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Taxonomic revision of *Paraustrosimulium* Wygodzinsky & Coscarón: reassignment of *Austrosimulium colboi* and description of *P. obcidens* n. sp. from Western Australia

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Abstract

The hitherto monotypic South American genus *Paraustrosimulium* Wygodzinsky & Coscarón is revised to accommodate two Australian species: *Austrosimulium colboi* Davies & Györkös and *Paraustrosimulium obcidens* **n. sp.** The generic diagnosis is updated and the eastern Australian species *Paraustrosimulium colboi* (Davies & Györkös) **n. stat.** is re-described, including the male for the first time. The Western, Australian sister species of *P. colbo*, namely *P. obcidens* Craig, Moulton Currie **n. sp.** is also fully described. The relationship of *Paraustrosimulium* to other simuliid genera is discussed, as are aspects of historical biogeography.

Key words: Australia, South America, Gondwana, Diptera, Simuliidae, *Austrosimulium, Paraustrosimulium, Cnesiamima*

Introduction

The relationships of the southern South American species described as *Simulium anthracinum* Bigot, 1888, has long intrigued students of Simuliidae. Edwards (1931) was the first specialist to recognize the close relationship between that species and *Austrosimulium* Tonnoir—a lineage that was, until then, considered endemic to Australia and New Zealand. Although only adult females were known at that time, most specialists accepted the position of *anthracinum* within *Austrosimulium* (*e.g*., Smart 1945, Wydozinsky 1953). Wygodzinsky (*loc cit.*) described the pupa for the first time and redescribed and figured the female. The larva was first described by Dumbleton (1960) who—although expressing doubts about a close relationship between *anthracinum* and *Austrosimulium*, nonetheless retained that taxonomy. Wygodzinsky & Coscarón (1962) described the male for the first time and addressed Dumbleton's reservations, proposing the monotypic subgenus *Paraustrosimulium* for *A. anthracinum*. That segregate was eventually elevated to full genus by Crosskey (1969: 17)—a status generally accepted by most subsequent workers to the present day (*e.g*., Wygodzinsky & Coscarón 1973, Adler & Crosskey 2017). Recent phylogenetic studies provide contradictory evidence about the relationship of *Paraustrosimulium* to *Austrosimulium*. An analysis of morphological characters by Gil-Azevedo & Maia-Herzog (2007) suggests a close (sister group) relationship between the two genera; in contrast, the molecular analysis of Moulton (2003) reveals that *P. anthracinum* is rather distantly related from all *Austrosimulium* species analyzed except "*A*". *colboi* Davies & Györkös 1988. Indeed, the position of the sister pair *P. anthracinum* + "*A*". *colboi* was so distant from other analyzed *Austrosimulium* spp. that Moulton (*loc. cit.*) suggested the latter species should be reassigned to *Paraustrosimulium*. The objectives of this paper are to (1) to reassess the current assignment of *colboi* in *Austrosimulium*, (2) provide an expanded definition of *Paraustrosimulium* to include *colboi*, plus a previously

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undescribed species from Western Australian, (3) redescribe *P. colboi,* including the male for the first time, (4) describe a new species of *Paraustrosimulium* from Western Australia, and (5) offer comments about historical biogeography and the relationships of *Paraustrosimulium* to other austral simuliid genera.

Material and methods

We follow terms for structures as in Craig *et al.* (2012), which were based mainly on those of Adler *et al.* (2004). One character infrequently referred to in the simuliid literature are projections from ventral sclerites of the adult cervix. Such structures were referred to as "cervical laterales" by Davies *et al.* (1962: 133) and "cervical sclerites" by McAlpine *et al*. (1981: 24). We adopt the latter term here. For locality data, individual labels are indicated by [ ], with a / indicating a line break. Male and female signs, where given, are as {M} and {F} respectively.

Davies & Györkös (1988) stated that type material of "*A*". *colboi* was deposited in the Australian National Insect Collection (ANIC); however, Bugledich (1999: 330) noted that it could not be found there. Rediscovery of that material was outlined by Craig (2011: 4). In short, the material was never sent to ANIC, and instead had remained in the D.M. Davies Collection at McMaster University until its rediscovery by DAC (*loc*. *cit*.). Only some of the original type material was recovered. Material examined of *P. anthracinum* was from the D.M. Davies Collection. Other material of *colboi* was also examined from that collection, plus specimens collected by the authors during three separate collecting trips between 1996 and 2014. Material of *P. obcidens* **n. sp.** was collected by JKM in 1996 and by JKM and DCC in 2014. All specimens described in this paper are deposited either in the Australian National Insect Collection, CSIRO, Canberra (ANIC), or the University of Alberta Strickland Museum (UASM), as indicated.

The generic affinities of *Austrosimulium colboi* Davies & Györkös, 1988

In 1968, D.M. Davies, McMaster University, was presented with a collection of Simuliidae by Ron Pilfrey, who had studied the Australian simuliid fauna under the guidance of specialist Ian Mackerras. Twenty years later, Davies & Györkös (1988) described two new and unusual species from that material, even though it was badly bleached. "*Cnephia*" *pilfreyi* and "*Austrosimulium" colboi,* were compared to a number of different genera from Australia, southern Africa and South American, and tentatively assigned to genus pending collection of additional material. The first specialist to seriously question the assignment of *colboi* to *Austrosimulium* was Moulton (2003: 53), whose molecular analysis of a broad spectrum of simuliid genera placed "*A*". *colboi* as sister to *Paraustrosimulium*—distantly separated from other species of *Austrosimulium* in his analysis. Moulton (*loc*. *cit*.) further noted possible morphological synapomorphies shared between "*A*". *colboi*, *P. anthracinum*, plus two other species: "*Cnephia" pilfreyi* and *Cnesiamima atroparva* (Edwards, 1931). Craig *et al*. (2012) lent support for this hypothesis by suggesting that "*A*". *colboi* could be reassigned to *Paraustrosimulium* based on features of the male genitalia and pupal gill. Further evidence can be found in a recently published neighbor-joining tree of COI DNA barcodes for species of austral Simuliidae (Hernández-Triana *et al*. 2017). Although such trees do not represent a phylogeny, "*A*". *colboi* and *P. anthracinum* were relatively closely placed on that tree, but distantly so from seven other species of *Austrosimulium,* which all clustered together. In view of this growing body of evidence, we formally reassign "*Austrosimulium*" *colboi* to *Paraustrosimulium*. The genus is here re-diagnosed to accommodate that species, plus a previously undescribed one from Western Australia.

Paraustrosimulium (Wygodzinsky & Coscarón)

Austrosimulium (*Paraustrosimulium*) Wygodzinsky & Coscarón 1962: 244. New subgenus. Stone 1963: 14.
Austrosimulium (*Paraustrosimulium*). Dumbleton 1963: 333. Dumbleton 1973: 484.
Paraustrosimulium. Crosskey 1969: 17. Raised to generic status. Wygodzinsky & Coscarón 1973: 189. Crosskey 1982: 16. Crosskey 1987: 438. Crosskey & Howard 1997: 18. 2004: 10: Adler & Crosskey 2017: 31.
Paraustrosimulium. Hernández-Triana *et al*. 2017: 350.

Re-diagnosis. *Adult*: Antenna with 8 flagellomeres; frons width variable; female mandible expanded subapically (*colboi, obcidens*), not so (*anthracinum*)**,** teeth on both sides; lateral cervical sclerites markedly expressed; antepronotal lobe markedly hirsute (*anthracinum*), or not (*colboi, obcidens*); anepisternal (aka pleural) membrane bare; metathoracic furcasternum with dorsal projections; wing with small to minute basal cell; costa with spiniform setae; apical end of R_1 with (*anthracinum*) or without fine spiniform setae; Rs not branched, but may be thickened apically with indication of branching; M appearing thickened apically; Cu curved; female thorax not markedly domed in Australian species, more so for *anthracinum*, katepisternal sulcus well defined; calcipala well expressed, rounded apically; pedisulcus as series of wrinkles (*anthracinum*) or definite depression (*colboi*, *obcidens*); claw with (*anthracinum, obcidens*) or without (*colboi*) definite tooth, when present separated from basal heel by distinct notch; spermatheca externally smooth, internally with sparse acanthae, pigment well extended along duct (*obcidens*), only slightly (*colboi*) or not (*anthracinum*); genital fork with short broad anterior stem, forwardly directed apodemes poorly expressed or absent, lateral arms short, apical lobes large; cercus rounded, anal lobe angulate proximally (*colbo, obcidens*), tapered (*anthracinum*); male gonostylus angulate with 2–4 terminal spines; ventral plate angulate laterally, with (*colboi, anthracinum*) or poorly expressed (*obcidens*) median keel, median sclerite well developed and M–shaped; parameres plate–like, numerous fine small parameral spines. *Pupa*: cocoon slipper–shaped, lacking anteroventral collar, well defined anterior edge, no marked medial projection, ventral floor present (*colboi*) or absent; pupal cuticle brown anteriorly; cephalic and thoracic cuticle with low tubercles; thoracic dorsocentral setae distinct and curled apically; cephalic plate with frontal and facial setae present; gill of simple construction, either annulated tapered tubular construction (*colbo, obcidens*) or, annulated flattened lamellae (*anthracinum*), concertinaed in histoblast; abdominal armature not markedly developed, distinct pleurites not present or markedly small; tergites III and IV with 4+4 hooks posteriorly, V to IX with spine combs anteriorly, sternum V with 4+4 hooks posteriorly, sternum VI and VII with 1+1 hooks, or all sternal hooks absent (*colboi*), small hooks on small pleurites VI and VII; poorly expressed spine comb on tergite IX, terminal spines short and blunt, grapnel hooks exacerbated. *Larva*: cervical sclerites small, subcircular to elongated, not fused to postocciput or slightly so; postgenal cleft well developed (*colbo, obcidens*) or shallow (*anthracinum*); antenna slightly longer than labral fan stem, medial plus basal antennomeres shorter than distal antennomere. Mandibles with apical teeth on narrowed extension, spinous teeth fine and pointed, mandibular serration and sensillum as separate structures; hypostoma with 13 teeth not arranged in distinct groups, underlain by ventral edge of hypostoma; abdominal cuticle bare, except for rectal scales only in *anthracinum*; anal sclerite X–shaped, with lateral thickening of medial region (aka interarm struts); accessory and semicircular sclerites absent; rectal papillae of three simple lobes.

Constituents. *Paraustrosimulium anthracinum* (Bigot) (South America), *Paraustrosimulium colboi* (Davies & Györkös) (Victoria, Australia), *P. obcidens* Craig, Moulton, Currie **n. sp.** (Western Australia).

Paraustrosimulium colboi (Davies & Györkös), 1988

(Figs. 1–42)

Austrosimulium colboi Davies & Györkös, 1988: 111. Original designation. Provisional placement to genus.
Austrosimulium (*Austrosimulium*) *colboi.* Crosskey 1989: 221.
Austrosimulium colboi. Crosskey & Howard 1997: 26. Unplaced to subgenus.
Austrosimulium (*Austrosimulium*) *colboi.* Bugledich 1999: 330.
"*Austrosimulium colboi*". Moulton 2003: 47.
Austrosimulium colboi. Crosskey & Howard 2004: 18. Adler & Crosskey 2009: 19; 2017: 30. Unplaced to subgenus.
?*Austrosimulium colboi*. Craig *et al.* 2012: 53.
Austrosimulium colboi. Hernández-Triana *et al*. 2017: 350.
Paraustrosimulium colboi. This work, new combination.

Redescription. *Adult female* (based on numbers of reared specimen). Body (Fig. 1): general body colour in alcohol evenly blackish brown; total length 1.9–2.3 mm. *Head* (Fig. 2): width 0.57–0.60 mm; depth 0.4 mm; postocciput black, hirsute; frons black; frons–head ratio (narrowest width of frons: greatest width of head) 1.0:6.3. *Eyes*: slightly bicolourous, interocular distance 0.09 mm**;** ommatidia 0.015 mm in diameter; 35–39 rows up and across at mid–eye. *Clypeus*: black; 0.17mm wide; vestiture of sparse black hairs. *Antenna* (Fig. 3): total length 0.41–0.46 mm; pedicel small, scape enlarged, both blackish brown, remainder brown; 8 flagellomeres, basal ones wider than long, distally ones more quadratic, overall tapered, apical flagellomere distinctly so. *Mouthparts*: substantial, *ca.*

0.7 length of head depth; maxillary palpus (Fig. 4), total length 0.45 mm, articles overall brownish black, 3rd article darker; proportional length of 3rd, 4th and 5th articles 1.0:0.8:1.5; sensory vesicle ovoid, 0.5x width of 3rd article, opening 0.3x width of vesicle; mandible (Fig. 5), broadly triangular apically, sharply pointed with 48–50 inner teeth and 9–11 finely pointed outer teeth; lacinia (Fig. 6) with 13–15 inner teeth and 22–26 outer teeth; cibarial cornuae (Fig. 7) (partly reconstructed) lacking apical fluting or sculpture, sharply terminated, central depression broad. Cervical sclerites markedly developed (Fig. 1). *Thorax*: moderately domed; length 0.80–0.96 mm; width 0.60–0.63 mm; scutum evenly blackish brown, vestiture of evenly distributed recumbent silver hairs; postpronotal lobe with longer hairs; antepronotal lobe with longer hairs; scutellum and postnotum concolourous with scutum; scutellar depression and scutellum with long substantial black hairs; pleuron and anepisternal membrane blackish brown, bare. *Haltere*: dark. *Wing* (Figs. 8, 9): length 2.1–2.4 mm; width 0.9–1.2 mm, veins lightly pigmented, costa not extended to wing apex with spiniform setae distally, absent from other veins; radial veins closely applied to costa; basal cell absent; a:b ratio 1.0:2.8. *Metathoracic furcasternum* (Fig. 10): dorsal arm with distinct projection. *Legs* (Fig. 1): overall blackish yellow; hind basitarsus about 5.5x as long as its greatest breadth, ventral row of stout spines absent, calcipala as long as wide 0.75x width of basitarsus, pedisulcus present, but not markedly developed (Fig. 11); tarsal claw (Fig. 12) with moderately developed basal heel and markedly small tooth. *Abdomen* (Fig. 13): abdominal scale black with dark hairs, not greatly extended; tergite II 5x wider than long, shallowly V–shaped, III–V as wide as long, rounded, VI 2x wider than long; dorsal vestiture of small black hairs increased in density posteriorly. *Genitalia*: sternite VIII vestiture of sparse coarse black hairs posterolaterally; hypogynial valves (Fig. 14) short, lightly pigmented with vestiture of sparse short hairs and triads of microtrichia; median edges slightly convex, slightly strengthened along edge, bluntly rounded apically; genital fork (Fig. 15) with anterior stem broad (not easily observed), but well sclerotized and pigmented narrowly medially, flared anteriorly, lateral arms broad, indications of lateral apodeme (as in *Gigantodax*), more distal apodeme (as in *Austrosimulium*) present only as ridge, lateral plates large, angular posteromedially, rounded posterolaterally; spermatheca ovoid (Fig. 16), surface un–patterned; sparse internal acanthae in pairs and triads; junction of spermathecal duct pigmented and slightly sculpted; cercus (Fig. 17) as wide as long, broadly rounded in lateral view, anal lobe shallow, angulate proximally.

Adult male (reared specimens and others). *Body* (Fig. 18): general colour evenly black; total length 2.2–2.6 mm. *Head* (Fig. 19): width 0.89 mm; depth 0.6 mm; wider than thorax. *Eyes*: upper ommatidia very dark red, 0.04 mm in diameter, *ca.* 14 across, 20 down; lower ommatidia almost black, 0.018 mm in diameter, *ca.* 35 across and 23 down. *Clypeus*: black; vestiture of very sparse black hairs; 0.15 mm wide. *Antenna* (Fig. 20): total length 0.51–0.55 mm; pedicel longer and wider than other divisions; first flagellomere longer than wide, others subrectangular; non–tapered, markedly narrow in comparison to that of female; scape and pedicel black, first flagellomere dark brown remainder evenly brown; flagellum markedly not hirsute. *Mouthparts*: poorly developed; length 0.26x head depth; mandibles insubstantial, finely tapered with apical hairs; laciniae as for mandible; maxillary palpus dark brown, 0.4 mm long, proportional lengths of 3rd, 4th and 5th articles 1.0:1.1:2.0, sensory vesicle small, occupying 0.33x width of article, opening 0.5x width of vesicle. Cervical sclerites markedly developed. *Thorax*: length 0.9–1.1 mm; width 0.8 mm; in alcohol, scutum evenly velvety black, vestiture of fine recumbent pale hairs; scutellum and postscutellum concolourous with scutum, coarse long black hairs. *Wing*: 2.1–2.4 mm in length, 1.0–1.1 mm in width; otherwise as for female. *Haltere*: tan. *Legs*: blackish brown; hind basitarsus about 5.5x as long as its greatest breadth, lacking row of stout spines; tarsal claw (Fig. 21) partially covered by grappling pad of *ca.* 20 hooks, distinct small basal tooth and heel. *Abdomen* (Fig. 22): black; abdominal scale with long fine hairs, tergites markedly broad, on tergites II–V hirsute laterally, less so on posterior others. *Genitalia*: ventral view (Fig. 23), ventral plate directed ventrally giving appearance of broadly concave apex, 1.5–2.0x wider than long, median keel well developed, with vestiture of fine hairs, plate roughly sculpted laterally; anteromedial depression broadly U to V–shaped, slight central convexity, basal arms short and pigmented (Fig. 24); median sclerite poorly expressed, broad and slightly divided apically; parameres present, moderately expressed, plate–like, apical rows of small spicules; adeagal membrane with sparse rows of minute microtrichia; gonocoxa 1.7x longer than basal width, markedly coarse black hairs on distal half; gonostylus (Fig. 25), approximately 3.0x longer than basal width, apically with 3 substantial terminal spines—variable and occasionally with one spine markedly displaced to outer apex.

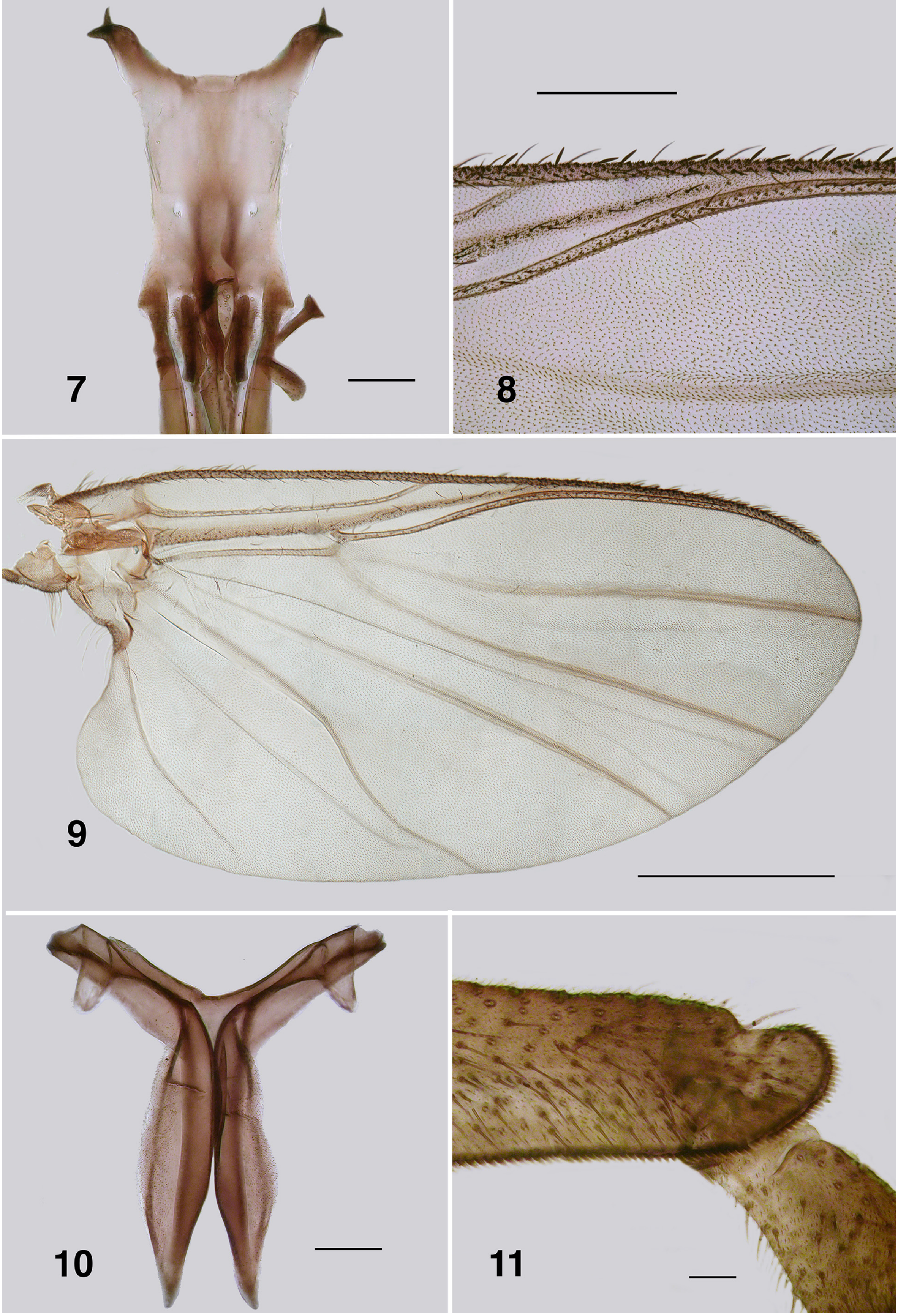
Pupa (based on numbers of specimens). (Fig. 26). *Body*: length, female 2.2–2.8 mm; male 2.2–3.3 mm. *Head*: frontal cephalic plate lacking dorsal depression; ratio of basal width to vertex width of female 1.0:1.5, for basal width to length 1.0:2.3, rounded apically (Fig. 28), male ratios 1.0:1.6 and 1.0:2.3 respectively (Fig. 29); evenly tuberculate, frontal setae absent, facial setae present, but insubstantial, ocular spine absent. *Thorax*. Dorsum with very small tubercles, no pattern (Fig. 30); dorsocentral setae spine–like and curled apically. *Gill* (Fig. 26, 27): basically a single expanded tapered tube directed anteroventrally, 1.7–2.1 mm, full length 0.3 mm at greatest width with *ca*. 19 annulations on the longer anterior portion with 2 or 3 on a stub–like posterior lobe (Fig. 27), fenestra normal (Fig. 30), fine filaments absent. *Abdominal armature*: sternal hooks absent, but sternite VIII with sparse multi–pointed scales; tergites I & II with 4–6 moderately expressed setae; tergite III with four hooks posteriorly per side, 3 or 4 other fine setae, no lateral hook; tergite IV as for III, but with single small hook laterally; tergites V–VIII with markedly poorly–expressed spine comb anteriorly, laterally morphing into low multi–pointed scales, four to five fine setae posteriorly; tergite IX with poorly–expressed broad row of low spines and scales anterad, terminal spines short, not markedly sharp, grapnel hooks well expressed (Fig. 31). *Cocoon* (Fig. 26). Surface smooth, fabric coarsely woven, silk filaments obvious, medium brown; distinctly slipper–shaped fully covering pupa with well defined anterior edge, slight median projection, complete ventral floor, close fitted to pupa.

