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Reassignment of Western Australia *Paracnephia gladiator* Moulton & Adler to a new genus, *Bunyipellum* (Diptera: Simuliidae)

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Abstract

With new material available of most stages of many known Australian *Paracnephia,* including new species, it is now clear that certain segregates warrant assignment to new genera. This applies to *Paracnephia gladiator* Moulton & Adler, a Western Australia simuliid with numerous unique character states. The species is fully redescribed and assigned to *Bunyipellum* **nov. gen.** A diagnosis is provided and relationships discussed, as is historical biogeography. *Bunyipellum* appears to be more closely related to elements of the South American simuliid fauna than to any other Gondwanan Australian species.

Key words: Western Australia, Gondwana, Simuliidae, *Bunyipellum* **nov. gen.**, bionomics, biogeography

Introduction

Distinctive Australian simuliids originally placed in the Holarctic genus *Cnephia* Enderlein by Mackerras & Mackerras (1948 *et seq.*) were assigned to Afrotropical genus *Paracnephia* Rubtsov by Crosskey & Howard (1997). Despite reservations by many specialists about the relationship of the Australian species to *Paracnephia s.s.* and to each other (*e.g.*, Davies & Györkös, 1988; Moulton *et al.*, 2004; Gil-Azevedo & Maia-Herzog, 2007; Currie & Adler, 2008), this assignment has persisted to the present day (Adler & Crosskey, 2017). In the phylogenetic remarks section of their description of *Paracnephia gladiator* Moulton & Adler, Moulton *et al.* (2004: 10) remarked that their generic assignment was a conservative move adopted for convenience, noting similarities between that species and the South American genera *Araucnephia* Wygodzinsky & Coscarón, *Araucnephioides* Wygodzinsky & Coscarón and *Paraustrosimulium* Wygodzinsky & Coscarón. Indeed, molecular data reveals that *Paracnephia gladiator* has no close relationship to any other Gondwanan Australian species (Moulton, unpublished).

With the availability of high quality material of many Australian Gondwanan simuliids, including new species (*e.g.* Craig *et al.* 2017), we now have the basis to confidently reassign *P. gladiator* to its own monotypic genus. We fully describe and illustrate the new genus, and offer brief comments about its relationships and historical biogeography. This is the second in a series of papers (*cf.* Craig *et al.* 2017) that aim to revise the Gondwanan Simuliidae of Australia.

Material and methods

This work is based on original material of adults and immature stages collected by JKM in 1996 and female adults collected by Andreas Zwick in 2003. Preparation techniques follow those of Craig *et al.* (2014). Images are all by DAC.

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For hypostomal teeth, rather than a system used by Currie (1986), as well as Adler *et al*. (2004) and others, we use a numbering system suggested by JKM, similar to that of Okazawa & Nodasaka (1982), but here the median tooth is designated '0' and those lateral on either side are numbered in sequence ‘1, 2, 3 .....’. Thence the 'lateral or corner tooth' is ‘4’ and the so-called ‘paralateral teeth’ are designated '5' and so on, if present (Fig. 36).

Bunyipellum **nov. gen. Craig, Currie, Moulton.**

Paracnephia gladiator **Moulton & Adler, 2004. Type species.**

Diagnosis. As noted by Moulton *et al.* (2004: 6) in their original description of *Paracnephia gladiator*, the larvae could be distinguished from those of all other species in the family by a suite of characters—namely, head capsule brown, hypostoma with eight equal-sized teeth, postgenal cleft squared and extended 1/4-1/3 distance to the hypostoma, body dark brown and gradually expanded posteriorly. Pupae were unique in having elongated spines on the head and thorax. Females were distinguished from those of all others by the orange scutum, maxillary palpomere V shorter than III and tarsal claws either lacking a tooth, or with a markedly small example. Males by the scutal colour and maxillary palp (as for female). With newer material available of most stages of the Australian Gondwanan simuliids, and with the recent reassignment of two such species to *Paraustrosimulium* (Craig *et al.* 2017), our reexamination of all stages of *Paracnephia gladiator* reveals that generic reassignment is also warranted for that species.

Adults: Nine antennomeres; body markedly tri-coloured with abdomen dark, antennae, legs and genitalia light yellow, thorax coloured; wings lacking colour spots, vein C with spine-like setae, Rs not branched, R and Rs not closely applied, small basal cell present, CuA_2 and M_1 sinuous. *Female*: Frons markedly broad; thorax yellowish orange; claw tooth absent to markedly small, heel colourless; spermatheca enlarged; hypogynial valves broadly rounded apically, anal lobe exacerbated. *Male*: Thorax reddish orange; genitalia protruded ventrally; gonostylus with two terminal spines; ventral plate as broad as long, narrow median carina, hirsute; paramere connector thin and closely applied to lateral edge of ventral plate, paramere plate-like, spines small and on bare aedeagal membrane. *Pupa*: Elongated spine-like setae (aka trichomes) on head and thorax; abdominal tergites ridged; pleurites absent; terminal spines elongated and sharp; 'grapnel hooks' as stiff straight setae. *Larva*: Body and head dark brown; labral fan stems short and broad; ray number and expression exacerbated; antenna subequal to fan stem length, basal antennomere markedly short and clear; hypostomal teeth small, in concave arrangement, tooth 5 forming 'lateral' tooth; anterior proleg circlet of hooks markedly small, similarly posterior proleg circlet, but hooks dark brown and enlarged.

Etymology. Named after the fearsome mythical beast of Australian Aboriginal mythology, the 'Bunyip'; said to lurk in the depths of billabongs (Holden & Holden, 2001).

