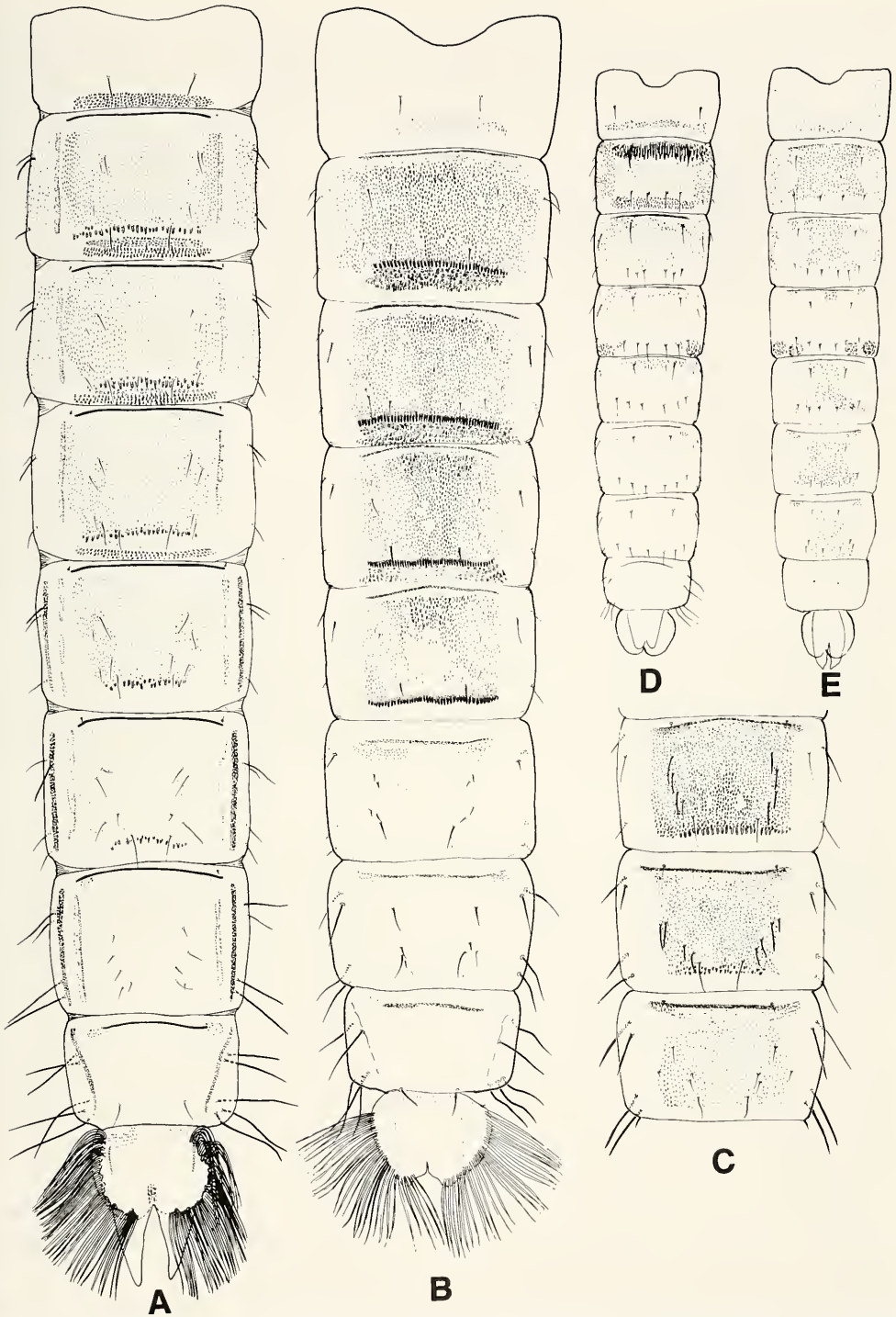


Fig. 2. *Austrobrillia* Freeman: pupal abdomina. A-C. Abdominal tergites. A. *A. longipes* Freeman. B. *A. chilensis*, spec. nov. C. T V-VII, *A. valereissia*, spec. nov. D-E. Sternites. D. *A. chilensis*, spec. nov. E. *A. valereissia*, spec. nov.

Adult female (n=5).