Larva (based on numbers of last instar larvae). *Body* (Fig. 32): overall grayish brown, stubby (head large in relation the body), thorax and anterior abdomen subequal in diameter, expanded smoothly posteriorly; total length 4.0–4.9 mm. *Head* (Figs. 33): distinctly bicolourous, background pale translucent yellowish brown, head spots marked, but not strongly pigmented, medial and posterior spots form distinct inverted T, mediolateral spots distinct; most spots with negative centre; probable males have a lighter head pattern than females; head length 0.69–0.70 mm, width 0.50–0.60 mm; distance between antennal bases 0.30–0.38 mm; lateral margins of head smoothly convex, more so posteriorly; cervical sclerites well developed and pigmented, rounded posteriorly but flared anteriorly, not fused to postocciput; anterolateral edges of apotome sharply pigmented; genae with darker 'eye brow' above stemmata. *Antenna* (Fig. 34): overall clear pale brown; total length 0.4 mm; well extended beyond labral fan stem; distal article slightly longer than other two articles combined; proportions of basal, median and distal article 1.0: 0.6: 1.8. *Labral fan*: stem markedly translucent; 62–64 fine rays, 0.56 mm in length, 0.01 mm in width; microtrichia as long as ray width, distinct pattern with *ca*. 5 microtrichia decreased rapidly in length. *Mandible* (Fig. 35): apical brush well developed with distinct pigmented base: apical teeth not markedly developed; subapical teeth small, 8–9 spinous teeth; 2 distinct serrations widely separated, sensillum distinct and finely pointed; blade region long, smooth and slightly concave. *Maxilla* (Fig. 36): lobe markedly cone–shaped, asymmetrical, palp longer than lobe, closely applied, 3x as long as basal width. *Postgenal cleft* (Fig. 37): small, but U–shaped with irregular anterior apex, sclerotized posterior tentorial pit cuticle extensive, pits ovoid; ratio of hypostoma, bridge and cleft 1.0:1.9:0.7; suboesophageal ganglion not pigmented. *Hypostoma* (Fig. 38): ventral edge as raised dome; 13 teeth, median tooth barely protruded beyond edge, two sublateral teeth smaller and subequal in length, other larger and protruded beyond edge, lateral teeth larger and well protruded, paralateral teeth smaller and sharp, variable expression, no others evident; no hypostomal serrations; four hypostomal setae per side. *Postgenal bridge*: pale and concolourous with genae. *Thorax*: (Fig. 39) anterior prothorax dark brown, remainder paler; pharate pupal gill as black, paddle–shaped horn; annulations of gill concertinaed. *Abdomen*: evenly medium brown, darkened posteriorly; abdominal segments expanded smoothly; posteroventral tubercles not markedly developed. *Anal papillae*: three simple lobes. *Posterior proleg* (Fig. 40): rectal scales absent; anal sclerite X–shaped with median region poorly expressed, anterior arms slightly flared, shorter than posterior arms, interarm struts distinct, posterior arms short; accessory sclerite absent, pigmented semicircular sclerite absent, but clear cuticle evident in that position. *Posterior circlet*: *ca*. 76–80 rows of 11–13 hooks (total *ca*. 930).

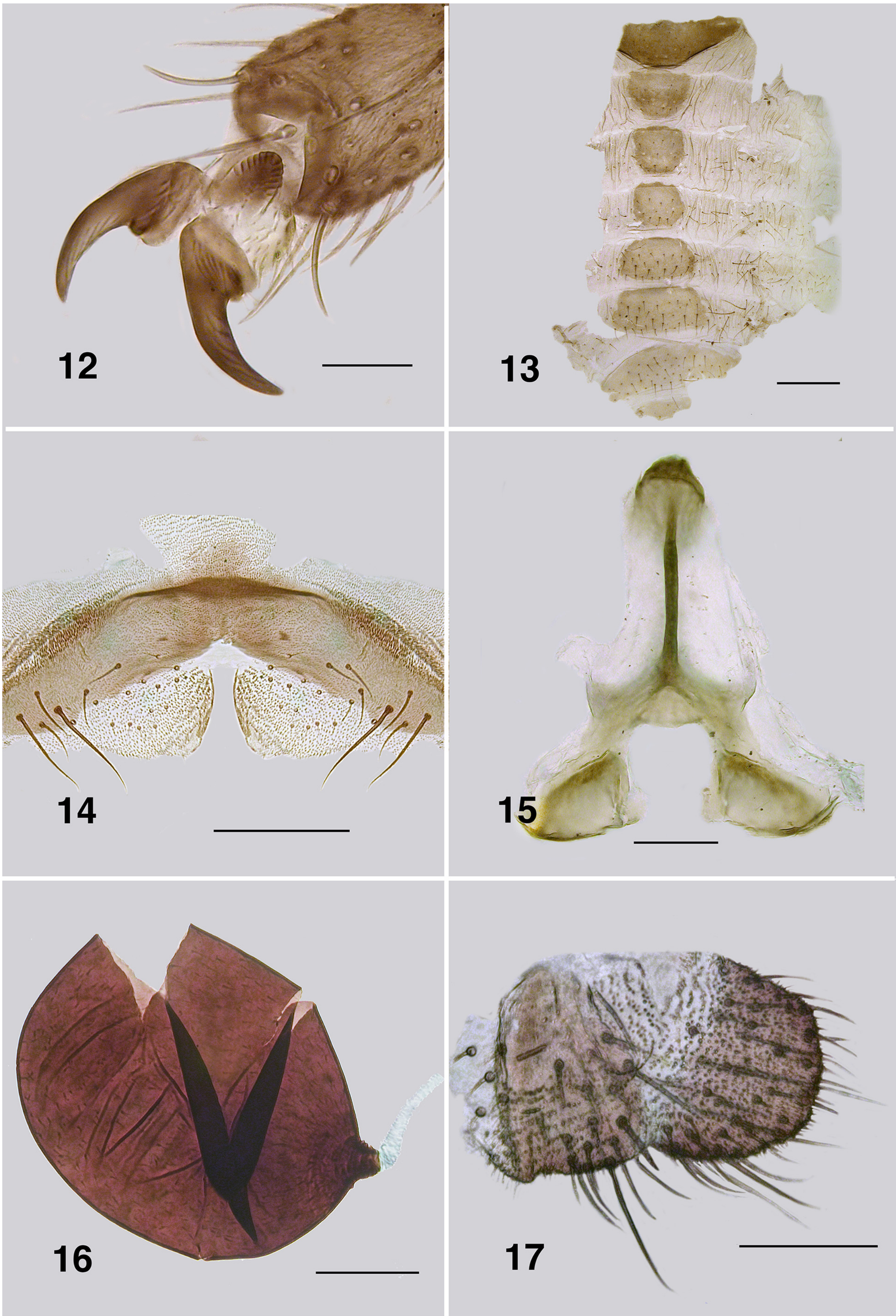
Etymology. Named by Davies & Györkös (1988) after Murray H. Colbo.

Types. The original type material as designated by Davies & Györkös (1988: 111) was stated to be a holotype pharate female with parts mounted on slides. Paratypes of 5 pupae, a pupal exuviae in alcohol with filaments on slides and 2 mature larvae mounted on slides. Label data as "Halls' Gap (37° 07´S/ 142° 07´E) in a slow flowing drain in a grassy forest, 26.viii.1958. I. M. Mackerras". As partially explained by Craig (2011), the dissected materials were never permanently mounted on slides and, when recovered, were still in depression slides, in glycerine, of which most had crept out of the depression. Alcohol material was dry—not surprising after some 20 years, or so. Much of the described material by Davies & Györkös (*loc. cit.*) was not recovered. That which was, was badly bleached and essentially useless. Some, however, was stained in Chlorozoal Black and examined to confirm it was of *P. colboi*, then placed in microvials, pinned, labeled as below and deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra.

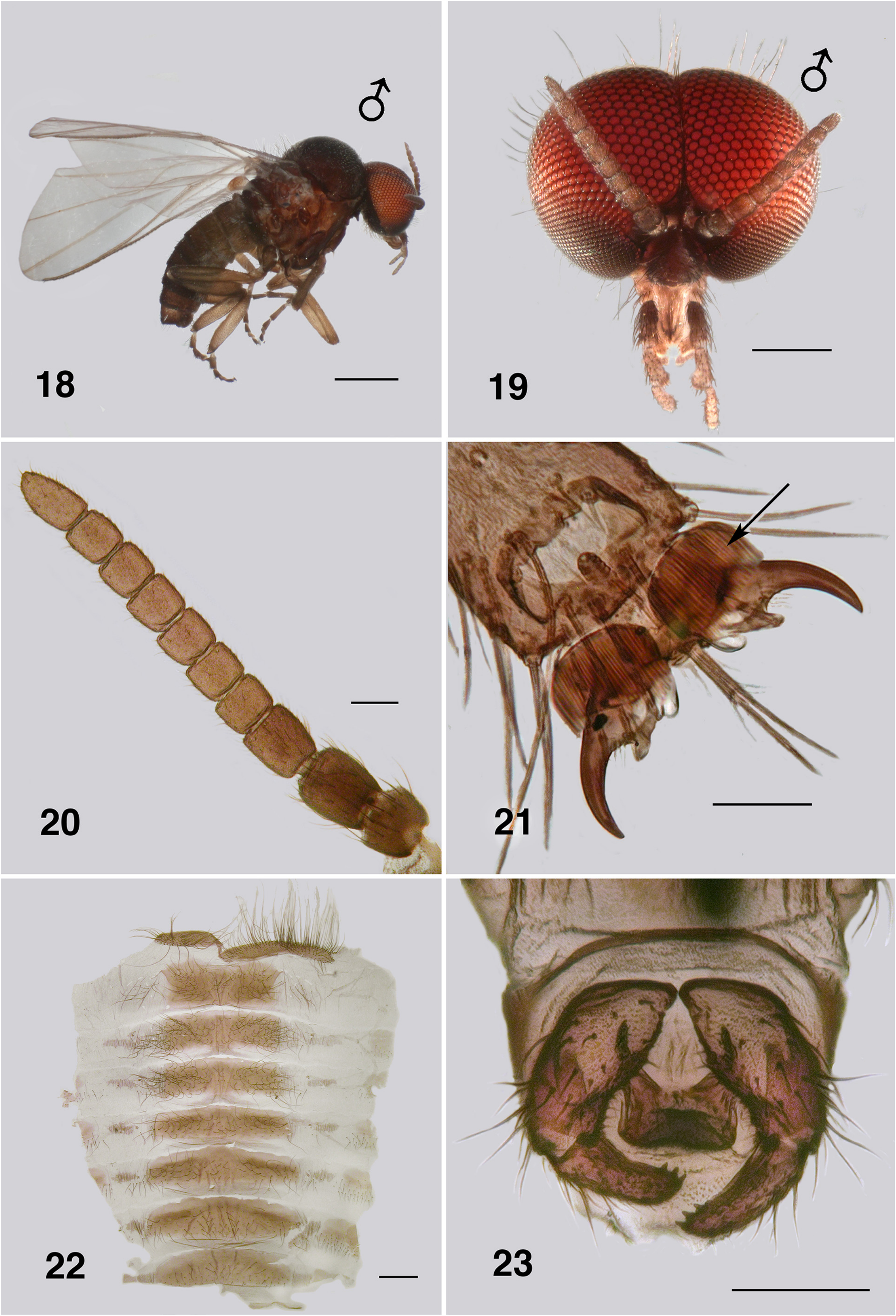
FIGURES 1–6. *Paraustrosimulium colboi* female. (1) Habitus. Reared. ETOH. Arrow indicates lateral cervicales. Scale bar = 0.5 mm. (2) Head. Frontal view. ETOH. Scale bar = 0.2 mm. (3) Antenna. Scale bar = 0.05 mm. (4) Maxilla. Scale bar = 0.05 mm. (5) Mandible. Note teeth on both sides. Scale bar = 0.02 mm. (6) Lacinia. Scale bar = 0.02 mm.



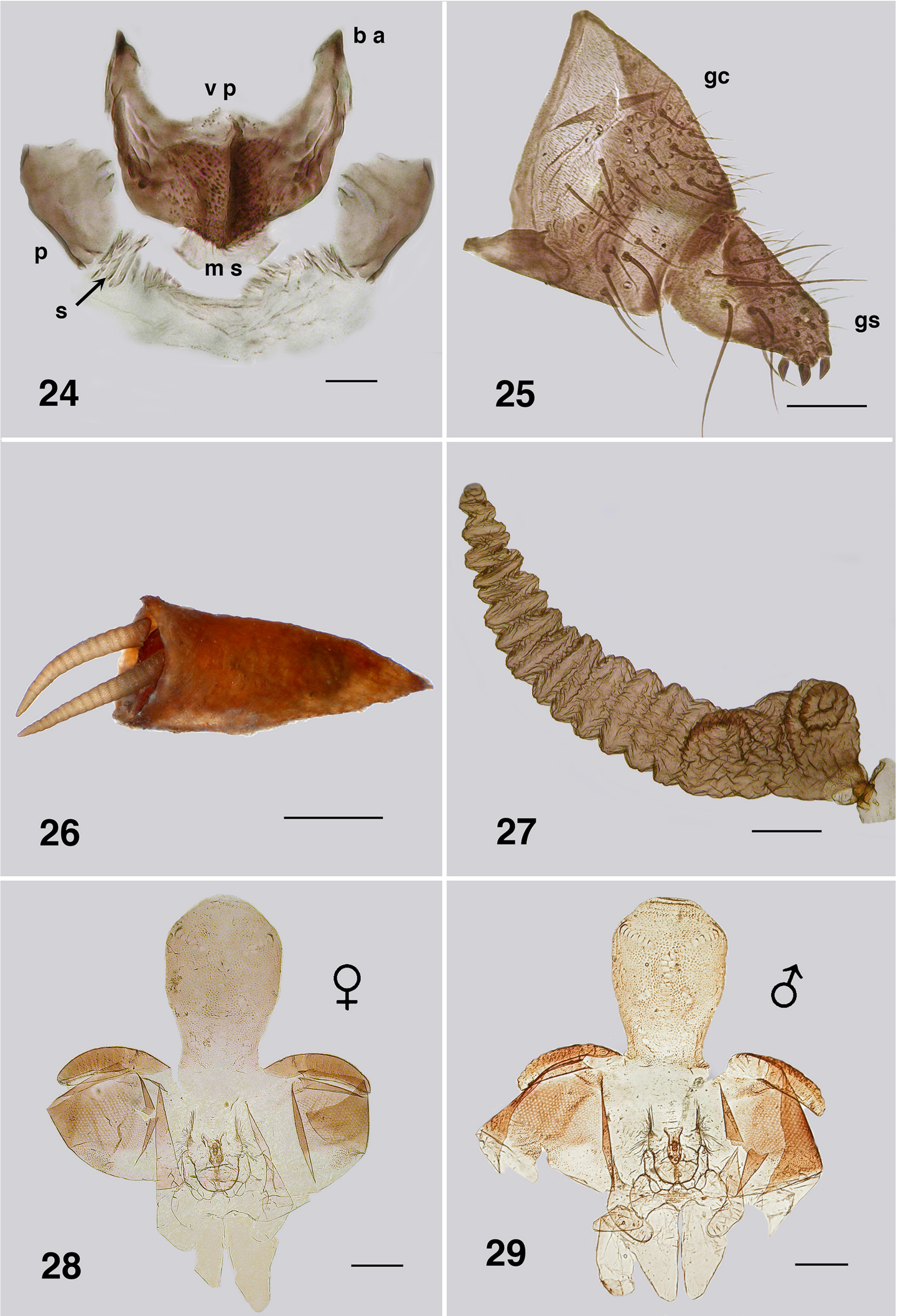
FIGURES 7–11. *Paraustrosimulium colboi* female. (7) Cibarium. (Partly reconstructed). Scale bar = 0.05 mm. (8) Wing veins. Scale bar = 0.2 mm. (9) Wing. Scale bar = 0.5 mm. (10) Metathoracic furcasterum. Scale bar = 0.05 mm. (11) Basitarsus, calcipala & pedisulcus. Scale bar = 0.02 mm.



FIGURES 12–17. *Paraustrosimulium colboi* female. (12) Claw. Scale bar = 0.02 mm. (13) Abdominal tergites. Scale bar = 0.2 mm. (14) Hypogynial valves. Scale bar = 0.1 mm. (15) Genital fork. Scale bar = 0.05 mm. (16) Spermatheca (flattened) Scale bar = 0.05 mm. (17) Cercus & anal lobe. Scale bar = 0.05 mm.

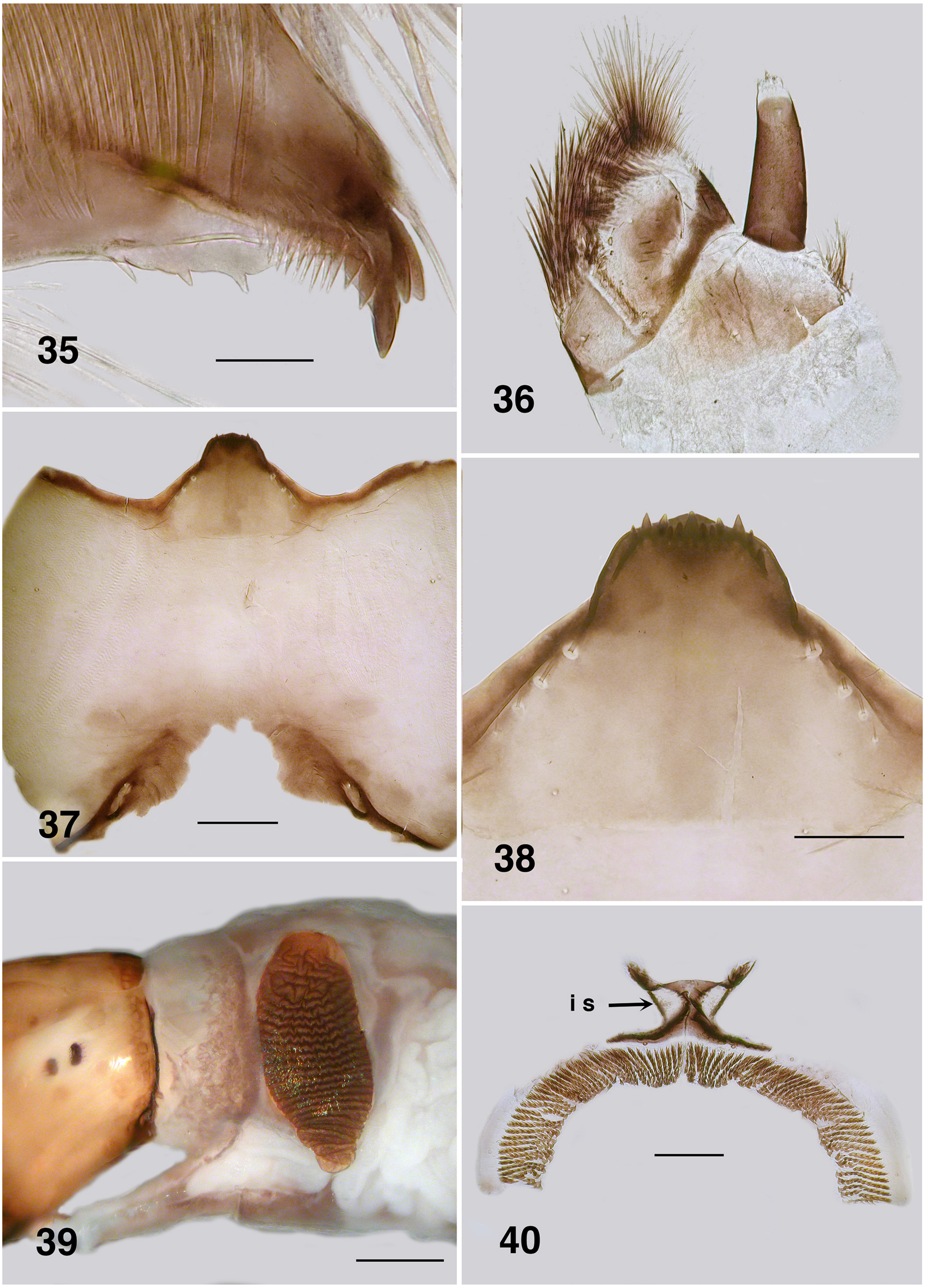


FIGURES 18–23. *Paraustrosimulium colboi* male. (18) Habitus. Reared. ETOH. Scale bar = 0.5 mm. (19) Head, frontal view. ETOH. Scale bar = 0.2 mm. (20) Antenna. Scale bar = 0.05 mm. (21) Claw. Arrow indicates grappling hooks. Scale bar = 0.02 mm. (22) Abdominal tergites. Scale bar = 0.2 mm. (23) Genitalia, ventral view, cleared, in glycerine. Scale bar = 0.1 mm.



FIGURES 24–25. *Paraustrosimulium colboi* male. **FIGURES 26–29.** *Paraustrosimulium colboi* pupa. (24) Ventral plate & parameres (slide mounted). Abbreviations: b a—basal arm, m s—median sclerite, p—paramere, s—spines, v p—ventral plate. Scale bar = 0.02 mm. (25) Gonocoxa—gc, gonostylus—gs. Lateral view. Scale bar = 0.05 mm. (26) Pupa and cocoon. Scale bar = 0.1 mm. (27) Pharate gill, slightly expanded. Scale bar = 0.2 mm. (28) Female cephalic capsule. Scale bar = 0.2 mm. (29) Male cephalic capsule. Scale bar = 0.2 mm.