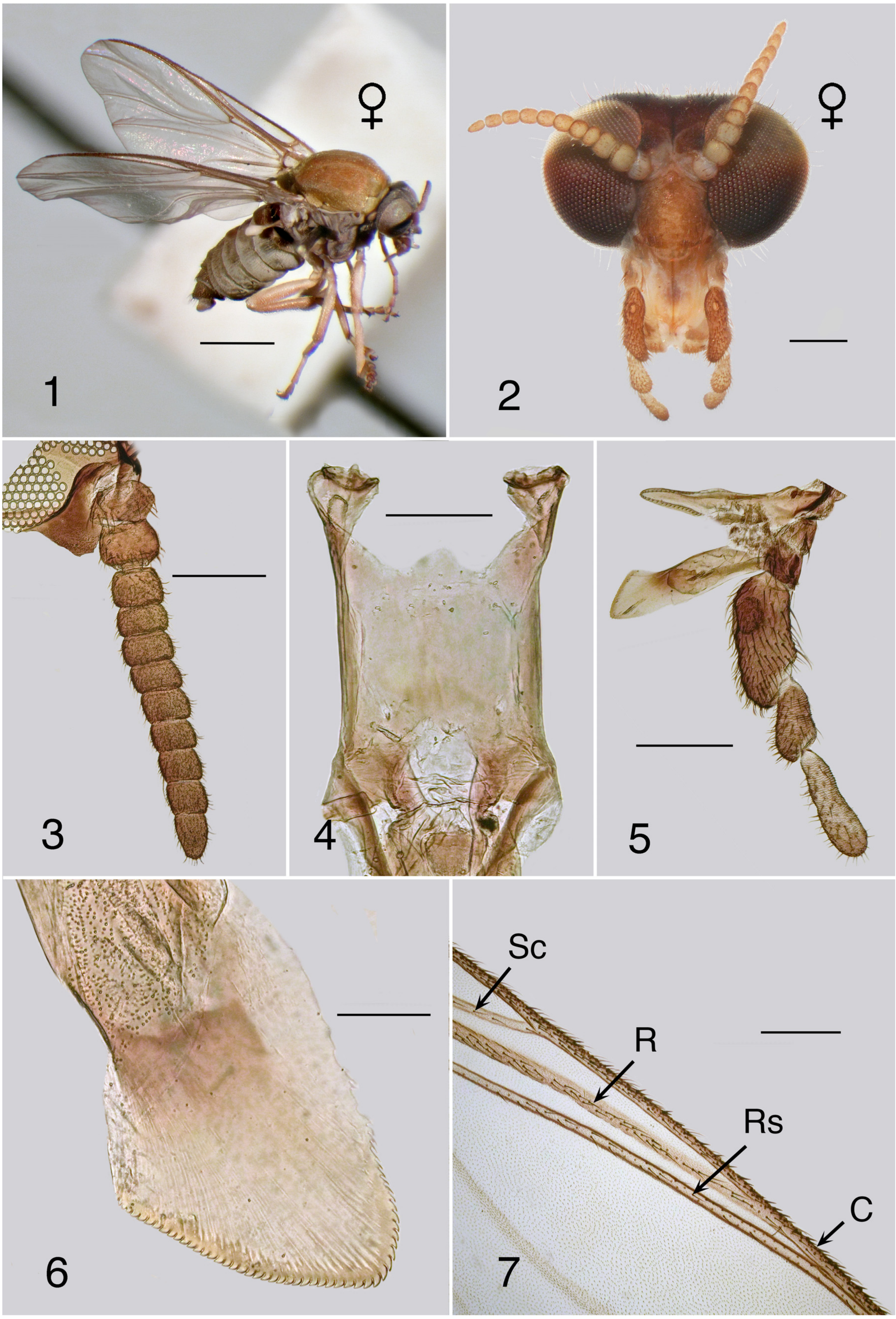
Bunyipellum gladiator **(Moulton & Adler) 2004. New Combination**

(Figs. 1–43)

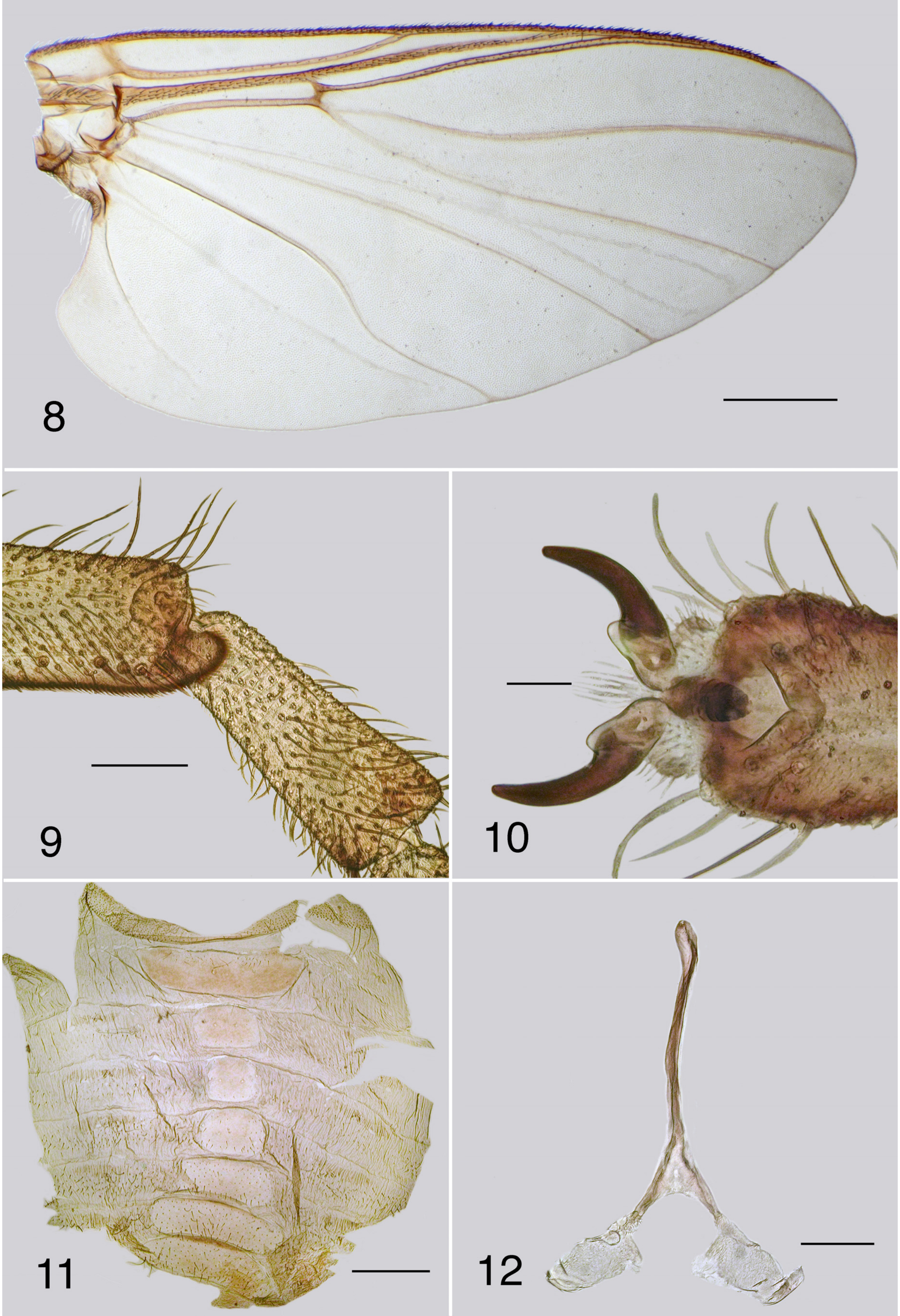
Cnephia "B", Bedo, in Rothfels 1979: 522. Cytospecies.
Paracnephia gladiator Moulton & Adler 2004: 3. Species designation (in Moulton *et al*. 2004).
Paracnephia gladiator, Adler & Crosskey 2008 *et seq*. 2017. Unplaced to subgenus.