As male, except body length 3.6-5.7 mm; wing length 2.5-3.5 mm, width 78-105, length:width ratio 3.1-3.3. Antenna with 6 flagellomeres each with sensilla chaetica, lengths 60-70, 63-77, 66-88, 60-108, 63-105, 105-133; AR 0.27-0.36. Head setation: 11-19 temporals including 6-11 inner verticals; 14-24 clypeals. Thorax: 6-13 lateral anteprenotals; 19-46 dorsocentrals, 5-6 prealars, 15-37 scutellars. Wing: 11-34 squamals, 19-38 R setae, 22-32 R₁, 38-41 R₄₊₅; VR 1.19-1.22. LR₁ 1.00-1.05, LR₂ 0.53-0.57, LR₃ 0.53-0.59. Spur lengths: p₁ 60-80, p₂ 49-73, 52-71, p₃ 70-105, 56-80.

Genitalia as in Figs 1D-F, with sternite VIII not forming floor under vagina, with numerous setae each side; tergite IX short, clearly divided into two parts with 27-36 setae each side; gonocoxite IX with 5-17 setae, not bulging; gonapophysis VIII divided, well developed rectangular ventrolateral lobe (vll) separated from strong dorsomesal lobe (dml); slender apodeme lobe (al) distinctly visible beneath dml, partially beneath vll; notum moderately developed; 3 seminal capsules: the median spherical, 80-90 × 71-80, the two lateral elongate ovoid 98-125 × 70-75; lateral seminal capsules weakly microtrichiose, with tapering necks, spermathecal ducts straight to slightly curved, dilated anteriorly, bearing special secretory cells medially; median spermathecal duct strongly microtrichiose, without neck; ducts end without bulbs at three separate opening. Labia microtrichiose. Tergite X broad, cerci well developed 205-230 long, postgenital plate distinct.

Pupa (n=5).

Length 5.0-7.8 mm. Pale yellow, with strongly pigmented transverse apophyses and dark brown tergal tubercles in transverse bands. All cephalic and thoracic setae strong, but non-taeniate: frontal setae 90-160 long; anteprenotal setae – MAps₁ 220-320, MAps₂ 168-315, LAps 30-115; precorneals – Pc₁ 160-240, Pc₂ 180-260, Pc₃ 85-125 (missing in 1 specimen); dorsocentrals – Dc₁ 35-90, Dc₂ 35-50, Dc₃ 70-105, Dc₄ 70-120; distances: Dc₁₋₂ 87-230, Dc₂₋₃ 56-98, Dc₃₋₄ 7-14. Thoracic horn (Fig. 3B) 190-415, slightly broadened medially, somewhat clubbed apically, with apical 75 % densely covered in fine spines.

Abdominal tergites (Fig. 2A): T I bare, with weak to strong pattern of pigment polygons on posterior; T II-VI with dense spinules, posteriorly with transverse band of irregularly-arranged, approximately biserial tubercles, weaker on more posterior tergites, with polygonal patterns on conjunctives II-IV associated with variably developed anteriorly-directed spinules; T VII-VIII bare. Pleurae II-III or IV (anteriorly) spinulose. Sternites much as in *A. chilensis* (Fig. 2D), with strong hyaline spines on II. Anal lobe with 74-99 taeniae.

Larva (n=6).

Length 7.5-9.2 mm. Body pale, usually with distinctive wood fibre-filled gut. Head capsule 580-790 long, golden yellow with slightly darker postoccipital margin, black mandibles, and dark brown mentum. Dorsal surface of head (Fig. 3C) comprising frontal apotome, fragmented clypeus (bearing S3) separated from more anterior sclerite (bearing S1 & 2) by golden-brown fragmentary pattern on clypeus; sclerites 1-5 otherwise indistinguishable from clypeus. Antenna (Fig. 3D) 4-segmented, lengths: 53-62, 11-14, 2-3, 3-4, AR 3.1-3.6, blade simple 33-42, annulate, extending well beyond antennal apex; style/peg sensillum 8-10 placed subapically on 2nd segment. Lauterborn organs absent. Ring organ in basal 1/3 of segment 1, with 1 or 2 (2nd minute) subsidiary pits adjacent.