FIGURES 30–31. *Paraustrosimulium colboi* pupa. **FIGURES 32–34.** *Paraustrosimulium colboi* larva. (30) Thoracic cuticle. Arrowhead indicates basal fenestra. Scale bar = 0.1 mm. (31) Abdominal terminal spines & grapnel hooks. NB: cocoon silk entangled in grapnel hooks & small terminal spines (arrows). Scale bar = 0.1 mm. (32) Last instar larva, habitus. Scale bar = 1.0 mm. (33) Head. Dorsal view. Scale bar = 0.2 mm. (34) Antenna. Scale bar = 0.1 mm.



FIGURES 35–40. *Paraustrosimulium colboi* larva. (35) Mandible apex. Scale bar = 0.02 mm. (36) Maxilla. Scale bar = 0.05 mm. (37) Genae, hypostoma, postgenal cleft. Scale bar = 0.1 mm. (38) Hypostoma. Scale bar = 0.05 mm. (39) Lateral view of pharate pupal gill. Scale bar = 0.2 mm. (40) Anal sclerite & circlet of hooks. Abbreviation: i s—interarm strut. Scale bar = 0.1 mm.


41


42

43


Holo-
type

Paraustrosimulium
obcidens

Western Australia
Styx River, S34.8845°
E117.1045°, alt. 50 m.
9-xi-2014, Coll. J.K.
Moulton

ANIC Database No.
29 026577

44

FIGURES 41, 42. *Paraustrosimulium colboi* habitats. **FIGURES 43, 44.** *Paraustrosimulium obcidens* holotype. (41) Earl's Culvert, Lodge Road, Grampians National Park, S37.16957º E142.34879º, 244 mabs, 10–vii–2011. (42) Culvert stream, Glenelg Road, Grampians National Park, S37.18138º E142.37428º, 228 mabs, 10–ix–2014. (43) Holotype, habitus (dried), (Styx River). Scale bar = 0.5 mm. (44) Holotype labels.

Holotype. Female head and hind legs. Label data:– [Holo–/type (red edges)] [*Austrosimulium colboi*/ Davies & Györkös 1988/ Victoria, Hall's Gap/ (37° 07'S/142° 07'E)/ 26.viii.l958/ I. M. Mackerras] [Exam/ prep./ DAC, 2011]. Stained with Chlorazol Black, in glycerine microvial on pin. (ANIC).

Paratypes. Labels as for holotype, but with [Para–/type (yellow edges)]. One mature last instar larva, head and pupal gill histoblasts separate, stained with Chlorazol Black, in glycerine microvial on pin. Female hind legs, ex–pupa, not stained, as above. Pupal gills and thoracic cuticle, stained with Chlorazol Black, as above. Four separate pupal gills, as above. (ANIC).

Additional material. Numerous specimens of larvae, pupae and reared adults. Two reared females and pupal exuviae. ETOH. Label data:– [Paraustrosimulium / colboi] [Australia, Vic., Grampians Nat. Prk.,/ Syphon Rd Bdg, Glenelg Rv, "Big Cord",/ S37.31232, E142.36711, 263 mabs, / 26–xi–2014, Coll. D.A.& R.E.G. Craig./ OZV14b] [UASM#/ 370849]. One reared female and pupal exuviae, as above, but with [ANIC Database No./ 29 026696].

Two tubes, ETOH of larvae, pupae, reared male and female. Label data:– [Paraustrosimulium / colboi] [Australia, Vic., Grampians Nat. Park,/ Glenelg Rd, upstream of culvert,/ S37.18138, E142.37428, 233 mabs,/ 10–ix–2014, Coll. D.A.& R.E.G. Craig./ OZV12.], one with [UASM/370850] the other [ANIC Database No./ 29 026697]. One tube, ETOH, larvae, pupae, reared females and males. Label data:– [Paraustrosimulium / colboi] [Australia, Vic., Grampians Nat. Park,/ Lodge Rd, Earl's culvert. S37.16957,/ E142.34879, 244 mabs, 11–vii–2011,/ Coll. D.A.& R.E.G. Craig. #8a.] [UASM #/ 370851]. One tube, ETOH, larvae and pupae. Label data:– [Paraustrosimulium / colboi] [AUSTRALIA/ Victoria/ Grampians N. P./ small stream X–ing/ Glenelg River Rd./ 28 September 1996/ JK Moulton] [ANIC Database No./ 29 026698]. Twelve slides of all stages. Label data:- [Paraustrosimulium/ colboi/ Aust. Victoria, Grampians/ Glenelg River/ 28-ix-1966/ Coll. JK Moulton] [UASM#/ 370868 -370879].

Distribution. Details given by Davies & Györkös (1988: 105) for the original material of *P. colboi* was that it had been collected in 1958 by Ian Mackerras from a site near Halls Gap, Grampians Nation Park, Victoria. However, map coordinates given locate that site in the Black Range State Park, some 30 km to the west of the Grampians and on checking (DAC pers. obs. 2011), the locality was not associated with running water. We are of the opinion that the longitude minutes given for the type locality is a typographical error, on the basis that it is the same as for the latitude, (*i.e.* 07'). For Halls Gap it should of *ca*. 32', but the exact location is unknown and original labeling missing. Other *P. colboi* material was found by JKM in 1996 in a stream to the southwest of Halls Gap and two other sites in that general area were established by DAC in 2011 and 2014—a markedly precinctive distribution (Fig. 85):

Victoria: Grampians National Park, small stream crossing Glenelg River Road. 28–viii–1996. Coll. J.K. Moulton. Grampians N. P., Lodge Road, Earl's Culvert, S37.16957° E142.34879°, 244 mabs, 10–vii–2011. Coll. D.A. & R.E.G. Craig. Grampians N. P., Glenelg Road, culvert, S37.18138° E142.37428°, 228 mabs, 10–ix–2014. Coll. D.A. & R.E.G. Craig.

Bionomics. Clearly an early spring species and univoltine, *Paraustrosimulium colboi* larvae and pupae occur in ephemeral, slowly–flowing streams (velocity 30–44 cm/sec) with generally colder water (temperature 9.6–14.5ºC) and sandy substrate. Larvae are restricted to trailing vegetation and woody debris. At the Earl's Culvert locality (Fig. 41), larvae of *P. colboi* occurred with those of *Austrosimulium furiosum* (Skuse)*, A. montanum* Makerras & Mackerras and *Paracnephia umbratora* (Tonnoir)—the later, too, almost an exclusively moderate–flow simuliid. At the Glenelg Road culvert stream (Fig. 42), *P. colboi* was the only simuliid present and in considerable numbers. Nothing is known about behaviour of the adults.

Remarks. There is little doubt that the material discovered since the original collection by Mackerras and described by Davies & Györkös (*loc. cite.*) is of *P. colboi*. There is good concordance of morphological character states with, however, some exceptions. They made the point that female adults possess mandibular teeth only on the inner surface, similar to mandibles of New Zealand *Austrosimulium*. Our material of *colboi* (and *obcidens* below) has definite teeth on the outer surface (Fig. 5), albeit they are small and were perhaps not noticed by Davies & Györkös? Known Australian *Austrosimulium* (*A.*) and *Novaustrosimulium* all lack outer mandibular teeth (Craig, pers. obs.). The anterior arm of the female genital fork is illustrated as being narrow (their Fig. 25), however, membranous areas to the side are not easily observed even in fresh material (Fig. 15), so in newer material the arm can be seen to resemble those of *Austrosimulium*, generally assumed to be unique in Simuliidae. Other character states of the fork are of similar expression. Then, too, is a discrepancy in the shape of the larval postgenal cleft—our material has a deeper cleft and is irregular (*cf.* Fig. 37 with their Fig. 29). Of further concern is the number of hooks comprising the larval posterior circlet—our material has more, as well there are differences in the illustration (their Fig. 33) of the anal sclerite and our material (Fig. 40), where the sclerite is markedly more substantive. Indicative of minor variation between populations? The colour of the larvae as described by Davies & Györkös (1988: 111) is paler than our recent material (Fig. 32)—perhaps not surprising given the age of their material.

Paraustrosimulium obcidens **Craig, Moulton & Currie, new species.**

(Figs. 43–85)

Description. *Adult female* (based on reared specimens). *Body* (Fig. 43): general body colour evenly dark brown, specimens from Styx River (Fig. 43) darker than from Deeside Coast (Fig. 45); total length 1.6–2.3 mm. *Head* (Fig. 46): width 0.54–0.60 mm; depth 0.35 mm; postocciput black with coarse hairs; frons blackish brown; frons–head ratio (narrowest width of frons: greatest width of head) 1.0:7.5. *Eyes*: dark red, interocular distance 0.06 mm;

ommatidia 0.014 mm in diameter; 35–39 rows up and across at mid–eye. *Clypeus*: blackish brown; 0.15mm wide; vestiture of sparse pale hairs. *Antenna* (Fig. 47): pedicel small, scape larger, both yellowish, first flagellomere yellowish basally, other flagellomeres black**,** subequal in size, apical flagellomere markedly elongate; total length 0.5 mm, markedly extended beyond head margin. *Mouthparts*: *ca*. 0.5 length of head depth; maxillary palpus (Fig. 48), total length 0.32–0.35 mm, 1st and 2nd articles pale, 3rd article semispherical and dark brown, sensory vesicle ovoid, 0.5x length and width of 3rd article, opening 0.25x width of vesicle; 4th article short, 0.5x 5th article length; proportional length of 3rd, 4th and 5th articles 1.0:0.5:1.0; mandible (Fig. 49), slightly expanded apically, sharply pointed with 7–9 irregularly arrayed, finely pointed outer teeth, 20–23 fine, small inner teeth apically, *ca*. 9 other poorly expressed teeth proximally; lacinia markedly with 12 or 13 inner and outer teeth; cibarial cornuae splayed, lacking apical fluting or sculpture, pigmented terminated, central depression shallow and broad (Fig. 50); cervical sclerites markedly developed (Fig. 45). *Thorax*: length 0.80–0.83 mm; scutum not markedly domed (Fig. 43, 45), evenly blackish brown, vestiture of evenly distributed recumbent silver hairs; postpronotal lobe with longer hairs; antepronotal lobe with longer hairs; scutellum and postnotum concolourous with scutum; scutellar depression and scutellum with distinct long substantial black hairs; pleuron and anepisternal membrane blackish brown, bare; katepisternal sulcus distinct. *Wing* (Fig. 51): length 2.1–2.4 mm; width 1.1–1.2 mm; veins not markedly pigmented; a:b ratio 1.0:3.2, otherwise as for *P. colboi*. *Haltere*: stem pale, knob dark. *Metathoracic furcasternum* (Fig 52): projections larger. *Legs*: overall yellowish; foreleg with coxa to tibia yellow then darker. mid leg slightly darker yellow, hind leg similar; hind basitarsus *ca*. 5.5x as long as its greatest breadth, ventral row of stout spines absent; calcipala well developed, 0.6x width of basitarsus, pedisulcus distinct (Fig. 53); tarsal claw with well developed tooth and basal heel, separated by distinct notch (Fig. 54). *Abdomen* (Fig. 55): slightly darker brown than thorax; abdominal scale darker, hairs not greatly extended; tergite II 3x wider than long, broadly V–shaped, other tergites not expressed; dorsal vestiture of small black hairs increased in density posteriorly. *Genitalia*: sternite VIII vestiture of sparse coarse dark hairs posterolaterally; hypogynial valves (Fig. 56) triangular, lightly pigmented with vestiture of sparse short hairs and triads of microtrichia; median edges slightly sinuous, strengthened along edge, divergent; genital fork (Fig. 57) with anterior arm short and broad, slightly sclerotized and pigmented narrowly medially, expanded and round anteriorly, lateral arms broad, indications of lateral apodeme (as in *Gigantodax*), more distal apodeme (as in *Austrosimulium*) present only as ridge, lateral plates large, angular posteromedially, rounded posterolaterally; spermatheca (Fig. 58) elongated ovoid, surface smooth; sparse internal acanthae; spermathecal duct pigmented well down duct, sculpting at junction absent; cercus (Fig. 59) as wide as long, broadly rounded in lateral view, anal lobe small, angulate proximally.

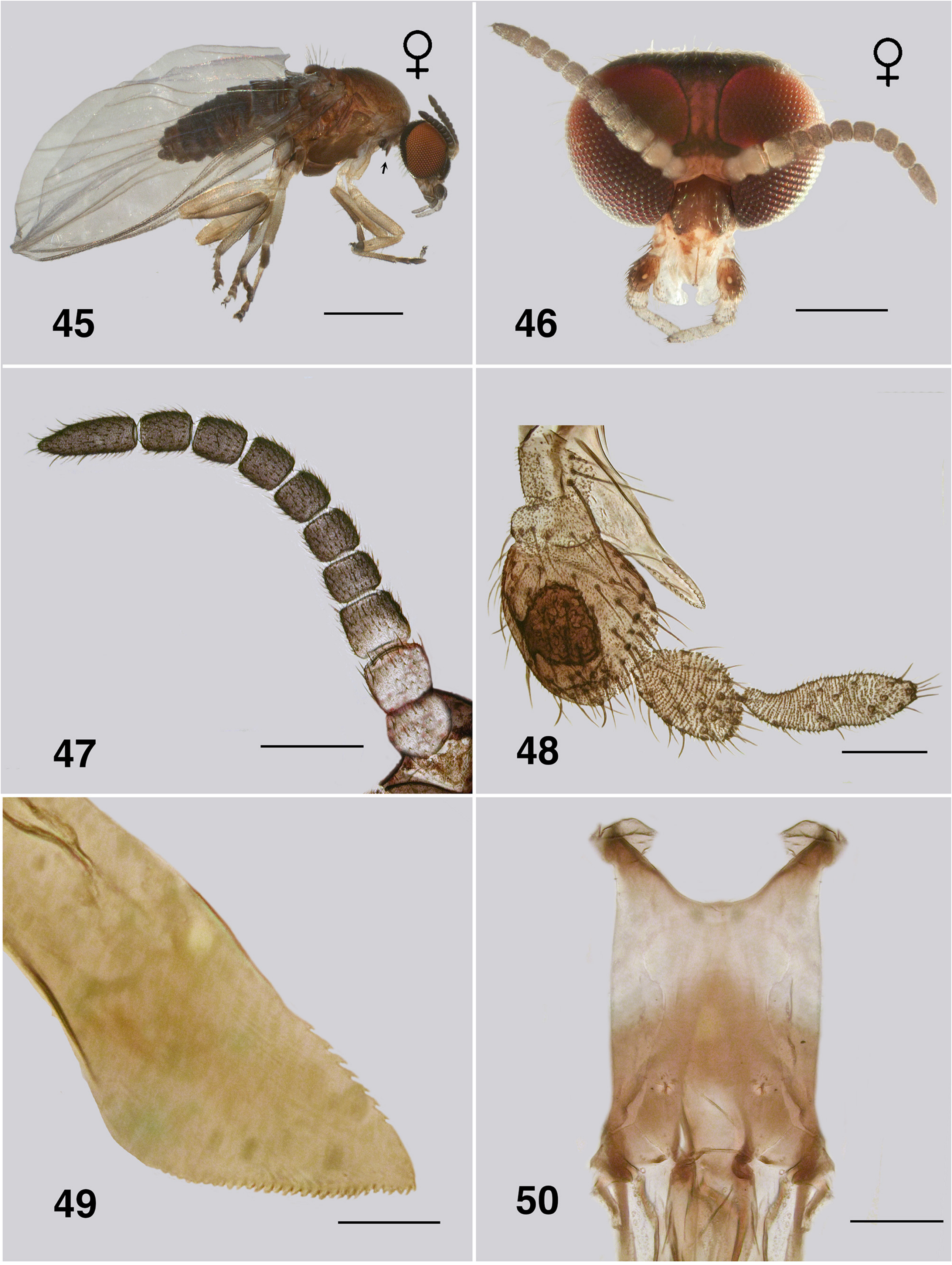
Adult male (based on 4 reared specimens). *Body* (Fig. 60): general colour blackish brown, relatively long legs; total length 1.5–2.0 mm. *Head* (Fig. 61): width 0.55–0.60 mm; depth 0.45 mm. *Eyes*: upper ommatidia blackish red, 0.03 mm in diameter, *ca*. 12 across and down; lower ommatidia almost black, 0.013 mm in diameter, *ca*. 20 across and down. *Clypeus*: black; 0.13 mm wide; vestiture of very sparse black hairs. *Antenna* (Fig. 62): total length 0.51–0.55 mm; scape and pedicel concolourous, pedicel lighter apically, first flagellomere lighter basally, otherwise concolourous; first flagellomere longer than wide, others subrectangular, becoming bead–like distally; non–tapered, distal flagellomere markedly wider than others; flagellum hirsute. *Mouthparts*: poorly developed; length 0.28x head depth; mandibles insubstantial, finely tapered with apical hairs; laciniae finely tapered apically with a few terminal hairs; maxillary palpus not markedly pigmented, 0.38 mm long, articles subequal in diameter; 3rd article slightly darker; proportional lengths of 3rd, 4th and 5th articles 1.0:0.9:1.6, sensory vesicle small, occupying 0.5x width of article, opening 0.75x width of vesicle. *Lateral cervicales* well developed (Fig. 60). *Thorax*: length 0.54–0.6 mm; in alcohol, scutum evenly velvety black, dry more yellow; vestiture of fine recumbent pale hairs; scutellum and postscutellum concolourous with scutum, coarse long black hairs. *Metathoracic furcasternum* (Fig. 63): with small projections. *Wing*: 1.9 mm in length, 0.9 mm in width; otherwise as for female. *Haltere*: tan. *Legs*: blackish brown; hind tibia slightly expanded medially; basitarsus about 6.4x as long as its greatest breadth, lacking row of stout spines; calcipala as for female; tarsal claw partially covered by grappling pad of *ca*. 20 hooks. *Abdomen* (Fig. 64): black; abdominal scale with long fine hairs, tergites not broad, increasing in size posteriorly, not markedly hirsute. *Genitalia*: in ventral view (Fig. 65); ventral plate directed ventrally giving appearance of flat apex, 1.8–2.0x wider than long (Fig. 66), curved giving appearance of a keel, roughly sculpted laterally at attachment of arms, vestiture of fine hairs, anteromedial depression shallowly U–shaped, proximal arms fine in ventral view, heavily pigmented apically, subequal in length to ventral plate, basal arms short and unpigmented; median sclerite well expressed, divided apically (M–shaped); parameres plate–like, but not markedly developed, strengthened laterally, apically with *ca.* 12 fine spicules, with *ca.* 5 larger spines meeting those from the other side; adeagal membrane densely covered with minute microtrichia; gonocoxa 2.5x longer than median width, coarse hairs on distal 2/3; gonostylus approximately 2.5x longer than basal width, angulate, apically with 2 or 3 substantial terminal spines, variable (Fig. 67).

Pupa (based on numbers of specimens) (Fig. 68). *Body*: length, 1.8–2.5 mm. *Head* (Fig. 72): frontal cephalic plate lacking dorsal depression; ratio of basal width to vertex width of female 1.0:1.5, for basal width to length 1.0:1.5, broadly rounded apically, male ratios similar; evenly covered with low clear tubercules, muscle scars distinct, frontal and facial setae present, insubstantial, ocular spine absent. *Thorax*: cuticle light brown to clear; dorsum covered evenly with small tubercles, no pattern (Fig. 69); dorsocentral setae spine–like, on raised bases, markedly black, slightly curled tips. *Gill* (Fig. 70): essentially as for *P. colboi*, 0.9 –1.3 mm full length with *ca.* 16–18 wrinkled annulations; stub–like posterior lobe absent; surface structure of annulations and regular trabeculae (Fig. 71). *Abdominal armature*: segment I and II lightly pigmented brown, tergite I with anteriorly directed substantial setae, II similar; III slightly tuberculated anteriorly, four hooks posterad, one small hook laterally; IV similar with slight pigmentation, two small hooks laterally; V with poorly expressed spine comb anterad, four fine setae posteriorly, two sternal hooks close together medially; VI as for tergite V, two sternal hooks wide apart; VII as for tergite VI, four sternal hooks; VIII spine comb present, but poorly expressed, four fine setae posteriorly, sternum with lightly expressed bed of scales; IX spine comb barely present, terminal spines markedly short and blunt, grapnel hooks exacerbated and pigmented (Fig. 73). *Cocoon* (Fig. 68). Essentially as for *P. colboi*, but not closely fitted to pupa; ventral floor absent; incorporated extraneous material rare.