Redescription. *Adult female* (based on numbers of specimens and original description). *Body* (Fig. 1): head dark brown, thorax reddish orange, abdomen blackish; total length 3.6–3.8 mm. *Head* (Fig. 2): overall dark in colour; width 0.94–1.10 mm; depth 0.54–0.60 mm; postocciput not markedly hirsute, frons expanded dorsally, broad, dark brown–black; frons-head ratio 1.0:4.5. *Eye*: interocular distance *ca.* 0.20–0.22 mm; all ommatidia similarly pigmented, diameter 0.012 mm; *ca.* 30 rows across and 36 down at mid–eye. *Clypeus*: width 0.23 mm, expanded ventrally; mottled medium brown, vestiture of sparse hairs. *Antenna* (Fig. 3): 9 flagellomeres, extended beyond head margin; total length 0.7–0.8 mm; evenly pale brownish yellow; pedicel smaller, scape larger than flagellomere I, others similar in size basally, slightly elongated distally, barely tapered to apex. *Mouthparts*: well developed, *ca.* 0.45x length of head depth; maxillary palpus (Fig. 5), relatively short, total length 0.68 mm, palpomeres I & II small, palpomere III darker brown than remainder, dense vestiture, IV small, V (distal) short; proportional lengths of palpomeres III–V 1.0:0.6:0.8; sensory organ ovoid, 0.3x length of palpomere III, opening broad, 0.6x width of vesicle; mandible (Fig. 6) with *ca.* 35 small inner teeth (44–50 in original description), 16 outer teeth; lacinia with *ca*. 17 and 13 teeth on inner and outer edge respectively; cibarium (Fig. 4) with cornuae broad and sclerotized apically, lightly sculpted, median gap broadly U-shaped with median projection, setae and armature absent. *Thorax*: length 1.4–1.7 mm; width 1.2–1.3 mm; evenly dark reddish orange with faint medial and lateral vittae and sparse black hairs; postpronotal lobe slightly paler, well developed; scutellum markedly pale with vestiture of long sparse lateral brown hairs; scutellar depression darker with sparse black hairs; postnotum dark brown, antepronotal lobe (aka propleuron) well developed with small array of vertical pale hairs, proepisternum and fore coxa with sparse pale hairs; pleuron brown, anepisternal (aka plural) membrane dark gray, lacking hairs; katepisternum darker, sulcus distinct and broad. *Wing* (Figs. 1, 7, 8): slightly fumose, length 3.4–4.4 mm; width 1.4–1.5 mm; anterior veins markedly brown, substantial**,** small basal cell distinct; a:b ratio 1.0:2.8; distal 2/3 of costa with hair-like setae proximally, mixed with spine-like setae distally, base of radius and R1 with hair-like setae dorsally, Rs with no trace of apical fork; false vein forked, M_1 appearing double; CuA_1 straight, not reaching wing margin (original description has it so), CuA_2 sinuous, reaching wing margin; A_1 curved distally, not reaching wing margin; A_2 with sclerotized base in anal angle. *Haltere*: stem tan, knob white to beige. *Legs* (Figs. 1, 9): evenly pale yellow; femora and tibiae slightly darker apically, hind basitarsus with ventral regular row of stout spines; calcipala small, less than 1/4 length of tarsomere II, with concentration of spines; pedisulcus essentially absent, as minor wrinkles; tarsomere II expanded distally, 2.5x longer than distal width; claws (Fig. 10) with talon smoothly tapered, basal tooth absent, rarely with small, sub-basal tooth, heel of claw moderately expressed and clear. *Abdomen*: in ETOH, dark greyish brown; basal scale (tergite I) mottled pale and dark grey with short pale hairs; anterior segments dark grey, segments posterior of V, darker brownish black; tergites poorly sclerotized and yellowish, tergite II markedly broad (Fig. 11), membranous areas grey. *Genitalia*: markedly small, yellowish; sternite VIII with distinct median region, vestiture of microtrichial arrays, large strong hairs posterolaterally; hypogynial valves (Fig. 14) markedly pale, vestiture of triads of microtrichia and strong hairs, median edges of valves distinctly concave, not strengthened, apices broadly rounded, insubstantial and colourless; genital fork (Fig. 12) elegant, anterior arm long and narrowed in expression, slightly expanded apically, no indication of membranous lateral areas, lateral arms narrowed, apodeme absent, posterolateral expansions well developed; spermatheca large, ovoid, (Fig. 13), surface smooth, internal fine spines (or acanthae) present in arrays of 4 to 5, small and hard to observe, clear area around junction with spermathecal duct small, sculpting minimal; cercus in lateral view ovoid, lightly pigmented; anal lobe rounded, substantial, more heavily pigmented (Fig. 15).