Labrum (Fig. 3E) with S1 simple, lanceolate; SII simple, SIII apically bifid; all S setae arranged transversely across labrum, with short SIVa & b lateral to SIII base. Premandible *Cardiocladius*-like, dark, broad and blunt, with one apical and one inner tooth, without brush. Spinulae and chaetulae simple spines. Labral lamellae of 5-6 fine, thin spines just anterior to S1 setae. Epipharynx (Fig. 3F) with medially fissured tormal bar, with "comb" of 3 rounded lobes on each side; pecten epipharyngis apparently absent, or indistinguishable from 6 robust simple chaetulae; very small chaetulae basales may be present.

Mandible (Fig. 3G) 120-170, unusually shaped (though aspect-dependent), somewhat conical/triangular and heavily sclerotised, with outer and inner margins smooth, with short outer (dorsal) tooth, "true" apical tooth subequal to width of first of 2 inner teeth, innermost tooth with notch. Seta subdentalis very narrow. Seta interna with 4-5 narrowly serrate branches.

Mentum (Fig. 3H) 100-115 wide, unique, with broad, medially indented area and 3 pairs of lateral teeth; no evidence of ventromental plates, beard absent.

Body not setose. Anterior parapods separate, with crown of elongate, simple, pale spines and claws. Posterior parapods separate, with apical group of simple claws. Procercus 45-60 long, 25-30