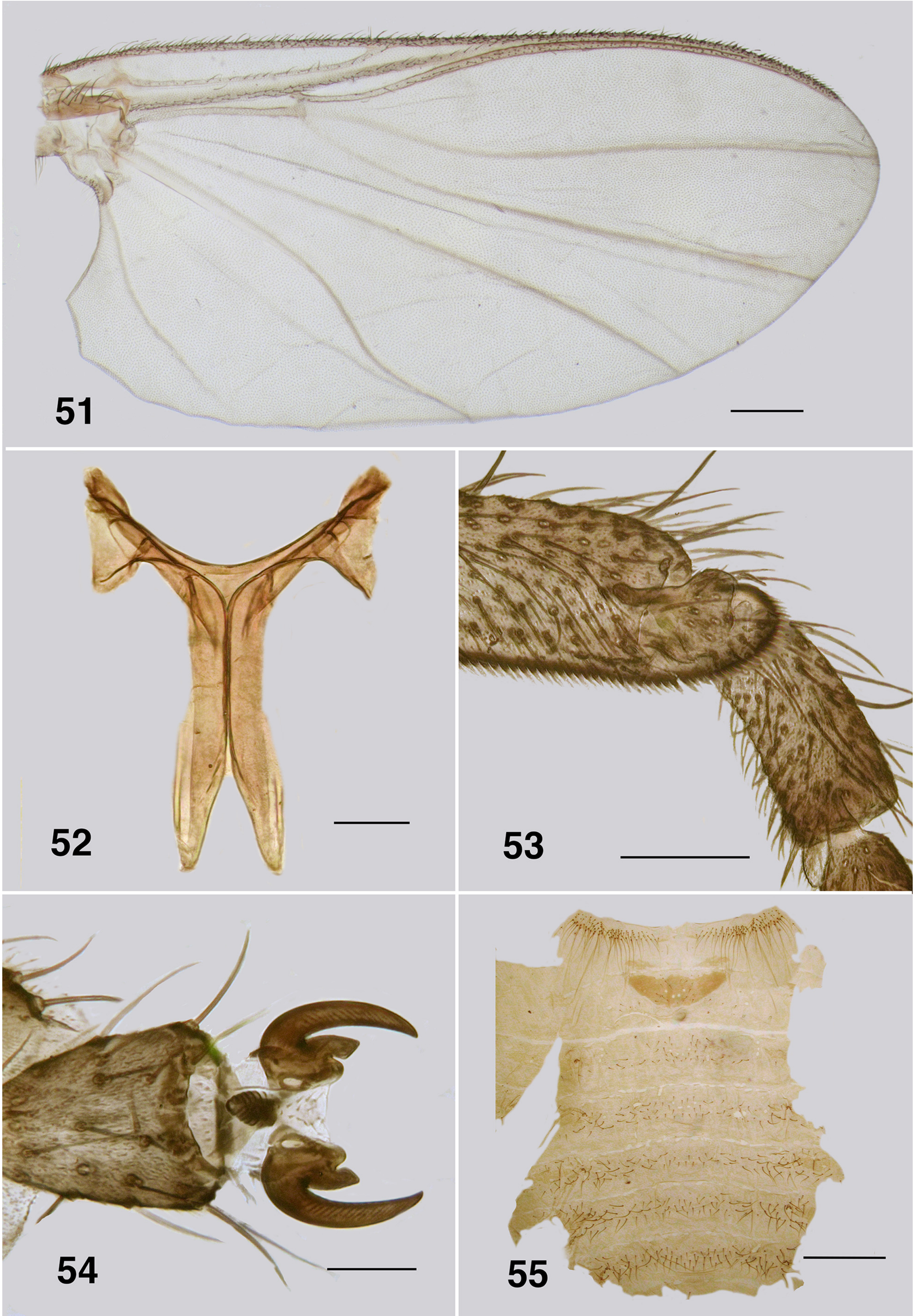
Larva (based on two last instar larvae). *Body* (Fig. 74): overall brownish, stubby (head large in relation to body), thorax and anterior abdomen subequal in diameter, expanded smoothly posteriorly; total length 4.2–4.9 mm. *Head* (Figs. 75): distinctly pale translucent yellowish brown, head spots poorly expressed, anteromedial spots not evident, posteromedial spots form distinct U–shape, mediolateral spots small and distinct; faint pigmentation along posterior of apotome; head length 0.60–0.70 mm, width 0.40– 0.43 mm; distance between antennal bases 0.25–0.27 mm; mandibular and antennal phragma lightly expressed; lateral margins of head subparallel, smoothly convex posteriorly; cervical sclerites small, distinct, not fused to postocciput; anterolateral edges of apotome sharply pigmented; genae lacking marked 'eye brow' over stemmata; ecdysial suture expanded posteriorly to behind stemmata then curved medially. *Antenna* (Fig. 76): overall clear pale brown; total length *ca.* 0.45 mm, extended well beyond fan stem, distal article longer than other two combined, proportions of basal, median and distal articles 1.0: 0.4: 1.7. *Labral fan*: stem light brown, darker along posterior edge; *ca.* 55 markedly fine rays, 0.60 mm in length, 0.01 mm in width; distinct pattern of microtrichia with longer one subequal to ray width, interspersed with *ca.* 5 shorter decreased rapidly in length. *Mandible* (Figs. 77, 78): apical brush well expressed: apical teeth finely expressed on narrow extension; apical tooth distinct, 11 fine spinous teeth; mandibular serrations separate and distinct, sensillum expressed as fine hair; blade region long, smooth and flat. *Maxilla* (Fig. 79): lobe cone–shaped, asymmetrical, palp longer than lobe, slightly separated, 2.6x as long as basal width. *Postgenal cleft* (Fig. 80): well expressed, U–shaped with sclerotized posterior tentorial pit cuticle, pits ovoid; ratio of hypostoma, bridge and cleft 1.0:1.6:1.0; suboesophageal ganglion not pigmented. *Postgenal bridge*: pale and concolourous with genae. *Hypostoma* (Fig. 81): ventral edge narrowly domed–shaped; 13 teeth, median tooth barely protruded beyond edge, two sublateral teeth smaller and subequal in length, other tooth larger, but only just protruded beyond edge, lateral teeth larger and slightly protruded, paralateral teeth smaller and sharp, variable expression, no others evident; no hypostomal serrations; four hypostomal setae per side. *Thorax*: pale; pharate pupal gill as black, paddle–shaped horn; annulations of gill concertinaed with annulations pleated and folded (Fig. 82). *Abdomen*: medium brown, lighter posteriorly; abdominal segments expanded smoothly; posteroventral tubercles not markedly developed. *Anal papillae*: three simple lobes. *Posterior proleg* (Fig. 83): rectal scales absent; anal sclerite X–shaped with medial region poorly expressed, anterior arms not flared, subequal in length to posterior arms, interarm struts distinct, posterior arms finely expressed; accessory sclerite absent, pigmented semicircular sclerite absent, but clear cuticle evident in that position. *Posterior circlet*: *ca.* 93 rows of 11–13 hooks (total *ca.* 1,100).

Etymology. From Latin *obcidens* [in reference to the 'west' and 'setting sun'].

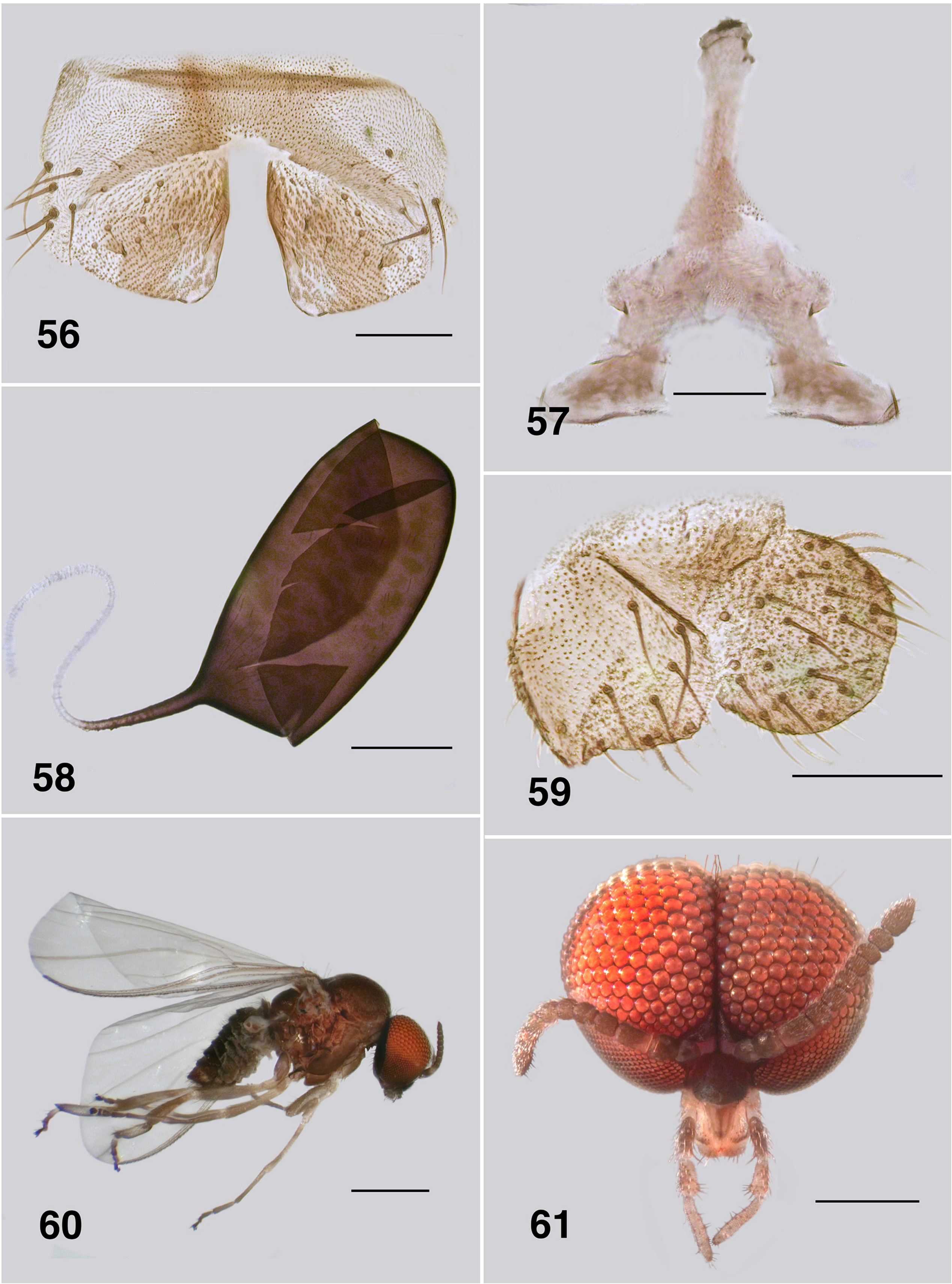
Types. *Holotype* (Fig. 43): micro–pinned reared female (dried with Pelldri II™) with pupal exuviae as subsidiary material in microvial. Label data (Fig. 44): [Holo/type (red)] [*Paraustrosimulium*/*obcidens*] [Western Australia/ Styx River, S34.8845°/ E117.1045°, alt. 50 m./ 9–xi–2014, Coll. J.K./ Moulton {F}] [ANIC Database No./29 026577].



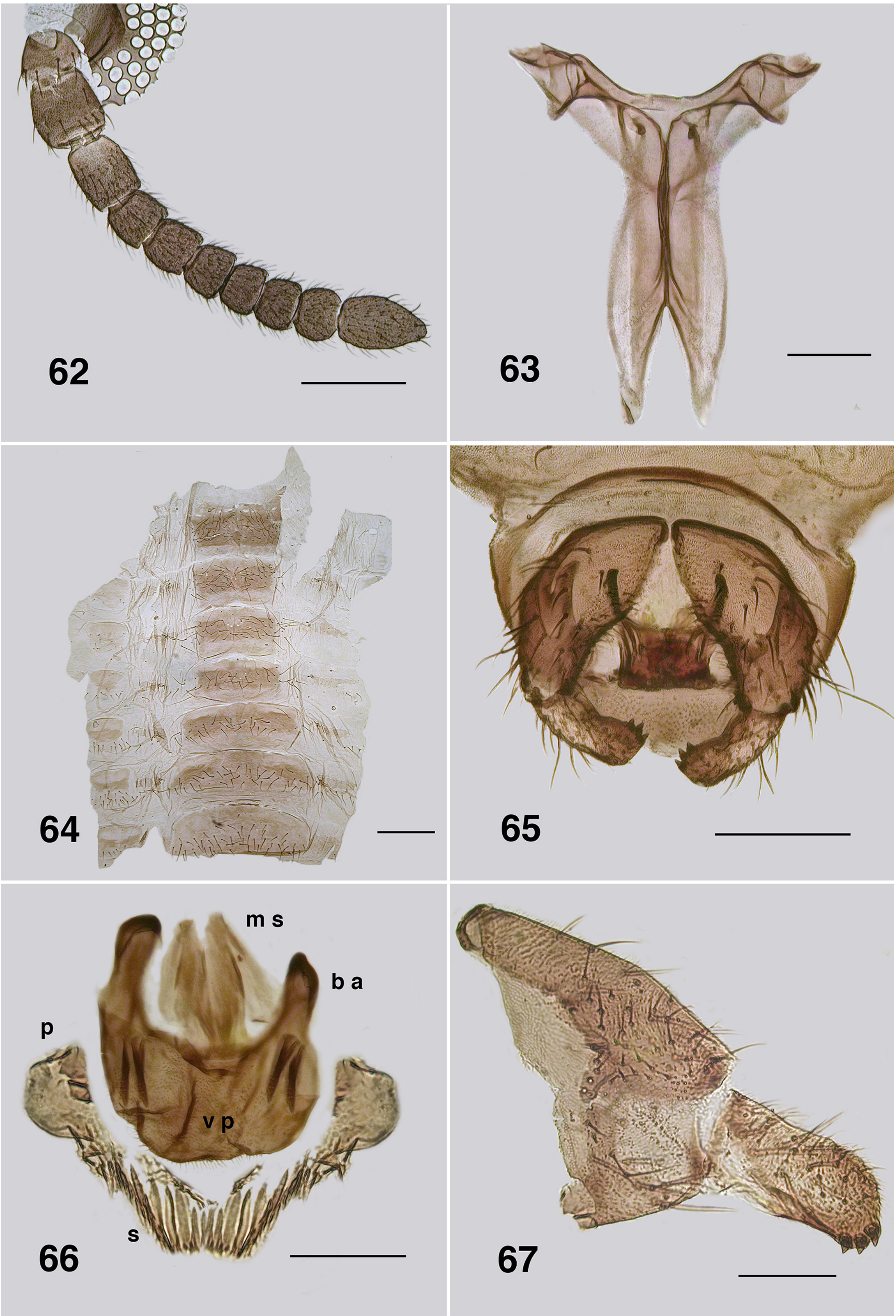
FIGURES 45–50. *Paraustrosimulium obcidens* female. (45) Habitus. ETOH. (Deeside Coast Road). Scale bar = 0.5 mm. (46) Head. Frontal view. ETOH. Scale bar = 0.2 mm. (47) Antenna. Scale bar = 0.5 mm. (48) Maxillary palp & lacinia. Scale bar = 0.05 mm. (49) Mandible. Note teeth on both sides. Scale bar = 0.02 mm. (50) Cibarium. Scale bar = 0.05 mm.



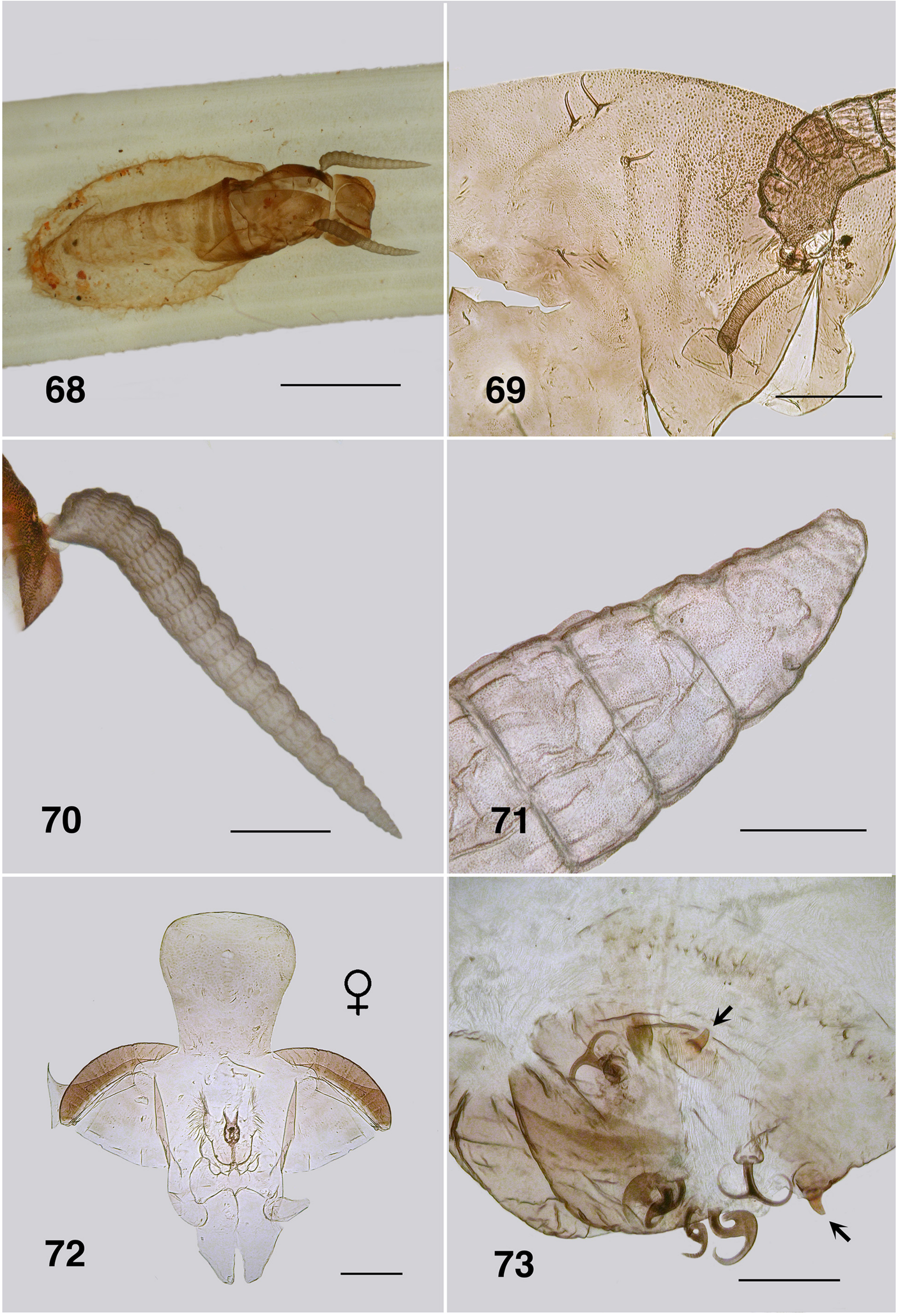
FIGURES 51–55. *Paraustrosimulium obcidens* female. (51) Wing. Scale bar = 0.2 mm. (52) Metathoracic furcasternum. Scale bar = 0.5 mm. (53) Calcipala & pedisulcus. Scale bar = 0.05 mm. (54) Tarsal claws. Scale bar = 0.02 mm. (55) Abdominal tergites. Scale bar = 0.2 mm.



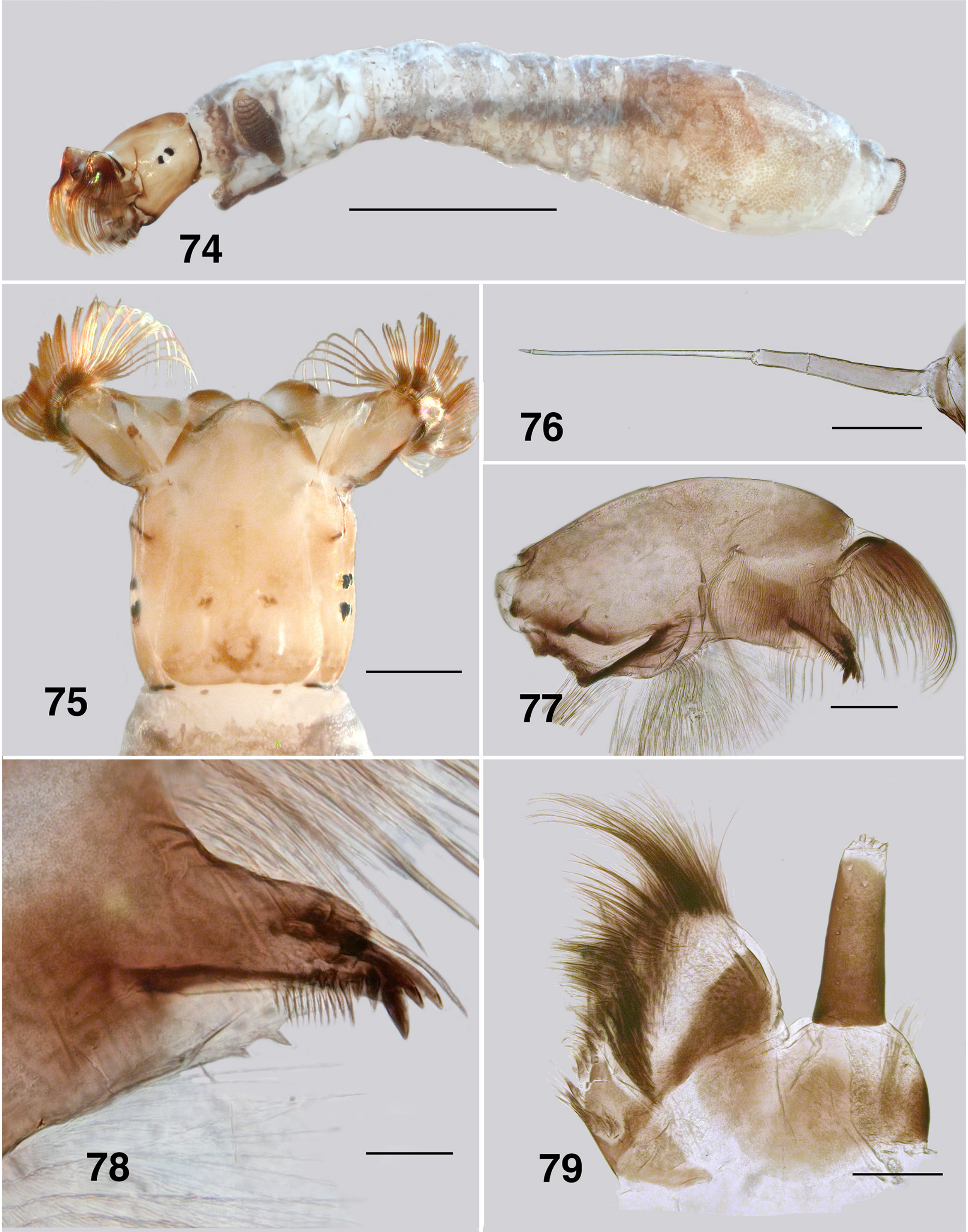
FIGURES 56–59. *Paraustrosimulium obcidens* female. **FIGURES 60, 61.** *Paraustrosimulium obcidens* male. (56) Hypopygial valves. Scale bar = 0.05 mm. (57) Genital fork (partially reconstructed). Scale bar = 0.05 mm. (58) Spermatheca (flattened). Scale bar = 0.05 mm. (59) Cercus and anal lobe. Scale bar = 0.05 mm. (60) Habitus of male. ETOH. (Styx River). Scale bar = 0.5 mm. (61) Head. Frontal view. ETOH. Scale bar = 0.2 mm.