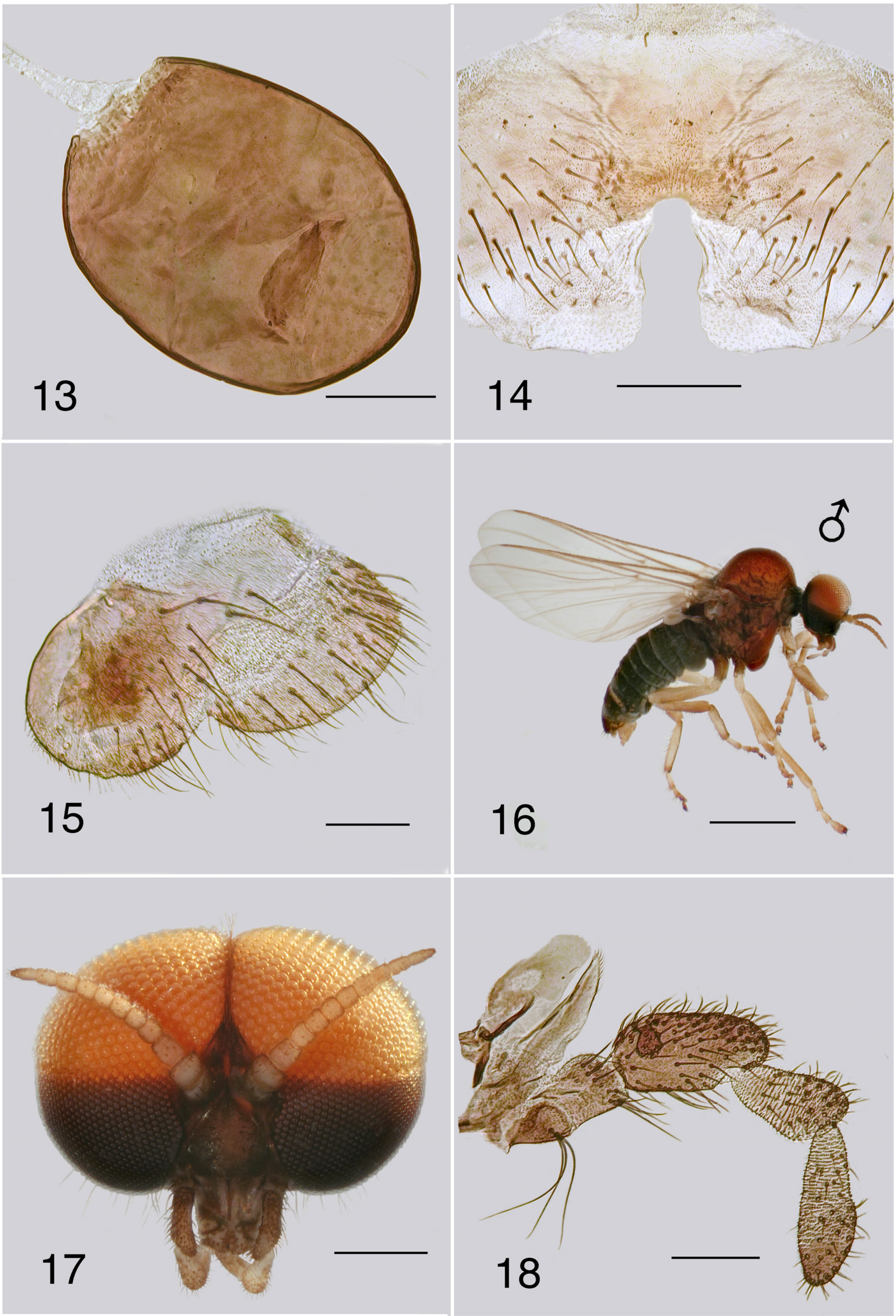
Adult male (based on numerous specimens and original description). *Body* (Fig. 16): overall tri-coloured, thorax reddish orange, legs pale yellow, abdomen black; total body length 2-6–3.3 mm. *Head* (Fig. 17): width 1.0 mm; depth 0.7 mm. *Eyes*: upper ommatidia colour dark orange, not markedly enlarge, diameter 0.033 mm, *ca.* 23 across and down; lower smaller ommatidia black to blackish orange, diameter 0.018 mm, *ca.* 24 across, 36 down. *Clypeus*: mottled black; width 0.2 mm; vestiture of sparse fine black hairs. *Antenna*: overall yellow, total length 0.71–0.73 mm; pedicel and scape dark brown; scape short, pedicel wider than broad, flagellomere I narrower than scape and longer than broad, remaining flagellomeres evenly yellow and tapered smoothly to elongated apical flagellomere. *Mouthparts*: insubstantial; length 0.3x head depth; maxillary palpus (Fig. 18) 0.6 mm long, palpomere III dark and tubular, extended distally, palpomeres IV smaller, palpomere V subequal in length to III, proportional lengths of III–V palpomeres 1.0:0.7:1.0, sensory vesicle minute, spherical, occupying 0.3x length of palpomere III, opening 0.33x width of vesicle; lacinia small with apical hairs; mandible lacking teeth. *Thorax*: markedly domed (Fig. 16), head angled anteriorly; length 1.2 mm; width 1.1 mm; postpronotal lobe concolourous with scutum, hairs longer; scutum mottled reddish orange, vestiture of sparse recumbent fine pale hairs, longer in scutellar depression; scutellum markedly paler than scutum with long black hairs laterally, postnotum darker than scutum, antepronotal lobe and proepisternum haired; pleurae darker than scutum, katepisternum dark brown, sulcus distinct, albeit shallow. *Wing* (Fig. 19): length 2.8–3.2 mm, width 1.4 mm**;** basal cell present, but minute; a:b ratio 1.0:3.0; otherwise as for female. *Haltere*: stem pale, knob grey. *Legs*: overall yellowish, hind basitarsus slightly expanded medially, ventral row of stout spines, calcipala and pedisulcus as for female; tarsal claw and grappling pad normal. *Abdomen* (Fig. 20): black; basal scale (tergite I) black, hairs pale and long, extended to posterior of tergite II, tergites all markedly broad and equally sclerotized; sternite I present, II absent, III and those more



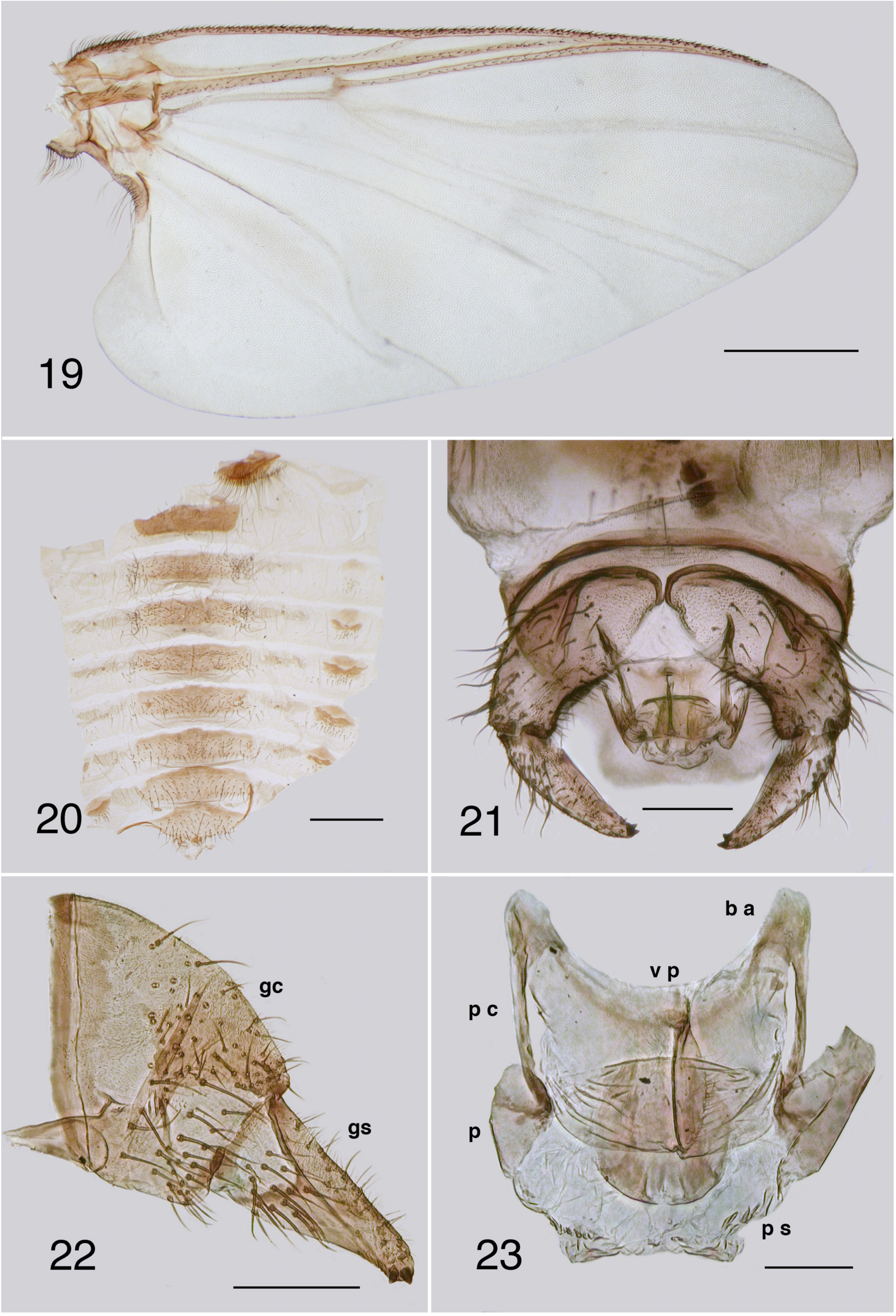
FIGURES 1–7. *Bunyipellum gladiator* female. (1) Habitus of female. Critical point dried from ETOH, colours muted. Scale bar = 1.0 mm. (2) Frontal view of head, ETOH. Scale bar = 0.25 mm. (3) Antenna. Scale bar = 0.2 mm. (4) Cibarium. Scale bar = 0.1 mm. (5) Maxilla, lacinia, mandible. Scale bar = 0.2 mm. (6) Mandible apex. Scale bar = 0.05 mm. (7) Wing veins. C = costa, R = radius, Rs = radial sector, Sc = subcosta. Scale bar = 0.2 mm.