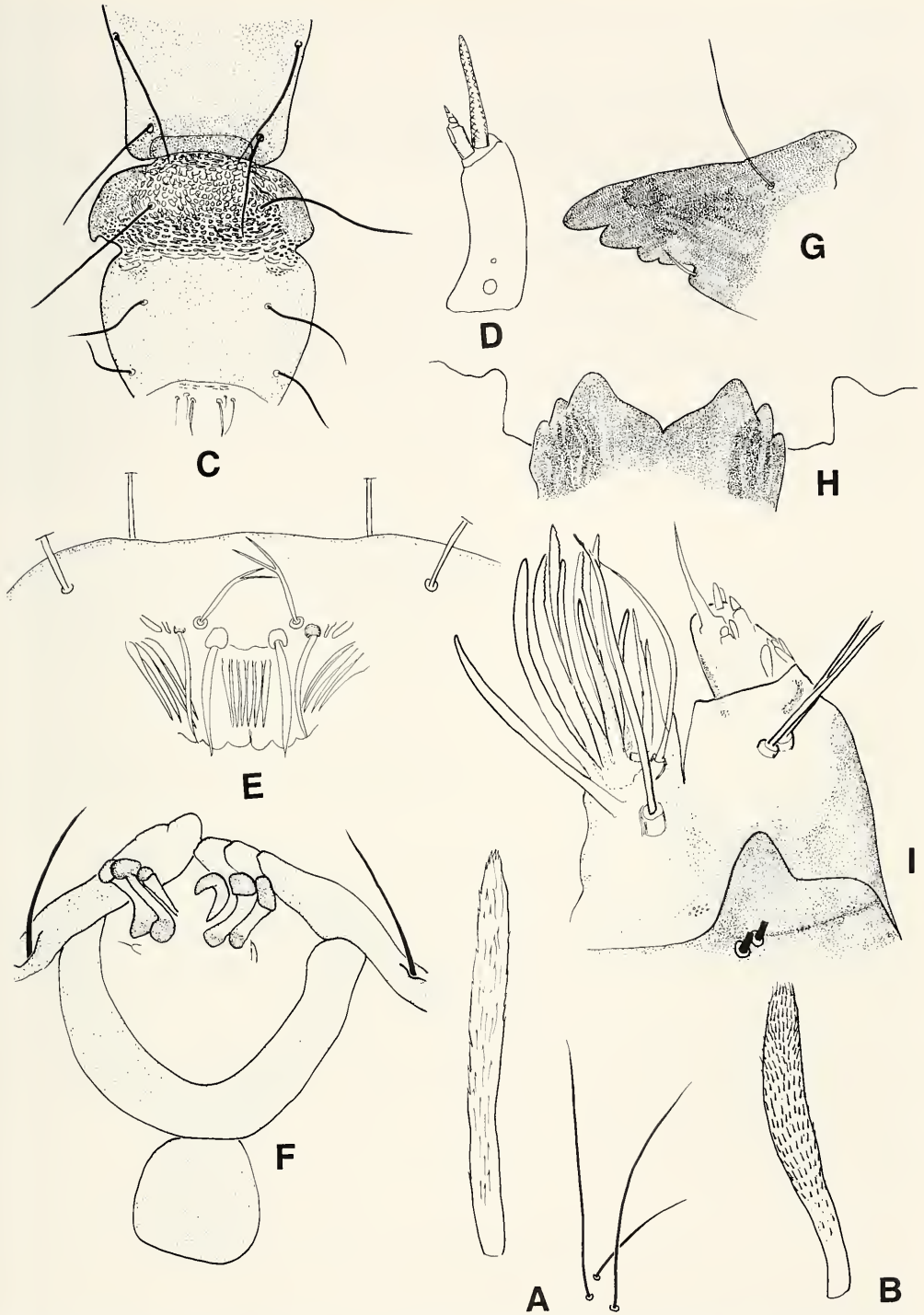


Fig. 3. *Austrobrillia* Freeman; immatures. **A, B.** Pupae: Thoracic horn. **A.** *A. chilensis*, spec. nov. **B.** *A. longipes* Freeman. **C-I.** Larva, *A. longipes* Freeman. **C.** Antero-dorsal head sclerites. **D.** Antenna. **E.** Labrum. **F.** Epipharynx. **G.** Mandible. **H.** Mentum. **I.** Maxilla.

wide, lightly pigmented, bearing 2 strong median setae and 7-8 anal setae of maximum length 480-580. Anal tubules short, cylindrical.

Comments

The larva of *Austrobrillia* has been reported in Australia as “nr *Eurycnemus*” by the Museum of Victoria (MV), a very appropriate code given the phylogenetic position (see below). This taxon, coded as MV69E, and that coded MV118E or “nr. *Eurycnemus* sp. 2”, appear identical (Richard Marchant, Museum of Victoria, pers. comm.)

In an unpublished thesis, Hergstrom (1974) recognised on adults two species of Australian *Austrobrillia*, splitting “*A. collessi*” (a not formally published, therefore unavailable name!) from the genotype by a narrower wing in both sexes, in the male by the degree of appression of the inner lobe (= inferior volsella) to the gonocoxite, and in the female by the “egg guide (= dorsomesal lobe of gonapophysis VIII) ending in a knob” (v. pointed). Although there is substantial variation, examination of material available to Hergstrom and additional specimens shows that the range of wing length:width ratios is less than described and does not fall into two groups. Furthermore, the assessment of genitalic features in both sexes seems to be due to distortions in some preparations. Examination of a large number of pupal exuviae shows that the species varies markedly in size, and consequently in allometric features, with thoracic horn length and density of anal lobe taeniae most variable. However, the reared material is still inadequate to assess how pupal relates to adult morphological variation, and at present the evidence is for a single, polymorphic species with clinal (Hergstrom 1974) or ecophenotypic variation.

Austrobrillia chilensis, spec. nov.

Figs 2B,D, 3A

Types. Holotype: Pe, slide-mounted in Euparal; Chile, Prov. Cautin, Rio Pirén, 4km o. (above) R. Queule, (Nr 17), 3.II.1986, M. Spies (ZSM).

Description

Pupa (n=1).

Length 6.5 mm. Pale, with brown transverse apophyses and dark brown tergal tubercles in transverse bands. Cephalic and thoracic setae weak, non-taeniate: frontal setae 50 long; anteprenotal setae – MAps₁ 73, Maps₂ missing, Laps₃ 66; precorneals – Pc₁ 165, Pc₂ 75, Pc₃ 155; dorsocentrals stubby – Dc₁ 20, Dc₂ 20, Dc₃ 50, Dc₄ 45; distances: Dc_{1,2} 160, Dc_{2,3} 125, Dc_{3,4} 5. Thoracic horn (Fig. 3A) 245, cylindrical, of even width, almost completely adorned with slender spines with elongate bases.