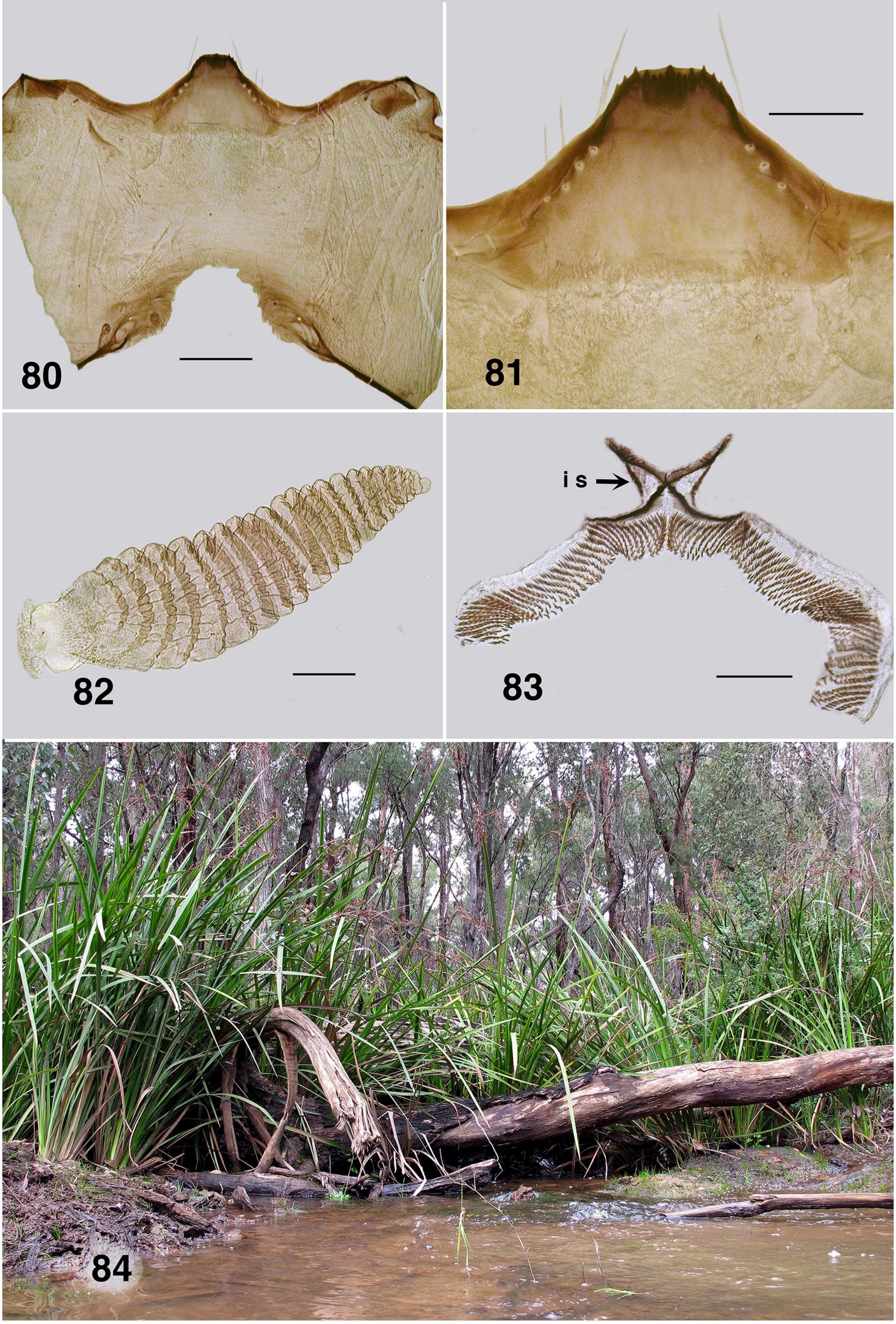
FIGURES 62–67. *Paraustrosimulium obcidens* male. (62) Antenna. Scale bar = 0.1 mm. (63) Metathoracic furcasternum. Scale bar = 0.05 mm. (64) Abdominal tergites. Scale bar = 0.2 mm. (65) Ventral view of genitalia. Cleared, in glycerine. Scale bar = 0.1 mm. (66) Ventral plate, parameres & spines (partly reconstructed). Abbreviations as for Fig. 24. Scale bar = 0.05 mm. (67) Gonocoxa and stylus, lateral view. Scale bar = 0.05 mm.



FIGURES 68–73. *Paraustrosimulium obcidens* pupa. (68) Pupal exuviae & cocoon on grass leaf. Scale bar = 1.0 mm. (69) Thoracic cuticle. Scale bar = 0.2 mm. (70) Pupal gill. Scale bar = 0.2 mm. (71) Gill surface structure. Scale bar = 0.05 mm. (72) Female cephalic capsule. Scale bar = 0.2 mm. (73) Abdominal segment IX, showing terminal spines (arrows) and grapnel hooks. Scale bar = 0.05 mm.



FIGURES 74–79. *Paraustrosimulium obcidens* larva. (74) Habitus, last instar. Scale bar = 1.0 mm. (75) Head. Dorsal view. Scale bar = 0.2 mm. (76) Antenna. Scale bar = 0.1 mm. (77) Mandible. Scale bar = 0.2 mm. (78) Mandible apex. Scale bar = 0.02 mm. (79) Maxilla. Scale bar = 0.05 mm.



FIGURES 80–84. *Paraustrosimulium obcidens* larva. (80) Genae, hypostoma, postgenal cleft. Scale bar = 0.1 mm. (81) Hypostoma. Scale bar = 0.05 mm. (82) Pharate pupal gill. Slightly expanded. Scale bar = 0.1 mm. (83) Anal sclerite & circlet of hooks. Abbreviation: i s—interarm struts. Scale bar = 0.1 mm. (84) Deeside Coastal Road stream, WA. *P. obcidens* habitat, S34.4380° E116.3863°, 183 mabs, 2-ix-2014,.

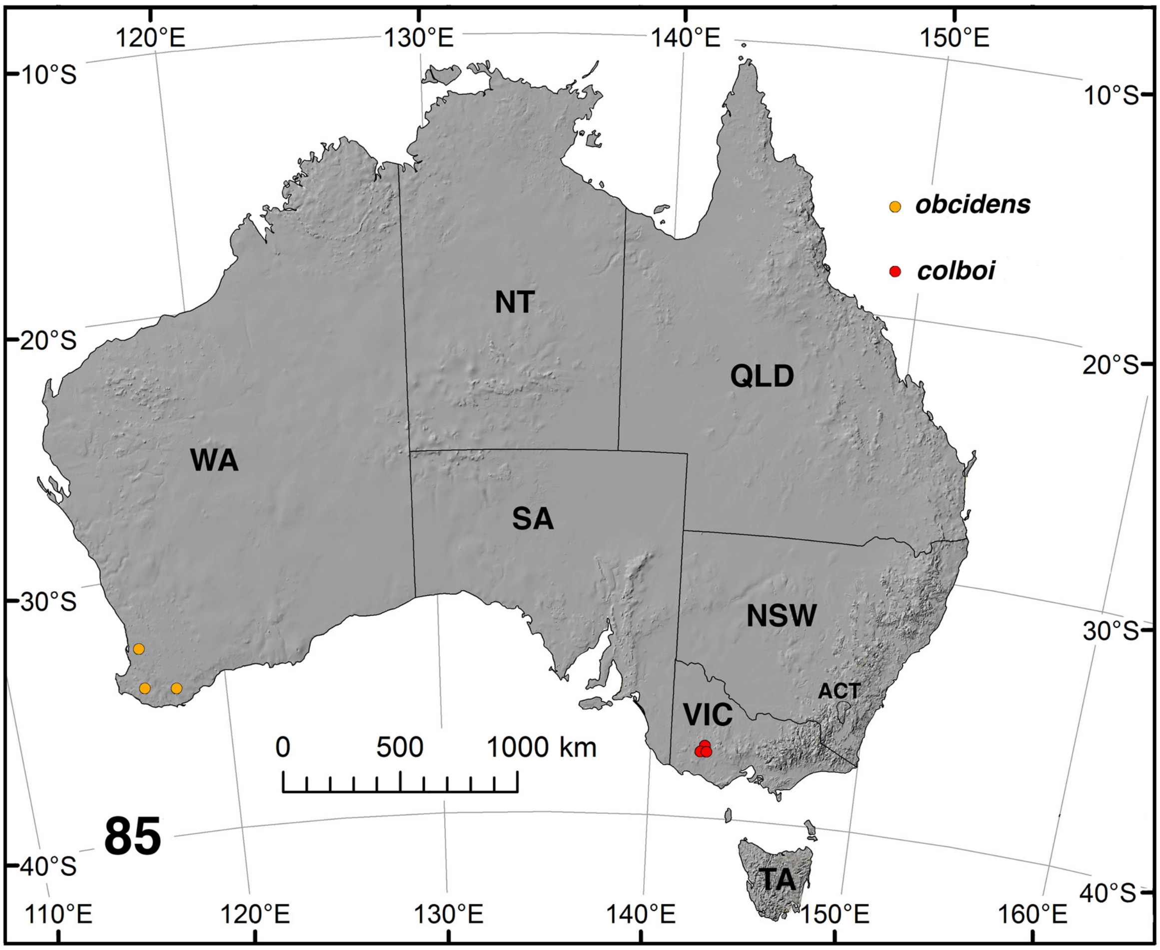


FIGURE 85. Distribution of Australian *Paraustrosimulium*.

Paratypes: six micro–pinned reared females (dried with Pelldri II™). Label data: [Para/type (yellow)] [*Paraustrosimulium/obcidens*] [Western Australia/ Deeside Coast Rd/ brook/ S34.4380° E116.3863°/ alt. 183 m. 9–ix–2014./ Coll. J.K. Moulton {F}] [ANIC Database No./29 026578-683]. One pinned male, label data as above, but with [{M}] [ANIC Database No./29 026584]. Two last instar larvae in ETOH. Label data: [Para/type (yellow)] [*Paraustrosimulium/obcidens*] [Western Australia/ Goldmine Gully, S32° 24'/E116° 12'/ 8 September 1996/ Coll: J. K. Moulton] [ANIC Database No./29 026626]. Five slide mounts—two, a male and female each from Goldmine Gully. Label data as above, but with [ANIC Database No./29 026627] and [ANIC Database No./29 026628]—one a last instar larva, with [ANIC Database No./29 026631]. Pupa [ANIC Database No./29 026629] and last instar larva from Deeside Coast [ANIC Database No./29 026630].

Additional material. ETOH. Mixture of males, female, larvae pupae and exuviae. Label data as for Deeside Coast [ANIC Database No./29 026632]. Slides, adults and one pupa; seven as [*Paraustrosimulium/obcidens*] [Western Australia/ Goldmine Gully/ Balmoral State Forest/ Jarradale S32.3900/ E116.2000. alt 280m/ 8-ix-1966. Coll. JK/ Moulton] [UASM #370880-370886], four as [*Paraustrosimulium/obcidens*] [Western Australia/ Deeside Coast Rd. brook/ S34.4380 E116.3863/ alt 183 m. 9-ix-2014/ Coll. JK Moulton] [UASM # 370887-370890].

Distribution (Fig. 85). *Western Australia*: Deeside Coast Road, S34.4380° E116.3863° alt. 183 m. 2 & 9–ix–2014. Coll. J.K. Moulton, D.C. Currie. Styx River, Fernlay Road, S34.8845° E117.1045°, alt. 50 m. 1–ix–2014, 9–xi–2014. Coll. J.K. Moulton, D.C. Currie. Goldmine Gully, Balmoral State Forest, Balmoral Road, Jarrahdale, S32.3900° E116.2000°, alt 280 m. 8–ix–1996. Coll: J.K. Moulton.

Bionomics. Little is known about this species. Collection dates suggest an Austral spring species. The small mouthparts of the female suggests non–biting behaviour, but the virtual absence of abdominal tergites (Fig. 55) and a well developed tooth on the tarsal claws (Fig. 54) imply otherwise. New Zealand *Austrosimulium* (Craig *et al.*

2012) blood–feeding species tend to have smaller tergites and it is known an enlarged tarsal claw tooth is common to bird–feeding simuliids (Adler *et al.* 2004), so perhaps *Paraustrosimulium obcidens* is ornithophilic?

Habitats of the larvae tend to be slow flowing streams (*e.g*., Fig. 84), with trailing grass and turbid water.

Remarks. The marked difference in the tarsal claw tooth between apparent sister species is surprising. *Paraustrosimulium colboi* females have little in the way of a tooth (Fig. 12), whereas those of *P. obcidens* have a markedly developed tooth separated by a distinct notch from a heel (Fig. 54), as do *P. anthracinum* (Fig. 96). A similar, smaller notch was noted by Craig *et al.* (2012) for some species of the *ungulatum*–group of New Zealand *Austrosimulium,* where otherwise, in that genus, a tooth is absent. The large tooth and notch are also seen in some species of *Gigantodax* (Wygodzinsky & Coscarón 1989). Of note too is the absence of the row of stout spines along the ventral edge of the basitarsus—this is also absent in the *ungulatum*–species group of *Austrosimulium*, and sporadically in others (Craig *et al.* 2012). The genital fork of female *P. obcidens* (Fig. 57) is almost an exact match of that for *P. anthracinum* (Fig. 99), whereas male genitalia of *P. anthracinum* (Fig. 109) are markedly similar to that of *P. colboi* (Fig. 24).

Paraustrosimulium anthracinum (Bigot)

(Figs. 86–128)

Simulium anthracinum Bigot, 1888: 15.
Simulium anthracinum. Kertész 1902: 285.
Simulium (*Austrosimulium*) *anthracinum*. Edwards 1931: 143.
Simulium (*Austrosimulium*) *anthracinum*. Pinto 1931: 671.
Austrosimulium anthracinum. Smart 1945: 499. Vargas 1945: 113. Wygodzinsky 1953: 293. Dumbleton 1960: 543.
Austrosimulium (*Paraustrosimulium*) *anthracinum*. Wygodzinsky & Coscarón 1962; 242. Coscarón 1968: 66.
Paraustrosimulium anthracinum. Crosskey 1969: 73. Crosskey & Howard 1997: 18; 2004: 10. Prosimuliini.
Paraustrosimulium anthracinum. Adler & Crosskey 2008: 26. Transferred to Simuliini.
Paraustrosimulium anthracinum. Adler & Crosskey 2017: 30.
Paraustrosimulium anthracinum. Hernández-Triana *et al*. 2017: 350.

Simulium moorei Silva Figueroa, 1917: 30.
Simulium (*Austrosimulium*) *moorei*. Edwards 1931: 144.
Simulium moorei. Pinto 1931: 29.
Simulium moorei. Vargas 1945: 166.
Austrosimulium moorei. Smart 1945: 499.
Austrosimulium moorei. Wygodzinsky 1953: 298. Synonymized with *A. anthracinum*.

Redescription. *Adult female* (based on 5 specimen and literature description). *Body* (Fig. 86): general body colour in alcohol evenly dark brown; total length 3.3 mm. *Head* (Fig. 87): width 0.76 mm; depth 0.49 mm; postocciput black, markedly hirsute; frons dark brown; frons–head ratio (narrowest width of frons: greatest width of head) 1.0:7.0. *Eyes*: evenly reddish brown, interocular distance 0.11 mm; ommatidia 0.012 mm in diameter; *ca*. 36 rows up and across at mid–eye. *Clypeus*: light brown; 0.23 mm wide; vestiture of sparse pale hairs. *Antenna* (Fig. 88): total length 0.68 mm; 8 flagellomeres, pedicel and scape small, wider than long, distal region of scape pale, remainder of antenna brown; flagellomeres quadratic, overall slightly tapered, apical flagellomere longer than broad. *Mouthparts*: well expressed, *ca*. 0.5 length of head depth; maxillary palpus (Fig. 89), total length 0.6 mm, articles brownish black, 3rd article black; proportional length of 3rd, 4th and 5th articles 1.0:0.8:1.2; sensory vesicle spherical, 0.5x width of 3rd article, opening 0.3x width of vesicle; mandible (Fig. 90), not markedly expanded apically, 27 inner teeth and 10–12 finely pointed outer teeth; lacinia (Fig. 90) with 11 inner teeth and 13 outer teeth; cibarial cornuae (Fig. 91) with marked sculptured edges, central depression broad and shallow. *Lateral cervicales*: well developed (Fig. 86). *Thorax*: length 1.5 mm; width 1.0–1.1 mm; scutum evenly dark brown, vestiture of evenly distributed recumbent silver hairs; postpronotal lobe with longer hairs; antepronotal lobe with markedly longer dense hairs; scutellum pale, and postnotum lighter than scutum; scutellar depression and scutellum with pale hairs; pleuron and anepisternal membrane dark brown, bare. *Wing* (Fig. 92, 93): length 3.0– 3.1 mm; width 1.6 mm, anterior veins lightly pigmented, basal cell distinct, costa not extended to wing apex with spiniform setae distally, also present on R_1 vein; radial veins not markedly closely applied to costa; a:b ratio 1.0:2.8; M thickened apically;

A_2 not approaching wing margin. *Haltere*: dark grey. *Metathoracic furcasternum*: dorsal arms with rounded projections (Fig. 94). *Legs*: overall dark brown; hind basitarsus *ca.* 5.7x as long as its greatest breadth, very slightly expanded medially, ventral row of stout spines present, calcipala moderately expressed, pedisulcus not markedly developed (Fig. 95); tarsal claw (Fig. 96) with moderately developed basal heel and markedly angulate tooth and notch. *Abdomen* (Fig. 97): abdominal scale black with dark hairs, not greatly extended; tergite II 3.2x wider than long, shallowly V–shaped, sparse black hairs, III, IV essentially bare, III–V as wide as long with rounded corners, VI 2x wider than long; dorsal vestiture of small sparse black hairs increased in density posteriorly. *Genitalia*: sternite VIII vestiture of sparse coarse black hairs posterolaterally; hypogynial valves (Fig. 98) broadly rounded; median edges slightly convex, not strengthened along edge, bluntly rounded apically, slightly crenulated laterally; genital fork (Fig. 99) with anterior arm broad (not easily observed), slightly sclerotized and pigmented medially (not so according to Wygodzinsky & Coscarón 1973), more so anteriorly, lateral arms broad, indications of lateral apodeme (as in *Gigantodax*), apodeme (as in *Austrosimulium*) present only as ridge, lateral arms broad, lateral plates large, pointed posteromedially, angulate posterolaterally; spermatheca ovoid (Fig. 100), length 0.14 mm, surface un–patterned; sparse internal acanthae; no clear area at junction of spermathecal duct, pigmentation not extended down duct; cercus (Fig. 101) broadly rounded apically, sloped ventrally, vestiture of evenly spaced hairs, anal lobe not angulate posteriorly.

Adult male (reared and other specimens). *Body* (Fig. 102): general colour dark brown to black; total length 2.3–2.6 mm. *Head* (Fig. 103): width 0.90 mm; depth 0.62 mm**.** *Eyes*: upper ommatidia very dark red, 0.03 mm in diameter, *ca.* 22 across, 20 down; lower ommatidia almost black, 0.01 mm in diameter, *ca.* 35 across, 26 down. *Clypeus*: blackish brown; vestiture of very sparse black hairs; 0.2 mm wide. *Antenna* (Fig. 104): total length 0.75 mm; scape and pedicel black, first flagellomere and remainder dark brown; pedicel longer and wider than other divisions; first flagellomere longer than wide, others subrectangular; non–tapered, narrow in comparison to that of female; apical article *ca.* 2x longer than wide. *Mouthparts*: moderately developed; 0.5x head depth; mandibles insubstantial, finely tapered with apical hairs; laciniae finely tapered apically with terminal hairs; maxillary palpus (Fig. 105), dark brown, 0.55 mm long, proportional lengths of 3rd, 4th and 5th articles 1.0:0.8:1.4, sensory vesicle small, occupying 0.25x width of article, opening 0.5x width of vesicle. Cervical sclerites well developed. *Thorax*: length 1.5 mm; width 0.9 mm; in alcohol, scutum evenly blackish brown, vestiture of fine recumbent pale hairs (often worn); scutellum and postscutellum concolourous with scutum. *Wing*: 3.0 mm in length, 1.5 mm in width; otherwise as for female. *Haltere*: tan. *Legs*: yellowish blackish brown; hirsute; hind basitarsus *ca.* 4.5x as long as its greatest breadth, slightly expanded medially, row of ventral spines present, not markedly stout; calcipala well expressed, pedisulcus barely evident (Fig. 106); tarsal claw partially covered by grappling pad of *ca.* 20 hooks, distinct basal tooth. *Abdomen* (Fig. 107): blackish brown; abdominal scale with long fine hairs, tergites markedly broad, tergites II–IV hirsute, less so on posterior others. *Genitalia*: ventral view (Fig. 108); ventral plate directed ventrally giving appearance of broadly concave apex, 1.5–2.0x wider than long, median keel well developed, vestiture of fine hairs, plate not sculpted laterally; anteromedial broad and slightly convex, basal arms fine, heavily pigmented, splayed apically (Fig. 109), paramere connectors well developed; median sclerite well expressed, broad and divided apically; parameres triangular, plate–like, strengthened laterally, spines as small spicules, not meeting medially; adeagal membrane with minute microtrichia; gonocoxa 2.0x longer than basal width, markedly sparse hairs; gonostylus approximately 2.0x longer than basal width, apically with 2–4 substantial terminal spines (Fig. 110).

Pupa (based on numbers of specimens). *Body*: length, female 3.2–3.5 mm; male 3.2–3.3 mm (Fig. 111). *Head*: frontal cephalic plate lacking dorsal depression; ratio of basal width to vertex width of female 1:1.5, for basal width to length 1:1.5, rounded apically (Fig. 113), male ratios 1.0:1.5 and 1.0:2.0 respectively (Fig. 114), evenly tuberculate, frontal and facial setae present, but insubstantial, ocular spine absent. *Thorax*: Dorsum with very small tubercles, no pattern; dorsocentral setae substantial, spine–like and curled apically, other more lateral setae also spine–like in expression (Fig. 115). *Gill* (Fig. 111, 112): fundamentally of three flattened laminae, curled along their length, with concertina marks from packaging in the histoblast appearing as annulations (Fig. 126, 127); anterior trunk 1.6–2.1 mm length (*ca.* 14 annulations), stub–like posterior lobe *ca.* 0.25 mm (*ca.* 6 annulations), ventral trunk *ca.* 0.6 mm in length (*ca.* 7 annulations); fine filaments, as such, absent. *Abdominal armature* (Fig. 116): tergites I & II with 4–6 fine setae, lightly tuberculate; tergite III with four hooks per side, 3 or 4 other fine setae, no sternal hooks; tergite IV as for III; tergite V with poorly expressed spine comb, 4 hooks on sternum, laterally small plurites; tergite VI with spine comb and four hooks ventrally, one on small pleurite; tergite VII as for

VI; VIII with a markedly poorly expressed spine comb anteriorly, spines reduced laterally; tergite IX with similar spines comb; terminal spines short, not sharp, grapnel hooks poorly expressed, as single hooks (Fig. 117). *Cocoon*. Surface smooth, fabric coarsely woven, silk filaments obvious, medium brown; distinctly slipper–shaped fully covering pupa, not close fitted, with well defined anterior edge, ventral floor absent.