FIGURES 8–12. *Bunyipellum gladiator* female. (8) Wing. Scale bar = 0.5 mm. (9) Calcipala and basitarsus II. Scale bar = 0.1 mm. (10) Claw. Scale bar = 0.02 mm. (11) Abdominal tergites. Scale bar = 0.5 mm. (12) Genital fork. Scale bar = 0.1 mm.



FIGURES 13–15. *Bunyipellum gladiator* female. **FIGURES 16–18**. *Bunyipellum gladiator* male. (13) Spermatheca. Scale bar = 0.1 mm. (14) Hypogynial valves. Scale bar = 0.1 mm. (15) Cercus and anal lobe. Scale bar = 0.05 mm. (16) Male habitus, ETOH. Scale bar = 1.0 mm. (17) Male head, ETOH. Scale bar = 0.25 mm. (18) Maxilla, lacinia, mandible. Scale bar = 0.1 mm.

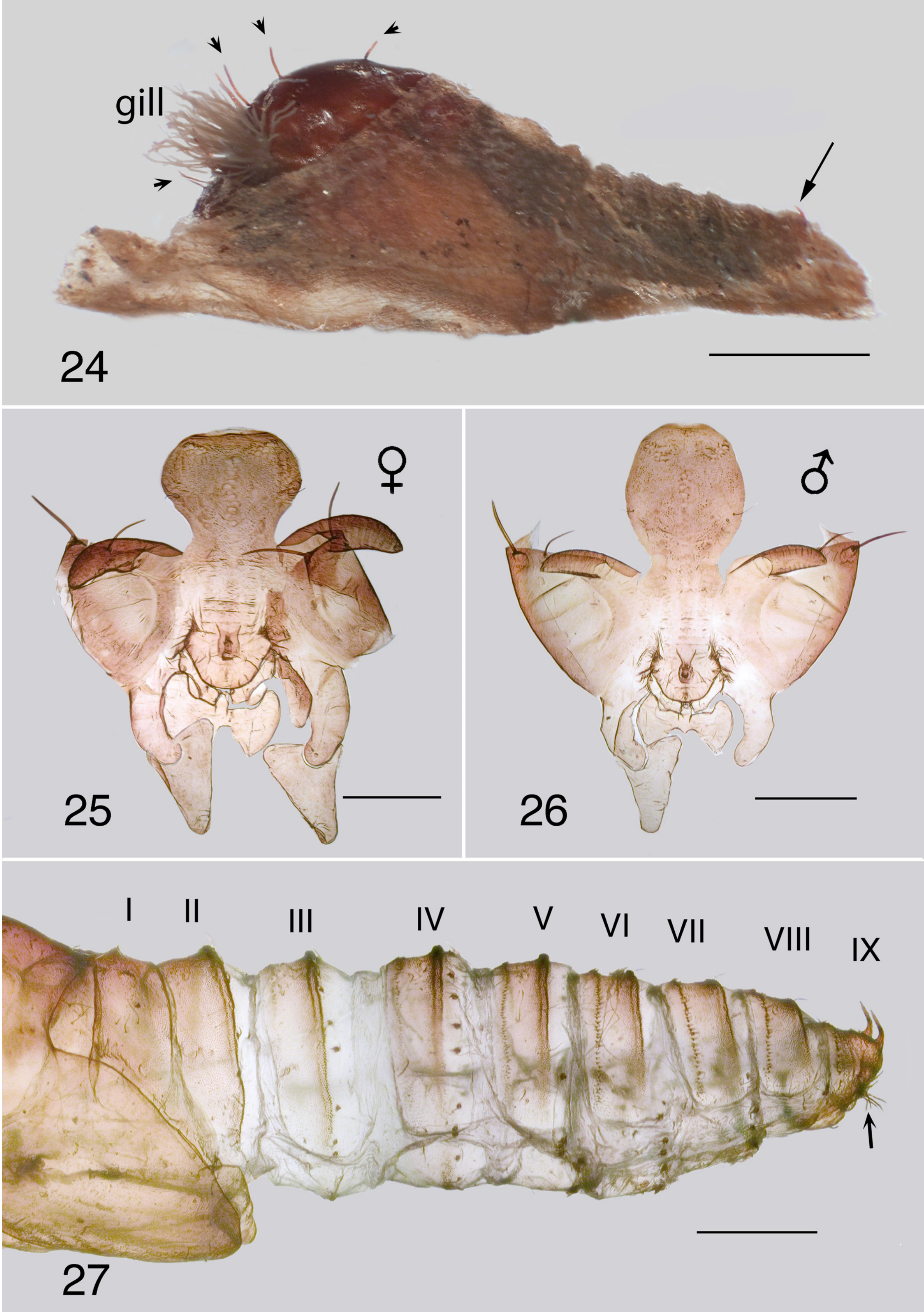


FIGURES 19–23. *Bunyipellum gladiator* male. (19) Wing. Scale bar = 0.5 mm. (20) Abdominal tergites. Scale bar = 0.5 mm. (21) Genitalia, ventral view. Scale bar = 0.1 mm. (22) Gonocoxa & gonostylus. Abbreviations; gc = gonocoxa, gs = gonostylus. Scale bar = 0.1 mm. (23) Ventral plate & parameres. Abbreviations; b a = basal arm, p = paramere, p c = paramere connector, p s = paramere spines, v p = ventral plate. Scale bar = 0.05 mm.