Abdominal tergites (Fig. 2B): T I bare, with faint polygonal pattern on posterior; T II-IV with dense spinules, posteriorly with transverse band of regularly-arranged and near-contiguous tubercles, anterior to broad conjunctival band of spinules arising from polygonal areas, on IV this band restricted to small lateral patches with wide median interruption; T V with posteromedially interrupted shagreen, anterior to monoserial even band of contiguous tubercles; T VI-VIII at most with weak shagreen. Pleurae with spinules on anterior of II and III. Sternites (Fig. 2D): I with posterior transverse band of shagreen, II with broad anterior band of elongate, translucent spines flanked by dense (pleural) spinules, and with posterior transverse band of shagreen; S III-V with sparser anterior spinules; IV also with pedes spurii A and nearby more medial patches (small); S VI with small anterolateral patches, VII-VIII bare. Anal lobe with 80 taeniae.

Etymology. Named for the country of provenance; adjectival.

Austrobrillia valereissia, spec. nov.

Figs 2C,E

Types. Holotype: Pe, slide-mounted in Euparal; ECU66 (Ecuador), NA (Napo), Sumaco, Cosanga, Bach mit Wasserfall (stream with waterfall), NÖ der Siedlung (NE of settlement), 2000m, (01-81/99-37), 13.I.1995, R. Gerecke (ZSM).

Description

Pupa (n=1).

Length 5.2 mm. Pale yellow, with tergal brown pigment associated with rectangular spinule patches, transverse apophyses and dark brown tergal tubercles in transverse bands. Cephalic and thoracic setae strong, near taeniate: frontal setae 80 long; antepronotal setae – MAPs₁ 130, MAPs₂ 170, LAPs₃ 70; precorneals subequal about 140; dorsocentrals stout – Dc₁ 35, Dc₂ 28, Dc₃ 50, Dc₄ 55; distances: Dc₁₋₂ 85, Dc₂₋₃ 115, Dc₃₋₄ 10. Thoracic horn 215, cylindrical, slightly tapering to apex, covered with slender spines with elongate bases.

Abdominal tergites (Fig. 2C): T I bare, with faint polygonal pattern on posterior; T II-VI with square patches of spinules, posteriorly with transverse band of irregularly-arranged, approximately biserial tubercles, weaker on VI, with polygonal patterns on anterior conjunctives, with broad transverse band of spinules on II-IV; T VII densely spinulose, VIII bare. Pleurae spinulose only on ventral (parasternae) of I-III. Sternites (Fig. 2E): SI with posterior and lateral bands of shagreen, II-III densely spinulose without long spines; IV with weak anterior shagreen, pedes spurii A and nearby more medial patches; S V-VII with median spinule patches, VI, VII also with anterolateral shagreen; SVIII bare. Anal lobe with 52 taeniae.

Etymology. Named to farewell (Latin: vale) my late, lamented colleague, Frieder Reiss; to be used as an adjective.

Key to pupae of *Austrobrillia* Freeman

1. Abdominal tergite VII spinulose (Fig. 2C). Sternite II without anterior transverse band of elongate hyaline spines, S V-VII extensively spinulose (Fig. 2E) *A. valereissia*, spec. nov.
 - T VII virtually bare (Figs 2A, B). S II with anterior transverse band of elongate hyaline spines, posterior sternites virtually bare (Fig. 2D) 2
2. T V with transverse band of closely approximated, uniserial tubercles, T VI without tubercles; conjunctival band on V medially interrupted (Fig. 2B) *A. chilensis*, spec. nov.
 - T V with transverse band of basally separated, unevenly biserial tubercles, T VI with tubercle band; conjunctival band on V continuous (Fig. 2A) *A. longipes* Freeman