Larva (based on numbers of last instar larvae). *Body* (Fig. 118): overall yellowish gray, anterior abdomen of smaller diameter than thorax, expanded smoothly posteriorly; total length 5.8–6.5 mm. *Head* (Figs. 119): evenly mid brown, head spots positive, but not strongly pigmented; head length 0.73–0.86 mm, width 0.66–0.67 mm; distance between antennal bases 0.50–0.51 mm; lateral margins of head smoothly convex; cervical sclerites well developed and pigmented, elongated and fused to postocciput; anterolateral edges of apotome not distinctly pigmented; genae lacking darker 'eye brow' over stemmata. *Antenna* (Fig. 120): apical article pale, others dark brown; total length *ca.* 0.4 mm; well extended beyond labral fan stem; distal article subequal in length to other two articles; ratio of basal, medial and apical articles 1.0:0.6:2.0. *Labral fan*: relatively small; stem translucent; 56–60 fine rays, 0.32 mm in length, 0.005 mm in width; microtrichia as long as ray width, substantial, interspersed with 2 or 3 smaller microtrichia. *Mandible* (Fig. 121, 122): apical brush moderately developed; apical teeth not markedly extended; subapical teeth small, 8–9 substantial spinous teeth; mandibular sensillum and serrations often complex, but not markedly so, sometimes as just a simple pair (as shown). *Maxilla* (Fig. 123): lobe markedly cone–shaped, asymmetrical, palp subequal in length to lobe, well separated, 2x as long as basal width. *Postgenal cleft* (Fig. 124): essentially absent; ratio of hypostoma, bridge and cleft 1.0:1.6:0.3; suboesophageal ganglion not pigmented. *Hypostoma* (Fig. 125): ventral edge broadly domed–shaped, more or less covering 15 teeth; median tooth barely protruded beyond edge, sublateral teeth smaller and subequal in length, barely protruded beyond edge, lateral tooth larger and protruded, paralateral teeth smaller and sharp, variable expression, no others evident; no hypostomal serrations; four hypostomal setae per side. Postgenal bridge: pale and concolourous with genae. *Thorax*: (Fig. 126) anterior prothorax brown, remainder paler; pharate pupal gill broad, inverted V–shape, concertinaed (Fig. 127). *Abdomen*: pale brown anteriorly, darker posteriorly; abdominal segments expanded smoothly; posteroventral tubercles present, but not markedly developed. *Anal papillae*: three simple lobes. *Posterior proleg* (Fig. 128): rectal scales present in large numbers; anal sclerite median region well expressed with lateral interarm struts distinct, anterior arms slightly flared, shorter than posterior arms, posterior arms irregular in outline; accessory and pigmented semicircular sclerites absent. *Posterior circlet*: *ca.* 80 rows of 15–17 hooks (total *ca.* 1,250).

Etymology. Not detailed by Bigot (1888: 15), but apparently from Greek 'ανθρακίτης' or Latin '*anthracite*', meaning 'coal–like'; no doubt in reference to colour of the male and, less so, the female.

Types. The lectotype female is housed in the Natural History Museum, London, along with a male and a female paralectotype (Crosskey & Lowry 1990: 203). Details of labeling unknown.

Material examined. Five tubes of ETOH material. Larvae, pupae, males, females. Label data:- [Paraustrosimuium/ anthracinum/ (Bigot)/ det. Coscarón 84] [Argentina Rio Negro/ Bariloche 11-ix-84/ Coll. Coscarón] [Ex-Davies Collection,/ McMaster. 2011] [UASM#/ 370852]. Larvae (damaged). Label data:- [Paraustrosimulium anthracinum/ Kerguen, Ao, Castillo, 21.9.84] [Ex-Davies Collection,/ McMaster. 2011] [UASM#/ 370853]. Larvae (damaged). Label data:- [Paraustrosimulium/anthracinum/ (Bigot)/ det. H. Gyorkos - '85] [Bariloche, Ao Villa/ Con Bosca. 19.ix. 84/ Col. Coscarón] [Ex-Davies Collection,/ McMaster. 2011] [UASM#/ 370854]. Males & females. Label data:- [Paraustrosimuium/ anthracinum/ (Bigot)/ det. Coscarón 92] [Chile. Magallanes/ Isla Deslit/ 9-xi-82. Col. Lanfranco] [UASM#/ 370855]. Larvae, pupae, male, female. Label data:- [Paraustrosimuium/ anthracinum/ (Bigot)/ det. Coscarón 82] [Chile. Chiloe/ rio Melitaba/ e/Huillinco/ y/ Chonchi/ 30-xi-92/ Col. Coscarón] [UASM#/ 370856]. Slides, fourteen, all stages:- [*Paraustrosimuium*/ *anthracinum*] [Chile/ Rio Melitaba y/ Chonchi/ 30-xi-92/ Col. S. Coscarón] [UASM#/ 370891-370904]; one, female [[Chile. Magallanes/ Isla Deslit/ 9-xi-82. Coll. Lanfranco] [UASM#/ 370905].

Distribution. Widespread in southern South American Andes—Wygodzinsky & Coscarón (1973) give details. In short, in Chile *P. anthracinum* extends from northern Terra del Fuego, northwards to Malleco. In Argentine, from Islas de los Estado off the coast of Terra del Fuego, northwards to southern Neuquen Province.

Bionomics. Wygodzinsky & Coscarón (1962) note that for their material of *P. anthracinum*, the aquatic stages were found attached to dead vegetation trailing in the water of a large stream, near the edge and just below the surface—the population was monospecific. Specimens reported by Dumbleton (1960) from Navarino Island similarly came from a large stream, however, those collected by Wygodzinsky (1953) some 1,200 km farther north in the Province of Rio Negro, Argentine, were obtained from smaller water courses. Hernández *et al.* (2009: 196) record larvae from a murky water stream on Isla Victoria, Lake Guillelmo, near Bariloche and the few females collected from that region were not markedly anthropophilic. Coscarón & Coscarón Arias (2007) noted that *P. anthracinum* was anthropophilic.

Dates of collections by Wygodzinsky & Coscarón (1973: 192) ranged from October to February. This covers the Southern Hemisphere spring and early summer, but there is no information regarding water temperatures, nor altitude as such. Some of the collections included all stages, so *P. anthracinum* would appear to be a multivoltine species.

Remarks. Given the wide–ranging distribution of *P. anthracinum*, variation between populations is perhaps to be expected. The earlier descriptions give variation in numbers of terminal spines on the male gonostyli and we see differences in the width of the female frons (see above). A more detailed examination of the species, involving molecular analysis will probably reveal cryptic species.

Character comparisons. We here make character-state comparisons between *Paraustrosimulium* (as re-defined) and related simuliids. While it is beyond the scope of this paper to undertake a comprehensive character analysis of austral simuliids, the following discussion of states provide the basis for identifying possible synapomorphies of *Paraustrosimulium*, and for offering remarks about its close relationship to other taxa, in particular *Austrosimulium*, "*Cnephia" pilfreyi* and *Cnesiamima atroparva.*

Adults. *Antenn*a: An antenna with 9 flagellomeres is inferred to be the ground plan condition in the Simuliidae based on the distribution of that character-state throughout the family (Adler *et al.*, 2004). *Austrosimulium* typically has only 8 flagellomeres (rarely nine), as do the three species now assigned to *Paraustrosimulium*. In fact, the shared presence of 8 flagellomeres was the main criterion by which Edwards (1931) originally assigned *anthracinum* Bigot to *Austrosimulium*. Both "*Cnephia" pilfreyi* and *Cnesiamima atroparva* exhibit the plesiomorphic condition.

Frons: Females of *Austrosimulium* s.str. have a markedly broad frons, with the lateral margins diverging dorsally. *Paraustrosimulium anthracinum* has a narrower frons, but with similar margins (Fig. 87); *P. colboi* (Fig. 2) also has a comparatively narrow frons, but with margins not as divergent; *P. obcidens* has by far the narrowest frons of the three *Paraustrosimulium* species, with its lateral margins subparallel (Fig. 46). Mackerras & Mackerras (1948: 248) illustrated (their Fig. 9) the female heads of *A*. (*Novaustrosimulium*) species *A. bancrofti*, *A. pestilens*, *A. furiosum* and *A. mirabile*. These are considerably closer in expression to *Paraustrosimulium* than to those of *Austrosimulium* (*Austrosimulium*).

Mandible of female: *Austrosimulium* females have mandibular teeth only on the inner apical surface. *Paraustrosimulium* female mandibles have teeth on both sides of the apex, albeit poorly developed on the outer edge (*e.g.* Figs. 5, 49); the mandible apex is also broadly triangular apically, unlike those of *Austrosimulium*. In their description of *P. colboi,* Davies & Györkös (1988) noted that teeth were present only on the inner surface of the mandible; however, given the poor quality of the material at their disposal, the outer teeth could easily have been overlooked. Mandibles of the females of "*Cnephia*" *pilfreyi* and *Cnesiamima atroparva* have teeth on both margins.

Maxillary palp: *Austrosimulium* (*Austrosimulium*) females tend to have the 3rd and 4th palpomeres more or less subequal in length, with the 5th palpomere 1.5x longer than the 4th. *Paraustrosimulium colboi* exhibits a similar condition (Fig. 4), whereas *P. obcidens* has a semispherical 3rd palpomere, a markedly small 4th palpomere, and with the 5th palpomere subequal in length to the 3rd (Fig. 48). The palp of *Paraustrosimulium anthracinum* (Fig. 89) is similar to that of *P. colboi*. *Austrosimulium* (*Novaustrosimulium*) females have a markedly narrowed 3rd palpomere, subequal in length to each of the more distal ones—a likely synapomorphy of that subgenus.

Cervical sclerites: All simuliid adult possess lateral cervical sclerites posteriorly on the neck. In *Paraustrosimulium* they are accentuated—markedly so in *P. obcidens* (Fig. 45) and *P. anthracinum* (Fig. 86). We consider this character state to be a synapomorphy of the genus.

Antepronotal lobe: Neither *P. colboi* (Fig. 1) nor *P. obcidens* (Figs. 43, 45) have noticeably hirsute antepronotal lobes, whereas those of *P. anthracinum* are markedly so, along with the postocciput of the head (Figs. 86, 87). This character is not well surveyed across austral simuliid taxa and is currently of limited phylogenetic value.

Wing: Spiniform setae on the costa of *P. anthracinum* are densely packed along the distal half, although relatively fine in expression (Fig. 93). In *P. colboi* and *P. obcidens* the spiniform setae are more widely-spaced and substantial (*e.g*. Fig. 8). *Paraustrosimulium anthracinum* has spinous hairs on the distal portion of the R_1 (Fig. 92), as does *Cnesiamima atroparva*. Such spines are absent from the other two species of *Paraustrosimulium* and

Austrosimulium. *Paraustrosimulium colboi* and *P. obcidens* have the apices of veins R_1 and Rs closely appressed or fused before joining C, as in *Austrosimulium*. The apices of veins R_1 and Rs are not as closely appressed in *P. anthracinum*, although the latter vein deflects markedly towards the anterior margin shortly beyond its base.

Leg Spines: The ventral row of stout spines that typically occur on the hind basitarsus is absent from *P. colboi*, *P. obcidens* (*e.g.* Fig. 11) and members of the *ungulatum*–species group of New Zealand *Austrosimulium.* The spines are present in most members of the *australense*–species group and in *P. anthracinum,* although in the latter species are longer and finer than is typical (Fig. 95).

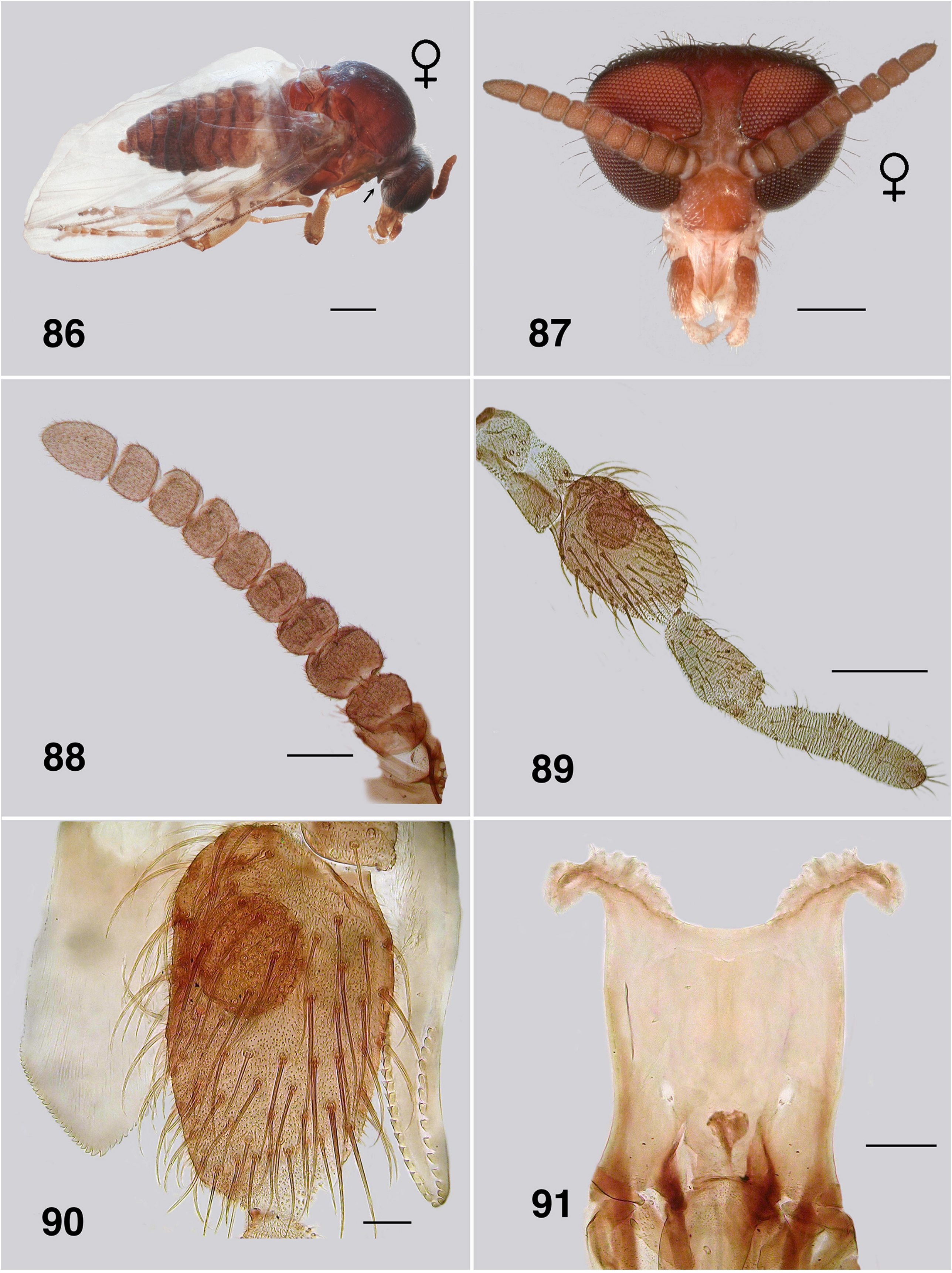
Tarsal claw basal tooth: Females of *Paraustrosimulium obcidens* and *P. anthracinum* each have a tooth that is markedly expressed, blunt, and with a distinct notch between the tooth and heel (Figs. 54, 96). The female claw of *Cnesiamima atroparva* is markedly similar in overall form. In contrast, the tooth in females of *P. colboi* is essentially absent (Fig. 12). The claw tooth in New Zealand *Austrosimulium* is present only in members of the *ungulatum* species-group, although not as markedly developed as in *P. obcidens* and *P. anthracinum*, and with only certain species having a notch between the tooth and heel. This type of claw is also present in the Australian species of the *ungulatum* species-group (*e.g.*, *A. crassipes* Tonnoir, *A. cornutum* Tonnoir). Members of the *mirable* species-group (*e.g. A.* (*A.*) *mirable*, *A.* (*A.*) *montanum*) possess a rather different claw from the others; specifically, a large basal tooth of different form that lacks both a notch and a heel. Species of subgenus *Novaustrosimulium* typically exhibit no expression of a tooth or heel, the only exception being *Austrosimulium* (*N.*) *magnum,* which possesses a small sharp tooth. Marked variation on basal tooth form makes this character suspect at higher phylogenetic levels, but has utility for characterizing groups of closely related species.

Genital fork: The three species of *Paraustrosimulium* have genital forks that are similar in overall form to those of the New Zealand *Austrosimulium*, although expression in the latter is rather varied (Craig *et al*. 2012). Other aspects of the genital fork, such as broad anterior arm, short broad lateral arms with variously expressed 'knee bends', small apodeme, and enlarged posterolateral lobes are similar to those of the *ungulatum*–species group. Such also occurs in the *bancrofti*–species group of *Novaustrosimulium*—but less so in the *furiosum*–species group. These variations notwithstanding, the genital fork of *Austrosimulium* and *Paraustrosimulium* differ from those of all other simuliids by the combination of a lack of intense pigment and the comparatively short and wide anterior- and lateral arms. In contrast, the genital forks of "*Cnephia*" *pilfreyi* and *Cnesiamima atroparva* is more distinctly pigmented and proportions of the anterior- and lateral arms are typical of other simuliids.

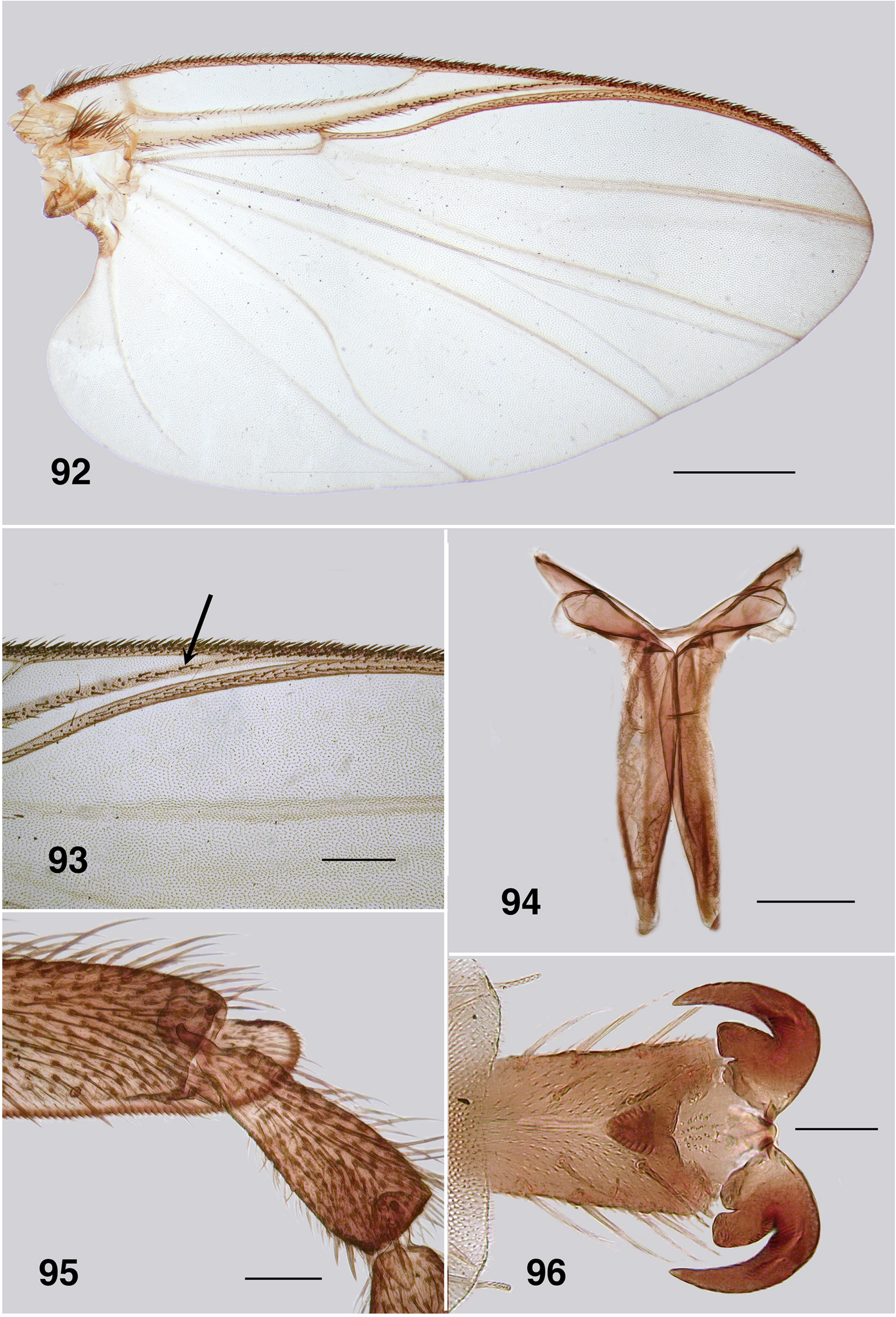
Spermatheca: None of the three species in *Paraustrosimulium* have patterning on the spermathecal surface, and all have sparse internal acanthae. *Paraustrosimulium obcidens* has considerable pigmentation down the sperm duct, but no sculpting at the junction (Fig. 58). *Paraustrosimulium colboi* has pigmentation for a short distance along the spermathecal duct and minor sculpting of the junction (Fig. 16). *Paraustrosimulium anthracinum* has neither pigmentation extended along the duct nor sculpting or clear area (Fig. 97). Most species of New Zealand *Austrosimulium* have a clear area at the duct junction, the only exception being *A. unicorne* Dumbleton of the *ungulatum*–species group. For all Australian *Austrosimulium,* for which material is available, the spermathecae are smooth externally, lack acanthae, and have a large clear area at the duct junction with sculpting at the pigmented edge of the spermatheca.