posterior distinct, pleural cuticle concertinaed. *Genitalia* (Figs. 16, 21–23): protruded ventrally, markedly pale yellow; gonocoxa 1.1x longer than basal width, vestiture of sparse hairs, slightly protruded ventral edge at gonostylus articulation; gonostylus in lateral view tapered markedly to narrow apex, approximately 1.8x longer than basal width, two short, blunt, apical spines; ventral plate poorly sclerotized, slightly wider than long, corrugated anterolaterally, vestiture absent, except for sparse hairs on narrow median carina, posterior apex broadly domed, membranous laterally, shallowly convex anteromedially, basal arms broadly expressed; median sclerite as two short sclerotized arms projected posteriorly beyond ventral plate; paramere connector thin and closely applied to lateral edges of ventral plate, parameres plate-like basally, slightly strengthened along one edge, tapered distally to unpigmented crenulated band of cuticle connected to sparse small spines on slightly strengthened area; adeagal membrane otherwise bare.

Pupa (based on numerous specimens). *Body* (Fig. 24): length, female 3.8–4.6 mm, male 3.6–4.1 mm, brown, markedly sclerotised cuticle. *Head*: frons of female short (Fig. 25), narrowed basally, angulate with ratio of basal width to vertex width 1.0:1.6 and width to length 1.0:1.4, that of male ovoid (Fig. 26), narrowed basally; ratios 1.0:1.8 and 1.0:2.3, respectively; cuticle with sparse granules in the male, more so in female; frontal and facial setae present, but poorly expressed, epicranial setae markedly expressed as long stiff spines, the dorsal-most extremely so, on raised bases. *Thorax*: shiny, smooth, generally lacking granules; setae spine-like in 4 transverse rows, anterior-most of 2 elongated and darkly pigmented spines, second row of 4; third row of 2 or 3 slender, hair-like setae, fourth row of 1 hair-like pair and 1 elongate, darkly pigmented pair of setae. *Gill* (Figs. 24, 38): *ca*. 60 light grey, non-tapered finger-like filaments arising directly from knob-like base, maximum length 0.8 mm; some filaments short, other branching once or twice at various length; filament surface lacking annulations, densely packed with trabeculae (Fig. 39). *Abdomen* (Fig. 27): sclerites light brown with dense granules; tergite I with 6–8 slender setae and central pair of short darkly pigmented spines on raised bases; tergites II–VII with raised ridge posteriorly, tergite II with 3 or 4 fine setae and 10–12 longer, stouter setae along posterior margin; tergites III and IV with 3 or 4 fine setae and 12–14 stout, anteriorly directed, darkly pigmented hooks; tergite V with 8 fine setae and 8 stout, anteriorly directed, darkly pigmented hooks; tergite VI with 9 or 10 fine setae and 2 anteriorly directed hooks (sometimes set in pleural membrane); tergite VII with 6–8 fine setae; tergite VIII with 10–12 fine setae; tergite IX with 4 darkly pigmented setae, terminal spines elongated and sharp; tergites IV–IX with anterior row of variously developed spine combs; pleurites absent; pleural membrane of segments IV–VII with 2 or 3 stout, darkly pigmented, anteriorly-directed hooks per side, that of segment VIII with 2 setae per side, segment IX with cluster of 4 or 5 elongate, darkly pigmented setae per side; abdominal sternites V and VI with 2–6 fine setae and 6 stout, anteriorly directed, darkly pigmented hooks; sternite VII with 4 stout, anteriorly directed, darkly pigmented hooks; sternite VIII with 2 slender setae; sternite IX lacking grapnel hooks, but with cluster of stiff, slightly curled spines (Fig. 28). *Cocoon* (Fig. 24): Close fitting, occasionally may cover complete pupa, extends beyond pupae ventrally, variable; dense weave; often retaining larval exuviae.

Larva (based on numbers of last instar specimens and original description). *Body* (Fig. 30): total length variable, 6.4–8.9 mm, substantial and muscular. Colour, overall, mottled dark brown. *Head* (Fig. 29): evenly medium brown, apotome slightly lighter than genae; head spot pattern poorly expressed, but tending to negative, irregular darker pigment posterolaterally; cuticle thickness exacerbated, with lateral corrugations; cephalic setae not evident; ecdysial sutures distinct, essentially straight, slightly expanded posteriorly; head depth and width increased markedly anteriorly, dimensions variable, length 0.86–1.20 mm, at mid head width 0.61–0.89 mm; distance between antennal bases 0.44–0.55 mm; head widest across base of fans; cervical sclerites elongated laterally with rounded region posteromedially, not obviously attached to postocciput. *Antenna* (Fig. 31): subequal in length to fan stem; usually directed more laterally and often posterolaterally (*e.g.* Fig. 29); total length 0.35–0.35 mm, apical and medial antennomeres subequal in length, basal antennomere clear except for lateral apical portion, markedly shorter than medial antennomere, that evenly dark brown, except for lateral apical portion, apical antennomere slightly expanded basally and apically, dark brown, proportional lengths of antennomeres 1.0:1.7:1.7. *Labral fan*: stalk markedly short, broad and sclerotized posteriorly, expanded anteriorly, 75–88 dark brown, markedly substantive rays, ten posterior rays slightly finer than remainder, bases exacerbated and darkly pigmented, ray length 0.92–1.02 mm, mid width 0.03 mm; microtrichia long, no pattern, length subequal to ray width. *Mandible* (Figs. 32, 33): well pigmented; apical brush exacerbated; apical teeth narrowed; outer teeth small, apical tooth moderately developed; preapical teeth small and subequal in length, *ca.* 12 spinous teeth of similar length; serration and sensillum as single unit; blade region short and straight. *Maxilla* (Fig. 34): lobe small, palpus



FIGURES 24–27. *Bunyipellum gladiator* pupa. (24) Lateral view of female pupa and cocoon. Arrowheads indicate spine-like setae on thorax and head; arrow the terminal spines. Scale bar = 1.0 mm. (25) Female head capsule. Scale bar = 0.5 mm. (26) Male head capsule. Scale bar = 0.5 mm. (27) Abdominal exuviae. Arrow indicates setae on sternite IX. Scale bar = 0.5 mm.