Systematic discussion

A data matrix derived to assess the phylogenetic position of *Parapsectrocladius* Cranston (Cranston 2000) has been expanded to include the *Brillia*-group (sensu Sæther & Wang 1992), in a first step limited to only those members known in all life history stages. This neglect of some taxa (*Irisobrillia* Oliver, *Tokyobrillia* Kobayashi & Sasa) is consistent with previously expressed views that combined data from all stages provide more robust phylogenetic estimation (e.g. Cranston & Edward 1998). The matrix (available from the author upon request) comprises 68 phylogenetically informative characters for larvae, pupae and adults of both sexes scored for 40 terminal taxa. It was analysed under parsimony with *Prodiamesa* Kieffer as outgroup, using Hennig86 (Farris 1988) operating within a Microsoft Windows shell of Tree Gardener 1.0 (Ramos 1996), employing the heuristic option mhennig* followed by bb*. Resultant trees (of low consistency and retention) are susceptible to variation in ordering multistate characters, although all have *Austrobrillia* either as sister to *Euryhopsis* Oliver + *Eurycnemus* v.d.Wulp, or the three in an unresolved trichotomy. The three other *Brillia*-group genera known in all stages, *Xylotopus*, *Brillia* and *Pseudobrillia*, lie as sister to the previous trio, or are unresolved, basal. Analyses adding pupal and adult characters for *Plhudsonia* Sæther, and adult characters for *Irisobrillia* and *Tokyobrillia*, demonstrate that these, too, are members of the clade, but the monophyly of *Austrobrillia* + *Euryhopsis* + *Eurycnemus* is not affected. Monophyly and internal relationships within the *Brillia*-group continue to depend upon nuances of weighting (additivity). Notably, in “all-additive” trees *Brillia* and *Pseudobrillia* cluster with *Irisobrillia* and *Tokyobrillia* as proposed by Sæther & Wang (1992). The *Brillia*-group is basal in all analyses, followed by “*Psectrocladius*” (Cranston 1996) followed by *Propilocerus* Kieffer, then *Diplocladius* Kieffer as successive clades – congruent with relationships

found in several of Sæther & Wang's (1992) analyses. Further progress in elucidating the relationships within the *Brillia*-group, and the basal Orthoclaadiinae in general, appears to require wider knowledge of the immature stages, and perhaps better micromorphological documentation of the female genitalia, including especially circum-vaginal morphology (number of openings of ducts, microtrichiation of labia, etc). Drift-collected pharate female pupae can provide much evidence as demonstrated by Reiss for *Plhudsonia* (Sæther 1992).

On balance, analyses provide evidence for the *Brillia*-group lying at the base of the Orthoclaadiinae phylogeny, with the autapomorphic direction (oblique), curvature, and length of wing vein RM providing strong evidence for monophyly, as noted by Sæther & Wang (1992), but less obviously developed in *Plhudsonia*.

The female genitalia are instructive also in identifying the relationship of *Spaniotoma* (*Orthoclaadius*) *eurycnemoides* Edwards, described from a distinctively patterned female adult from Patagonia (Edwards 1931: 284). As redescribed by Sæther (1979) it was transferred to *Psectrocladius*, but re-evaluation by Sæther & Wang (1992) showed it to be a member of the *Brillia* group, probably within *Eurycnemus*. The bare wing and the genitalia resemble *Plhudsonia* and also *Austrobrillia longipes*, suggesting a possible association of *eurycnemoides* Edwards with one of the two pupal exuviae described above. However, the strong development of the pulvilli, which caused Edwards confusion and initially led Sæther (1979) to place the taxon in *Psectrocladius*, does not debar its inclusion in the *Brillia*-group, but presently precludes it from congenericity with *Austrobrillia*.

Ecology and biogeography

The larvae of *Austrobrillia longipes* are found on wood and leaves, and within wood immersed in streams in the southeast of Australia, and their guts contain predominantly fibres of wood (McKie & Cranston 1998). This appears to be a mode of living common to many, if not most, members of the *Brillia*-group. For example, the larvae of *Xylotopus par* (Coquillett) mine in decaying, water-logged hardwood in North American streams (Kaufman 1983, Oliver 1985). The larvae of *Pseudobrillia komorii* Niitsuma were found on fallen leaves in Japanese streams as early instars, and as miners in decomposing wood in later instars (Niitsuma 1991). Species of *Brillia* include both grazers in leafpacks and wood miners in the northern hemisphere. It may be surmised that the immature stages of additional taxa whose larvae are unknown may be found in similar habitats. Furthermore, given the basal phylogenetic position of the *Brillia*-group in the subfamily (see above), it might be inferred that grazing on leaves and mining in wood forms a plesiotypic behaviour in the orthoclaids.

The discovery of another taxon with a specialised immature biology that occurs in both South America and Australia adds further weight to arguments that the radiation of the Chironomidae at the taxonomic level of still extant monophyletic clades (genera) predates the fragmentation of Gondwana, followed by great stasis in biology and pupal morphology over a period in excess of 38 million years since Australia and South America were contiguous through Antarctica. The current distribution of the *Brillia*-clade suggests an even more ancient, Pangaean origin.

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