Cercus and anal lobe: The cercus of all three *Paraustrosimulium* species is rounded apically—a common condition in the Simuliidae. The anal lobe *P. colboi* and *P. obcidens* is angulate proximally, similar in form to those of *Gigantodax* species (Wygodzinsky & Coscarón 1989). In contrast, the anal lobe of *P. anthracinum* is tapered proximally.

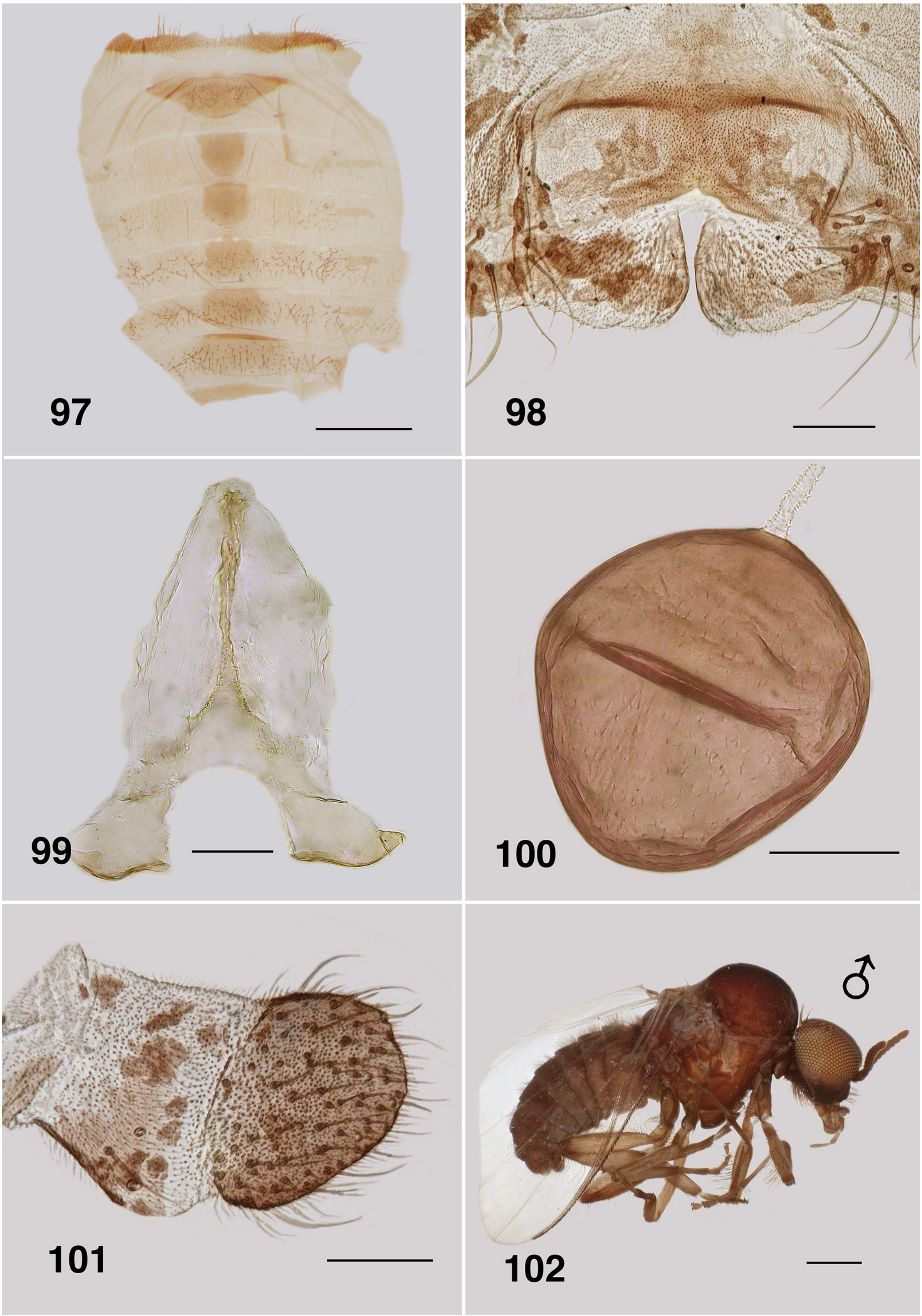
Male genitalia: In New Zealand *Austrosimulium* (*Austrosimulium*) the parameres are either absent or represented at most by a slender twisted rod of cuticle. Further, parameral spines are entirely lacking from such species (Craig *et al*. 2012). There is little or no mention of these character states by Dumbleton or the Mackerras'; however, examination of Australian *Austrosimulium* (*Austrosimulium*) species (Craig *per. obs.* 2014) reveals they are similar to New Zealand species, as described above. The subgenus *Novaustrosimulium* also has a weakly expressed paramere, but small spines are present in members of the *furiosum*–species group. These were illustrated by Mackerras & Mackerras (1949: 393. their Fig. 13c for *A.* (*N.*) *crassipes*). *A. bancrofti* has small parameres, but lacks spines (DAC pers. obs.). The ventral plate of members of the *furiosum*–species group possess a keel, and thus resemble those of *Paraustrosimulium*; the angulate gonostyli are also shared between members of these two taxa. In contrast, the gonostyli of *Austrosimulium* (*Austrosimulium*) and members of the *bancrofti*–species group of *Novaustrosimulium* are more tapered.



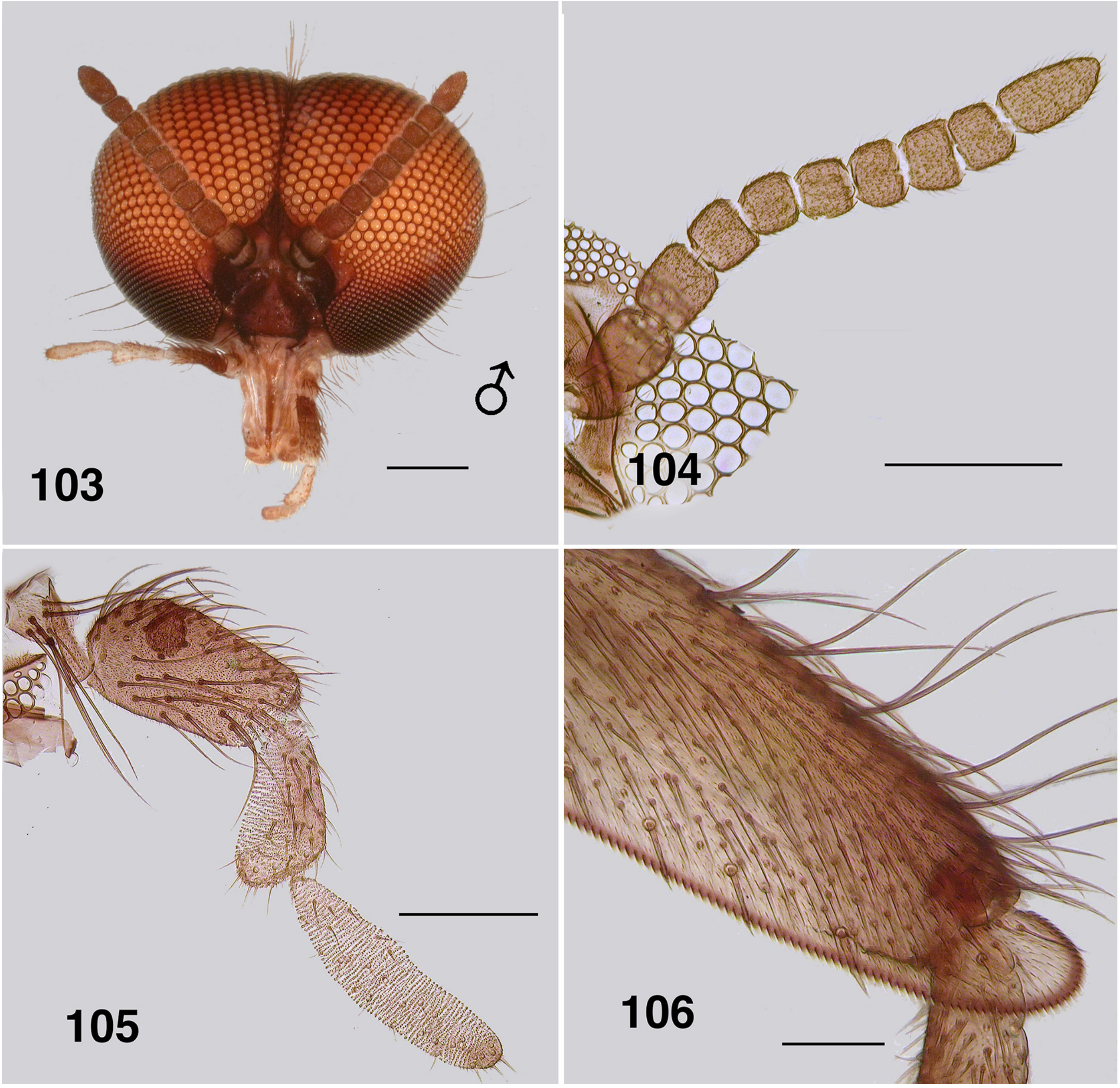
FIGURES 86–91. *Paraustrosimulium anthracinum* female. (86) Habitus. ETOH. Scale bar = 0.5 mm. (87) Frontal view of head. ETOH. Scale bar = 0.2 mm. (88) Antenna. Scale bar = 0.1 mm. (89) Maxillary palp. Scale bar = 0.1 mm. (90) Mandible apex, lacinia. Scale bar = 0.02 mm. (91) Cibarium. Scale bar = 0.05 mm.



FIGURES 92–96. *Paraustrosimulium anthracinum* female. (92) Wing. Scale bar = 0.5 mm. (93) Wing veins. Arrow indicates spiniform setae on R_1. Scale bar = 0.2 mm. (94) Metathoracic furcasternum. Scale bar = 0.1 mm. (95) Basitarsus & calcipala. Scale bar = 0.05 mm. (96) Claw. Scale bar = 0.02 mm.



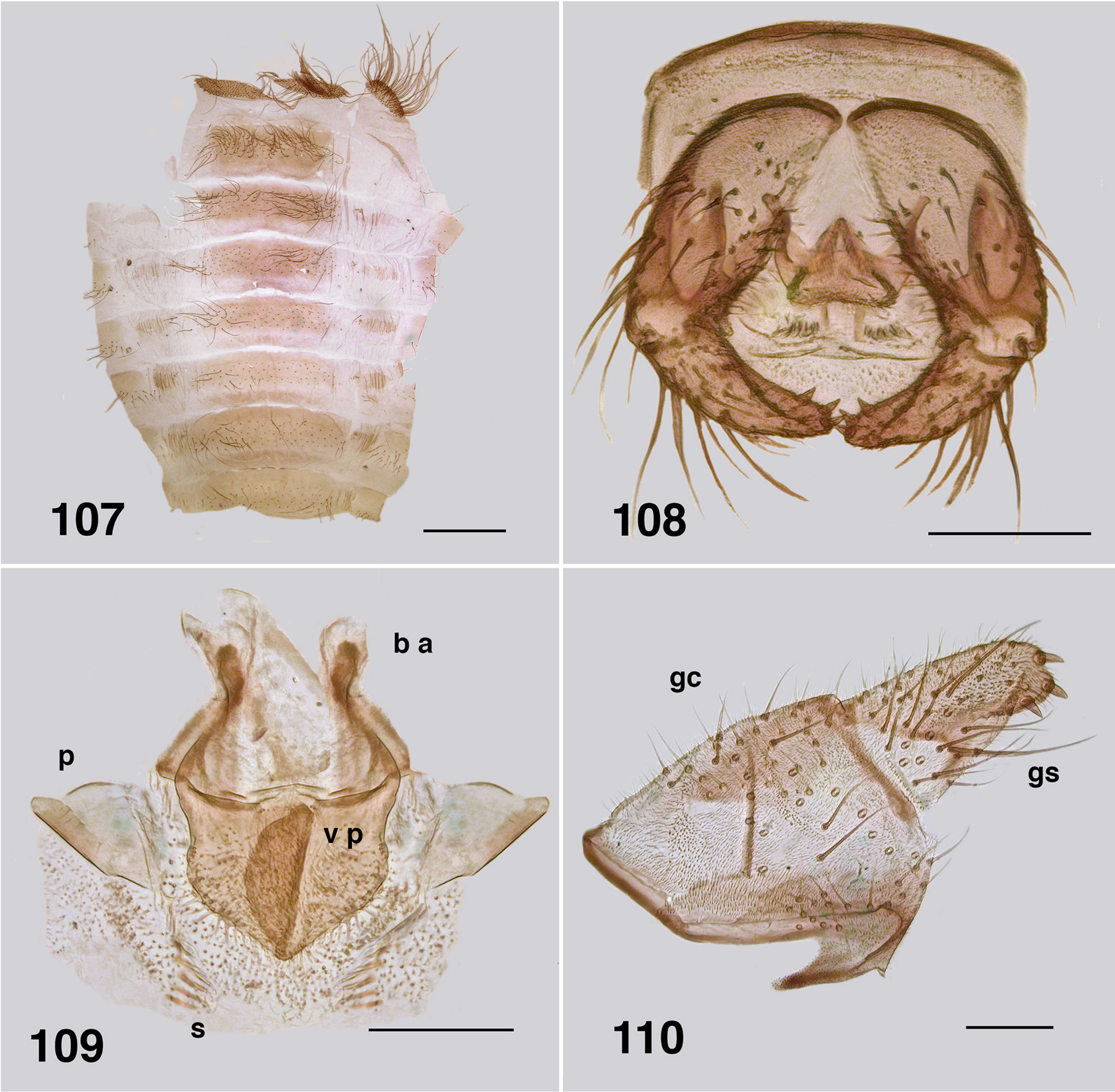
FIGURES 97–101. *Paraustrosimulium anthracinum* female. **FIGURES 102.** *Paraustrosimulium anthracinum* male. (97) Abdominal tergites. Scale bar = 0.5 mm. (98) Hypopygial valves. Scale bar = 0.05 mm. (99) Genital fork. Lightly stained with Chlorazol Black. Scale bar = 0.05 mm. (100) Spermatheca. Scale bar = 0.05 mm. (101) Cercus & anal lobe. Scale bar = 0.05 mm. (102) Male habitus. Scale bar = 0.5 mm.



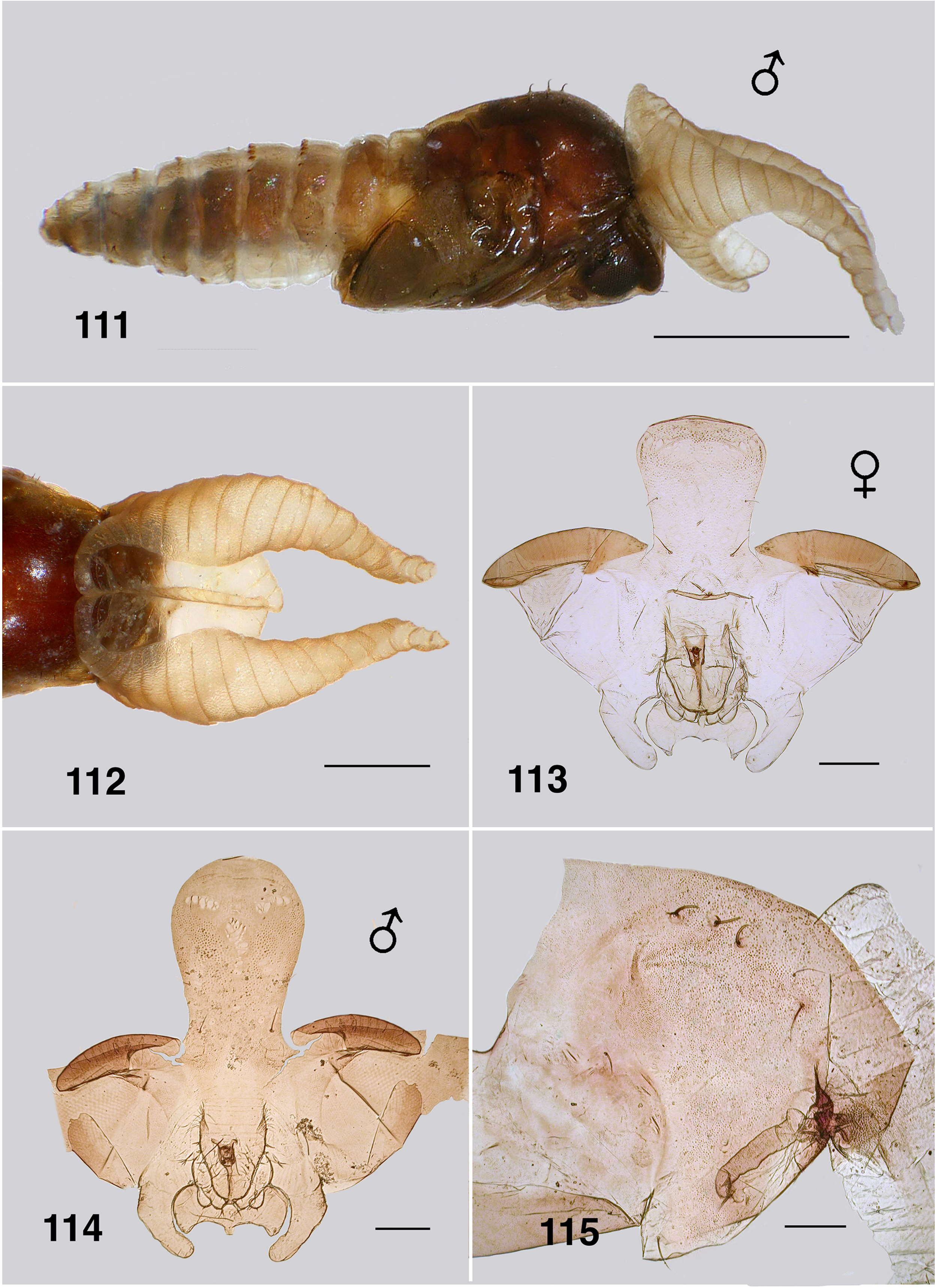
FIGURES 103–106. *Paraustrosimulium anthracinum* male. (103) Frontal view of head. ETOH. Scale bar = 0.2 mm. (104) Antenna. Scale bar = 0.2 mm. (105) Maxillary palp. Scale bar = 0.1 mm. (106) Calcipala and pedisulcus. Scale bar = 0.05 mm.

Pupa. *Gills*: The gills of *P. colboi* and *P. obcidens* (Fig. 26, 70) are inflated, tubular, structures that are similar in form to those of *Cnesiamima atroparva,* except for the presence of sparse fine filaments in the latter species (Coscarón 1991: 74, his Fig. 14 C). The gill of "*Cnephia*" *pilfreyi* is also an inflated, tubular, structure, although consisting of 6 filaments (as opposed to a single, large, cornuate structure, as in the previously mentioned species). The gills of *P. anthracinum,* while superficially similar in appearance to the other two species of *Paraustrosimulium*, are actually not tubular in form. Rather, they consist of flattened elongated curled laminae. The *P. anthracinum* gill appear to be more similar in form to that of *Simulium* (*Hemicnetha*) *canadense* (Hearle 1935: 14–15; Adler *et al*. 2004: 538) or to those of certain members of the *cormonsi*–species group of *Gigantodax* (Wygodzinsky & Coscarón 1989). While the external structure of gills seems to be rather varied in *Paraustrosimulium*, the way they are packaged within the gill histoblast of the last instar larva appears to be similar. When fully inflated, the pupal gill of *P. obcidens* is *ca*. 0.90 mm long with a maximum diameter of 0.09 mm (Fig. 70). The dimensions of the same gill when contained within the histoblast of a late last-instar larva is *ca*. 0.58 mm in length and 0.21 mm maximum breadth—a packaging ratio of *ca*. 1:2 for the length. This is achieved by each distal annulation being concertinaed sequentially into a larger more proximal annulation. The packaging of gills is further enhanced because each annulation is pleated laterally (Fig. 82), further reducing the diameter of each annulation—an elegant piece of biological engineering. Similar packaging is seen to the gill histoplast of pharate pupal *P. anthracinum* (Figs. 111, 112, 126, 127). Although the packaging of pupal gills has not been widely surveyed in the Simuliidae, it seems possible that the mechanism described above is synapomorphic—at least for *Paraustrosimulium* and perhaps also for *Paraustrosimulium* + *Cnesiamima*.