FIGURE 28. *Bunyipellum gladiator* pupa. **FIGURES 29–30.** *Bunyipellum gladiator* larva. (28) Pupal abdominal apex; exuviae. Arrow indicates setae on sternite IX. Scale bar = 0.2 mm. (29) Dorsal view of head, last instar larva. Scale bar = 0.5 mm. (30) Habitus, last instar larva. Scale bar = 1.0 mm.

black, 2.2x as long as basal width; hair tuft at base of palp markedly developed. *Postgenal cleft* (Fig. 35): angulate, V-shaped apex; posterior tentorial pits not markedly developed; postgenal bridge not markedly lighter than genae; elongated posteroventral muscles spots distinct; ratio of hypostoma: genal bridge: cleft, 1.0:2.0:1.0; ventral cuticle of head with lateral corrugations. *Hypostoma* (Fig. 36): darkly pigmented; not markedly extended anteriorly, anterior margin concave; teeth short, blunt, subequal in height; tooth 0 (median) small and sharp, as is tooth 1 (sublateral), tooth 2 & 3 similar, all partially obscured by ventral edge of hypostoma, tooth 4 (lateral) sharp medially, flanged laterally to tooth 5—the most prominent, albeit largely obscured by hypostomal edge, teeth 6 & 7 barely evident, all teeth variable; lateral serrations absent; 2 or 3 setae per side, short. *Thorax* (Fig. 37): pupal gill histoblast with *ca.* 8 filament bases visible; with head to the right filaments descend vertically then curl slightly clockwise, with filament tips then slightly angled counterclockwise; gill (Figs. 38, 39) as described under pupa. *Anterior proleg* (Fig. 40): proximally well expressed, but circlet of hooks small, two hook sizes, lateral sclerites absent (described as present in original description). *Abdomen*: medium to dark greyish brown, anterior segments banded, posteriorly not; gradually expanded posteroventrally to seventh segment, sharply contracted at last segment. Integument with minute, subparallel, crenulate ridges dorsally (Fig. 41) and rounded granules ventrally. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 42): markedly finely expressed; anterior arms short and flared distally, median region not markedly developed, posteroventral arms twice as long as anterior arms, finely tapered, distal half crenulated. *Rectal papillae*: three simple lobes. *Posterior circlet*: overall small, but with hooks darkly pigmented and distinct; numbers of hooks low, 44–48 rows with 7–11 hooks per row (total *ca*. 440).

Etymology. As given in Moulton, Adler & Prince (2004: 6), the species name refers to the stout, elongated setae (aka trichomes) on the pupal head and thorax.

Types. The holotype and some paratypes are deposited in the Western Australia Museum, Perth. Additional paratypes are in the Australian National Insect Collection (ANIC), Canberra; Natural History Museum, London; United States National Museum of Natural History, Washington, DC; Canadian National Collection, Ottawa; and Clemson University Arthropod Collection, Clemson, South Carolina (Moulton *et al*. 2014: 3).

Additional material Some material of all stages is now in the Strickland Museum, University of Alberta; ETOH (UASM# 354037–354050); slides (UASM# 353351–353359). Five dried pinned females from Deeside Coast Road are deposited in ANIC (ANIC Database No./29 026585, 29 026737–29 026740). The remainder of the original material is in the personal collection of J. K. Moulton (JKM).

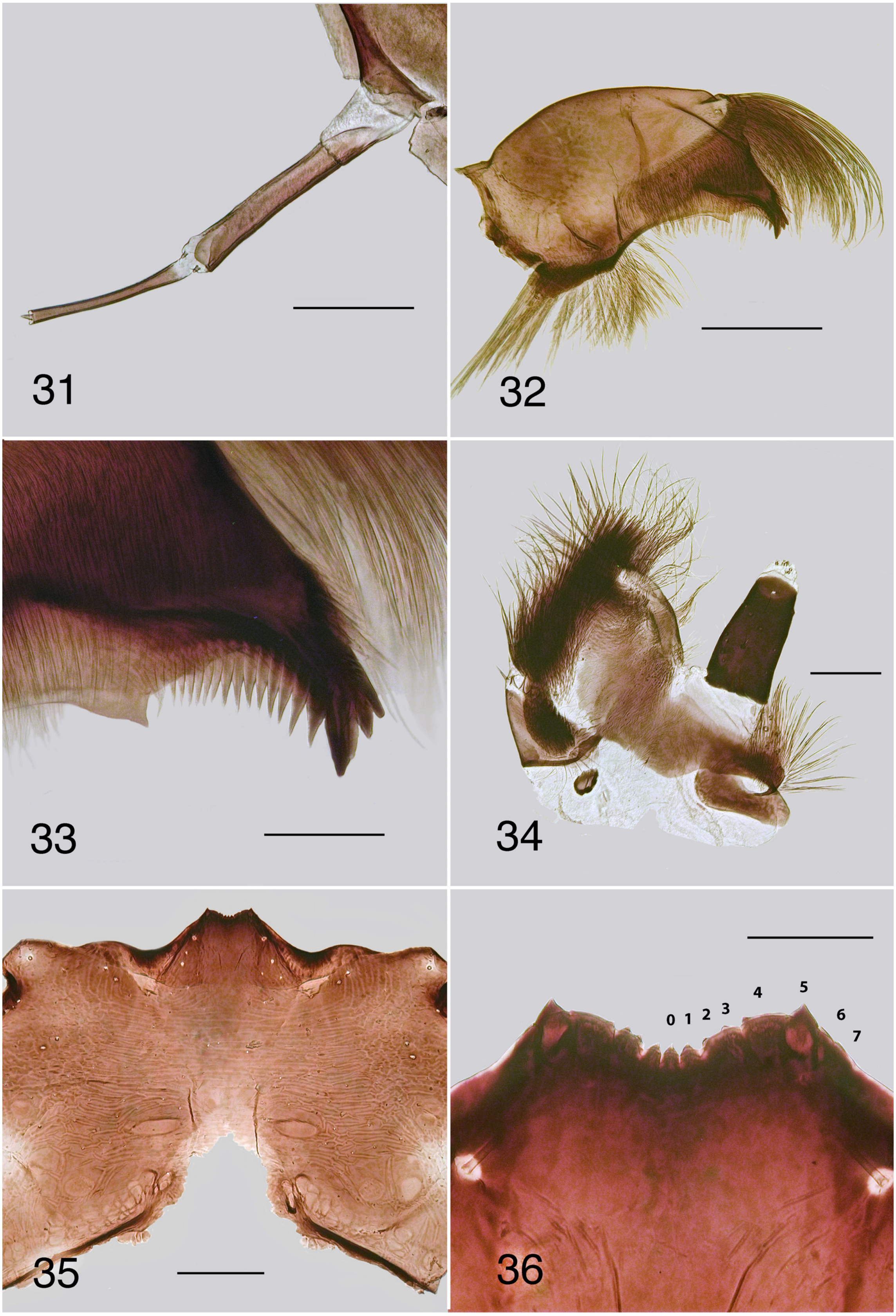
Distribution (Fig 43). Known only from the Jarrah Forest and Warren regions of Western Australia.