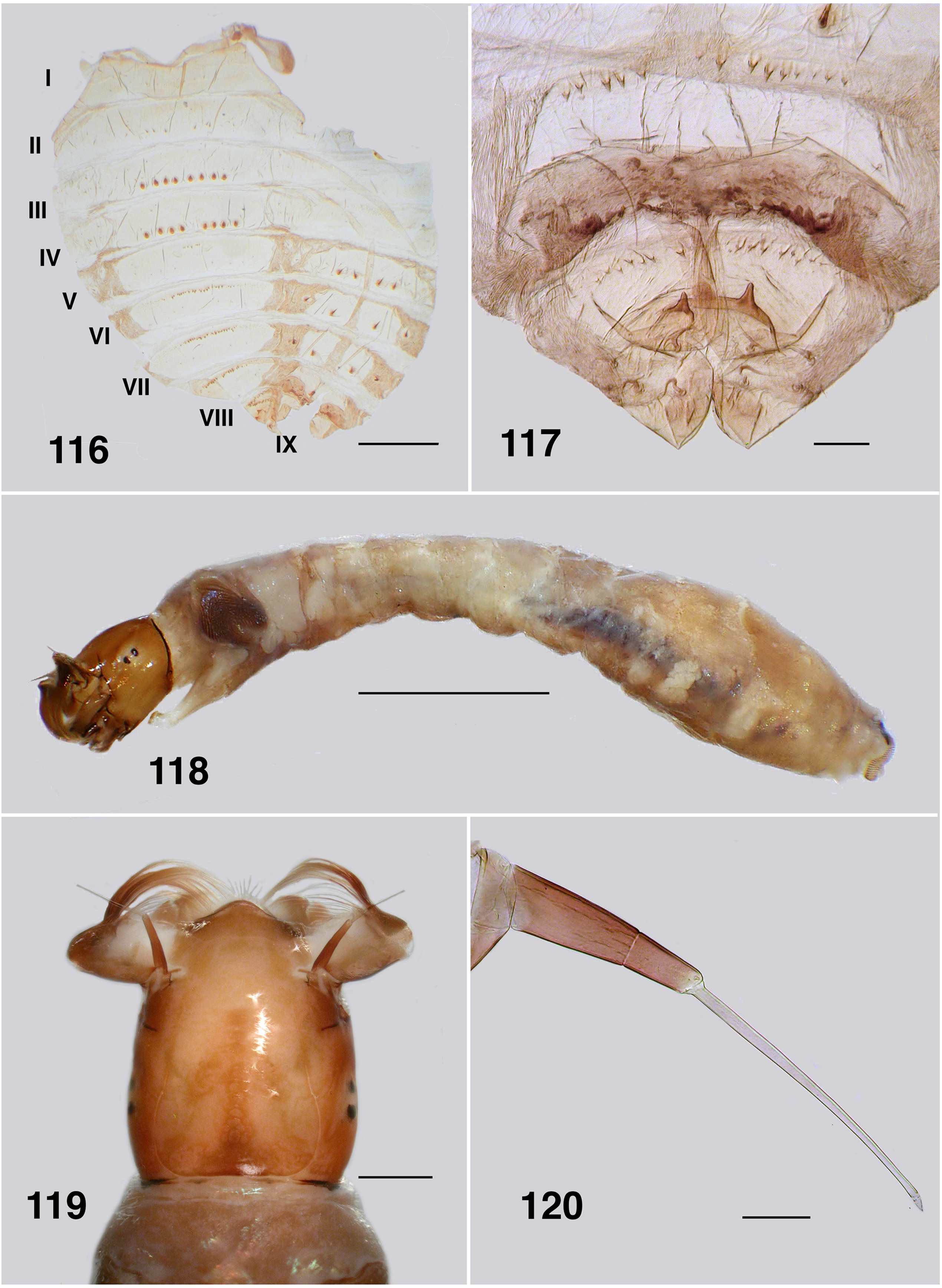
Cephalic plate: A character of considerable taxonomic utility for *Austrosimulium* is a marked depression of the vertex in the cephalic plate of the pupa. Craig *et al.* (2012) considered this state to be a synapomorphy of the *australense*–species group. It is absent from both members of the *ungulatum*–species group and the three species of *Paraustrosimulium*.



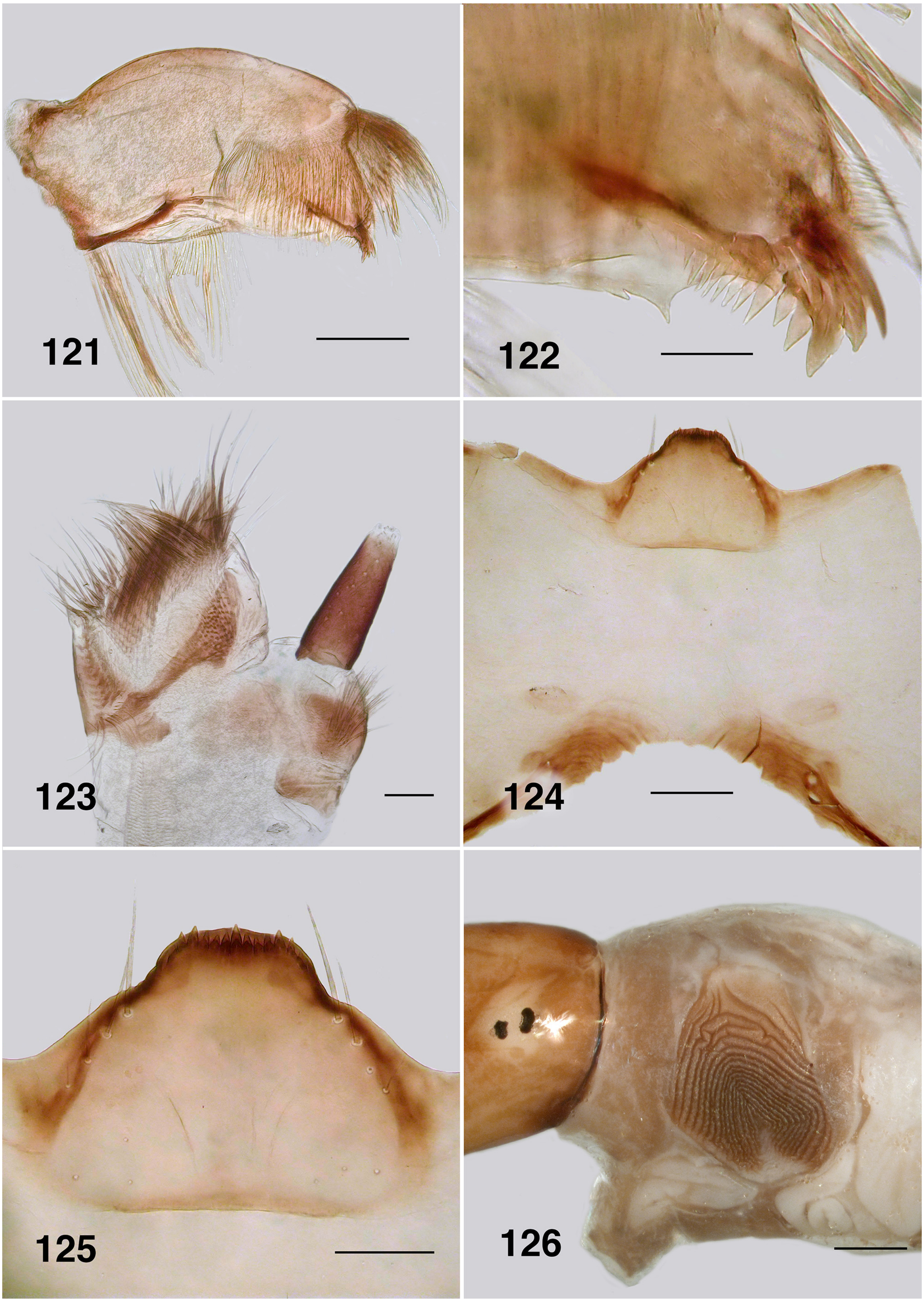
FIGURES 107–110. *Paraustrosimulium anthracinum* male. (107) Abdominal tergites. Scale bar = 0.2 mm. (108) Ventral view of genitalia. Cleared, in glycerine. Scale bar = 0.1 mm. (109) Ventral plate, parameres & spines. Slide mounted. Abbreviations: b a—basal arm, p—paramere, s—spines, v p—ventral plate. Scale bar = 0.05 mm. (110) Lateral view, gonocoxa—gc, gonostylus gs. Scale bar = 0.05 mm.



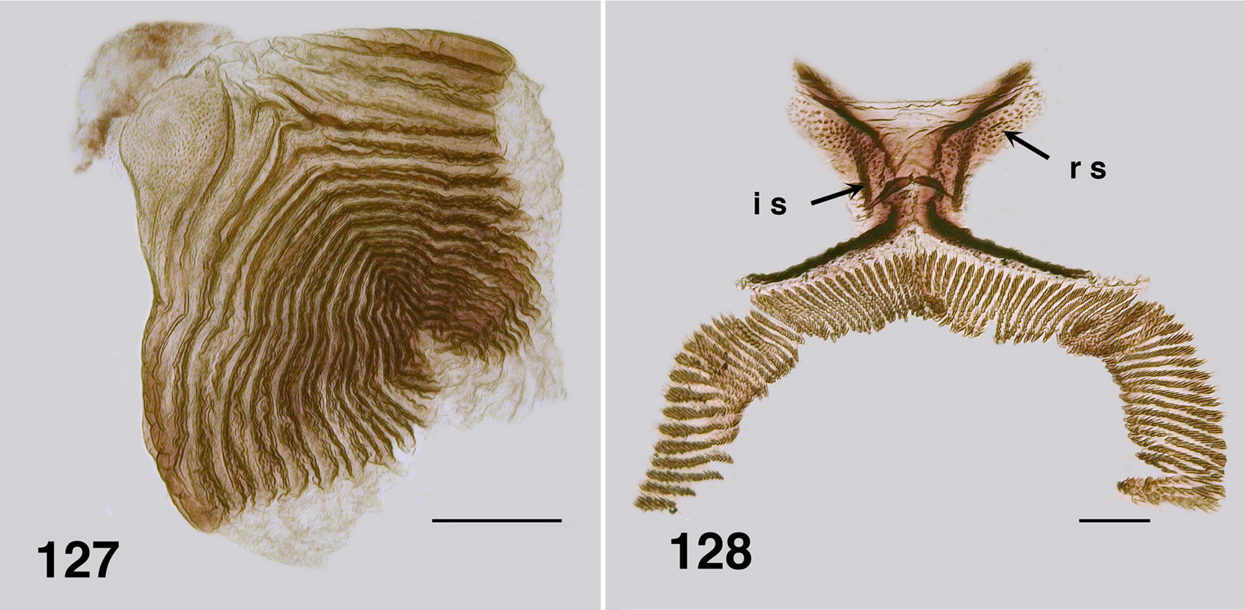
FIGURES 111–115. *Paraustrosimulium anthracinum* pupa. (111) Right lateral view of male pupae. Scale bar = 1.0 mm. (112) Dorsal view of pupal gills. Scale bar = 0.5 mm. (113) Frontal view of female head capsule. Scale bar = 0.2 mm. (114) Frontal view of male head capsule. Scale bar = 0.2 mm. (115) Thoracic cuticle. Scale bar = 0.2 mm.



FIGURES 116, 117. *Paraustrosimulium anthracinum* pupa. **FIGURES 118–120**. *Paraustrosimulium anthracinum* larva. (116) Abdominal armature. Scale bar = 0.5 mm. (117) Terminal segments. Scale bar = 0.05 mm. (118) Habitus, last instar larva. Scale bar = 1.0 mm. (119) Dorsal view of head. Scale bar = 0.2 mm. (120) Antenna. Scale bar = 0.05 mm.



FIGURES 121–126. *Paraustrosimulium anthracinum* larva. (121) Mandible. Scale bar = 0.1 mm. (122) Mandible apex. Scale bar = 0.02 mm. (123) Maxilla. Scale bar = 0.05 mm. (124) Genae, hypostoma, postgenal cleft. Scale bar = 0.1 mm. (125) Hypostoma. Scale bar = 0.05 mm. (126) Thorax showing pupal gill histoblast. Scale bar = 0.2 mm.



FIGURES 127, 128. *Paraustrosimulium anthracinum* larva. (127) Pupal gill histoblast, showing pleating. Scale bar = 0.2 mm. (128) Anal sclerite & circlet of hooks. Abbreviations: r c—rectal scales, i s—interarm strut. Scale bar = 0.1 mm.

Abdominal armature: Pupae of *Austrosimulium* and *Paraustrosimulium* have reduced abdominal armature, in particular ventral hooks which are absent in certain species of *Austrosimulium* and *P. colboi*. The terminal spines are also markedly reduced in members of those two genera, as well as in *Cnesiamima* and "*Cnephia*" *pilfreyi*. In *Paraustrosimulium* and *Cnesiamima*, the role of holding onto cocoon silk has evidently been assumed by a series of terminal grapnel hooks (Figs. 31, 73). Similar grapnel hooks are present in the pleura of abdominal segments VIII and IX of pupal *Metacnephia* Crosskey; however, this is almost certainly an independently derived state based on the relatively derived phylogenetic position of that genus (Adler *et al*., 2004). The stiff apically curved dorsocentral setae of the thorax (*e.g.* Fig 69) perhaps serve a similar role in *Paraustrosimulium* and *Cnesiamima*, but are comparatively less-well developed in *Austrosimulium*. Spine combs on tergite IX of *Austrosimulium* and *Cnesiamima* are absent, and only weakly expressed in *Paraustrosimulium* (Figs. 31, 73)—an unusual character-state that, in combination with the reduced size of the terminal spines, is considered synapomorphic for these three segregates.

Cocoon: The three *Paraustrosimulium* species all possess a more–or–less similar slipper-shaped cocoon. Those of *P. anthracinum* and *P. obcidens* (Fig. 68) have a well-defined anterior opening, no floor, and a well-defined ventral edge on the substrate. That of *P. colboi* is more substantial (Fig. 26) and has a distinct floor. Similar cocoon shapes can be seen in *Austrosimulium* and *Cnesiamima*. That of "*Cnephia*" *pilfreyi* differs in that it has a raised anteroventral collar, giving the cocoon a distinctive shoe-shape (Davies & Györkös, 1988).

Larva. *Antenna*: Larval antennal proportions of *Paraustrosimulium* species are all similar, with the ratios of basal, median and distal antennomeres 1.0:0.6:2.0. (Figs. 34, 76, 120). Antennae of New Zealand *Austrosimulium* larvae have somewhat variable proportions for the basal two antennomeres; but all have an elongated distal antennomere that is conspicuously longer than the combined length of the proximal antennomeres (Craig *et al*. 2012: their Figs. 367–383). The only *Austrosimulium* species in which the distal antennomere is shorter than the combined length of the proximal antennomeres are members of the subgenus *Novaustrosimulium*. In that segregate, the two proximal antennomeres are of approximately equal length and the distal antennomere is shorter than as described above, with ratios ranging from 1.0:1.1:1.5 to 1.0:0.8:1.1. The elongate condition of the distal antennomere is clearly derived within the Simuliidae. The only other austral simuliids exhibiting a similar condition is *Cnesiamima* and "*Cnephia*" *pilfreyi*. It seems possible that an elongate distal article could be synapomorphic for *Paraustrosimulium*, *Austrosimulium*, *Cnesiamima* and "*Cnephia*" *pilfreyi*; albeit, implying a reversal in *A.* (*Novaustrosimulium*).

Mandible: Mandibles of Australian *Paraustrosimulium* larvae have apical teeth that are finely expressed and narrowly projected apically (*e.g.*, Fig. 35). Such is also expressed in the Australasian *Austrosimulium* s.str. and *A.* (*Novaustrosimulium*). The apical teeth in *P. anthracinum* are comparatively more substantive. The mandibular sensillum and serration (Craig 1977) in all *Austrosimulium* larvae are complex (Craig *et al*., 2012), unlike the simple projections in the three *Paraustrosimulium* species (Figs. 35, 78, 122).

Hypostoma: All three species of *Paraustrosimulium* have the ventral wall of the hypostoma extended anteriorly such that it obscures the hypostomal teeth, which in turn are not grouped in a distinctive fashion (Figs. 38, 81, 125). In this respect, the hypostoma of *Paraustrosimulium* is virtually identical to those of *Austrosimulium* and "*Cnephia*" *pilfreyi*. The hypostomal teeth of *Cnesiamima atroparva* are also obscured by the ventral wall of the hypostoma (Coscarón 1985: 69); however, unlike the previously mentioned taxa, the outermost sublateral, lateral, and paralateral teeth are clustered onto a prominent lobe. The relatively extended ventral hypostomal wall might constitute evidence of common ancestry among these taxa.

Postgenal cleft: The cleft is essentially absent in *P. anthracinum* (Fig. 124) but relatively well developed in *P. colboi* (Fig. 37) and *P. obcidens* (Fig. 80)—similar in expression to the New Zealand *Austrosimulium*. The cleft is of variable expression in the Australian *Austrosimulium*, for example ranging from absent in *A.* (*A.*) *montanum* to well developed in *Novaustrosimulium* species. The postgenal cleft is absent from both *Cnesiamima atroparva* and "*Cnephia*" *pilfreyi*.

Anal sclerite interarm strut: This character-state is clearly derived within the Simuliidae based on its absence from members of the Parasimuliinae and Prosimuliini. Tonnoir (1925) used the presence of interarm struts, in part, to characterize members of the genus *Austrosimulium*. However, that state is now known to be more widely distributed among simuliine genera, including *Paraustrosimulium* and *Gigantodax*. In larvae of *Austrosimulium* and *P. anthracinum* (Fig. 128) the interarm struts appear to be the lateral strengthened edge of a broad medial region that bridges the dorsal and ventral arms; in most examples, the cuticle between the struts is pigmented. The condition in *P. colboi* (Fig. 40) and *P. obcidens* (Fig. 83) is similar except the interarm struts are somewhat more closely approximated (giving the sclerite a more distinctive X–shaped appearance), and the cuticle between the interarm struts is sparsely pigmented. Superficially, therefore, the laterally strengthened edges appear more definitely as independent struts, as opposed to being part of a more integrated medial sclerotized area between the dorsal and ventral arms. In this respect, the interarm struts in *P. colboi* and *P. obcidens* more closely resemble the condition in *Gigantodax* than in *P. anthracinum* and *Austrosimulium*. However, phylogenetic studies based on morphological (Gil–Azevedo & Maia–Herzog 2007: 60) and molecular (Moulton, 2003) datasets reveal that *Gigantodax* is distantly related to *Paraustrosimulium* and *Austrosimulium*. Accordingly, interarm struts must have evolved independently at least twice within the Simuliidae. Coscarón & Coscarón Arias (2007: 94) remarked that the anal sclerite of *Cnesiamima* was without or with "only faint" interarm struts (*cf.* their figure 22N), perhaps suggesting a close relationship with *Austrosimulium* and *Paraustrosimulium*. Davies & Györkös (1988) reported that interarm struts were absent from the anal sclerite of "*Cnephia*" *pilfreyi*; however, their material was badly bleached so it is conceivable the arms are actually present but weakly expressed. Examination of more freshly collected material is needed to confirm the presence or absence of interarm struts in "*C.*" *pilfreyi*.

Semicircular sclerite: Homologies of the semicircular sclerite that surrounds the circlet of hooks in many *Austrosimulium* species is of similar concern to the interarm struts. While the presence of this sclerite appears to be of considerable taxonomic value in *Austrosimulium*, similar structures occur in larvae of other taxa, such as *Parasimulium* Malloch (Adler *et al*., 2004), *Crozetia* Davies (Craig *et al*. 2003), *Gigantodax* (Wygodzinsky & Coscarón, 1973) and *Simulium* (*Gomphostilbia*) *palauense* Stone (Takaoka & Craig 1999). Dumbleton (1973: 563) provided examples of the varied forms of semicircular sclerite known at that time. Reasons for not considering these structures to be homologous, in all instances, include: (1) differences in expression of the junction of the semicircular sclerite to the ventral arm of the anal sclerite and, (2) semicircular sclerite expression is merely a product of the degree of sclerotization and pigmentation of the ring of cuticle that surrounds and supports the outer edge of the circlet of hooks (Fig. 83). Apparently, such a ring (whether darkly sclerotized or not) is present in all simuliid larvae (Craig *et al*. 2012: 48). Accordingly, while the presence of a particularly expressed semicircular sclerite may prove to be synapomorphic for a given lineage, interpretations of homology must be made with caution.

The relationships of *Paraustrosimulium* and biogeographic considerations

Evidence presented here and in accordance with most previous studies is that *Paraustrosimulium*, *Cnesiamima*, *Austrosimulium* and "*Cnephia*" *pilfreyi* all share an immediate common ancestry (*e.g*., Wygodzinsky & Coscarón, 1972, Gil-Azevedo & Maia-Herzog 2007, Craig *et al*. 2012). This is somewhat at odds with Moulton's (2003) comprehensive analysis of molecular data, in which *Austrosimulium* was placed as the sister group of all other simuliine genera analyzed—distantly removed from a strongly supported monophyletic lineage including "*Cnephia*" *pilfreyi*, *Paraustrosimulium* and "*Austrosimulium colboi*" (note that *Cnesiamima* was not among the taxa sampled in Moulton's analysis). Whether the unexpected position of *Austrosimulium* was a product of long-branch attraction—as suggested by Gil-Azevedo & Maia-Herzog (2007), remains an open question. Monophyly of this clade of austral simuliids is supported by up to 4 synamporphies: *viz*. reduced abdominal armature in the pupa, hypostoma with ventral wall extended anteriorly to obscure teeth, larval antenna with distal antennomere markedly longer than the two proximal antennomeres combined (condition reversed in members of *A. Novaustrosimulium*) and presence of interarm struts in anal sclerite (yet to be definitely confirmed in "*Cnephia*" *pilfreyi.*

Monophyly of *Paraustrosimulium*, as currently defined, is supported by just one synapomorphy: namely, presence of markedly expressed cervical sclerites in the adults. Wygodzinsky & Coscarón (1973) established the monotypic genus *Cnesiamima* based solely on adults, but acknowledged the overall similarity of that segregate with *Paraustrosimulium*. Had the immature stages of *Cnesiamima* been known to those authors, as they are now, we wonder whether they would have described it as a separate genus. Nonetheless, the phylogenetic analysis of Gil-Azevedo & Maia-Herzog (2007) has *Cnesiamima* as the sister group of *Paraustrosimulium* + *Austrosimulium*—a reasonable placement based on available evidence. "*Cnephia*" *pilfreyi* wasn't included in Gil-Azevedo & Maia-Herzog's (2007) analysis, but Moulton's (2003) molecular analysis placed that species in a trichotomy with *Paraustrosimulium* (as here defined) plus a cluster of northern Holarctic genera. More freshly collected material of "*C*" *pilfreyi* is needed to better understand its relationships with other members of this austral clade.

In terms of relationships within *Paraustrosimulium*, it seems likely that *P. anthracinum* is the sister of *P. obcidens* and *P. colboi* together, supported, in part, by geography and shared pupal gill structure in the latter two species (*cf*. Figs 26, 70, 112).

Paraustrosimulium, *Cnesiamima*, *Austrosimulium* and "*Cnephia*" *pilfreyi* exhibit marked structural heterogeneity, and the relictual distribution of their members bespeaks a relatively early origin for their common ancestor. Separation of southern Western Australia and Antarctica was complete *ca*. 95 Mya (Rix *et al*. 2015). Given the morphological similarities between *P. anthracinum* and *P. obcidens*, plus a predilection for cooler water, a reasonable assumption is that that tectonic movement was the vicariant event separating their precursor. The last connection between South America and Antarctica was at 41–35 Mya, with formation of the Drake Passage. Final separation of Australia and Antarctica was *ca*. 32 Mya, well to the east, when Tasmania separated and the Antarctic Circum–Polar Current was established. A secondary vicariant event that probably separated the precursor of *P. obcidens* and *P. colboi* was the inundation of the Nullarbor Plain region by the Eromanga Sea at *ca.* 25 Mya. The Nullabor marine incursion did not end until *ca*. 14 Mya (Toussaint *et al*. 2016), followed by a mid–Miocene climatic optimum. We consider *P. colboi* to be the more derived taxon of the two Australian species.

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