Kangaroo Gully, Brookton Hwy. (Rt. 40), Jarrah Forest, Darling Reserve, S32.1170° E116.1500°, alt. 230m., 21 August 1973, Coll. J. Prince; 7 September 1996, Coll. J.K. Moulton. Quinine Gully, Ashendon Hwy., S32.1500° E116.1920°, alt. 260m., 7 September 1996, Coll. J.K. Moulton. Churchman's Brook, Canning Dam Road, S32.1879° E116.1163°, alt. 282m., 8 September 1996, Coll. J.K. Moulton. Goldmine Gully, S32.4054° E116.2023°, alt. 270m., 8 September 1996, Coll. J.K. Moulton. Mumballup, S33.5300° E116.1100°, alt. 133m., 13 September 1974, Coll. D.G. Bedo. Shannon National Park, Deeside Coast Road, S34.7767° E116.3157°, alt. 80m., 5 November 2003, Coll. A. Zwick.

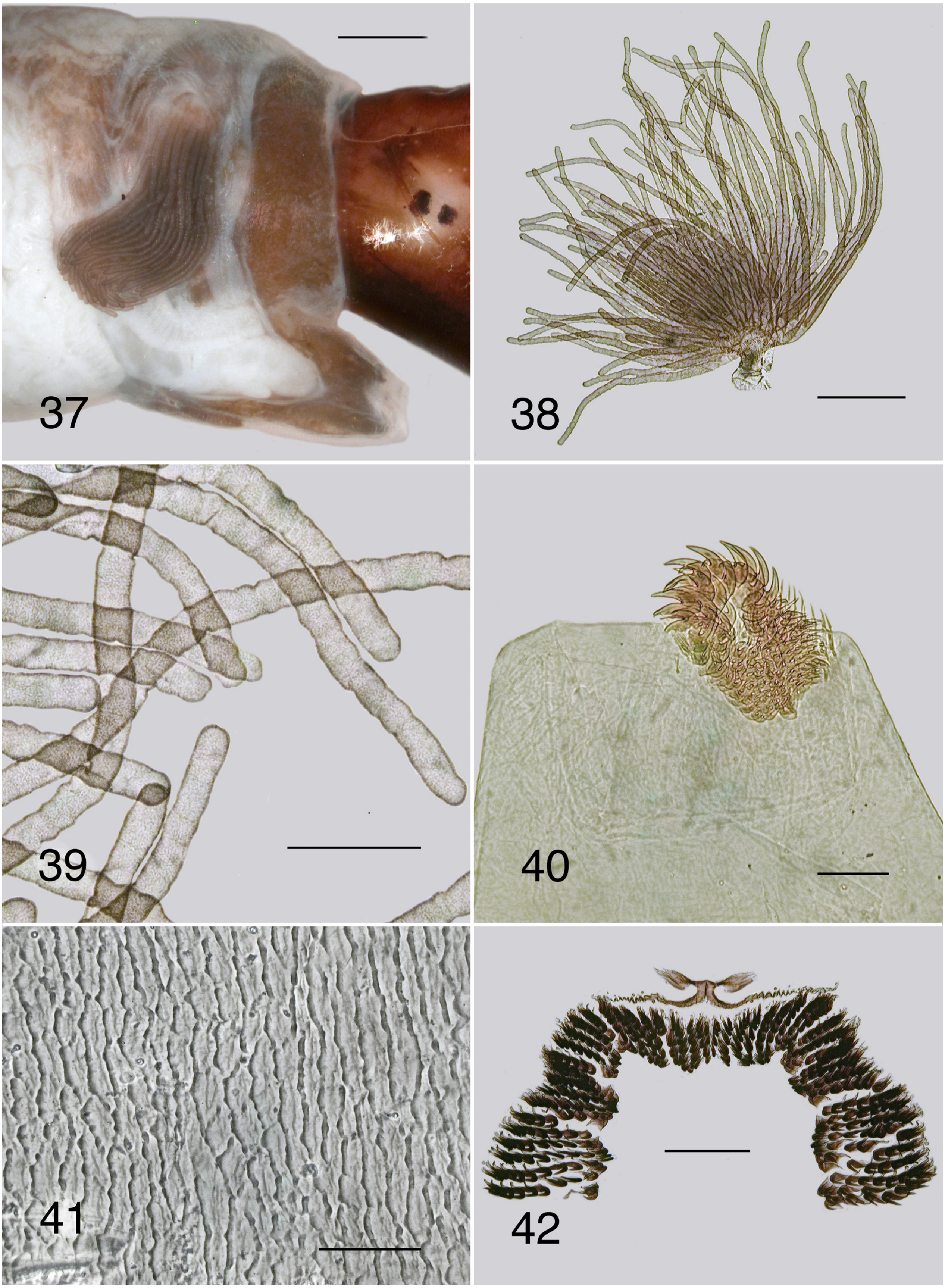
Bionomics. Moulton *et al*. (2004: 8) note that larvae and pupae occupy riffles in shaded small to medium-sized streams in the Jarrah Forest region of the Darling Range in Western Australia. Found only during the Austral late winter and early spring, *Bunyipellum gladiator* is assumed to be univoltine. Females are attracted to humans but are not known to blood feed on such hosts. The substantial mouthparts (Fig. 2), well-toothed mandible (Fig. 6), plus relatively small abdominal tergites (Fig. 11) suggest that females of *B. gladiator* are capable of blood feeding. Presence of a simple claw (Fig. 10) indicates that the species is not ornithophilic (Adler *et al*. 2004).

Remarks. Female adults, apart from possessing large mouthparts, have a maxillary palp (Fig. 5) unique for Australian simuliids. Palpomeres I and II are larger than others, III is subequal in length to palpomere V, with IV markedly small. For the wing, the radius and radial sector veins parallel one another and are not closely applied as in *Austrosimulium* (Craig *et al*. 2014: 210). The calcipala possess a clump of spines and this condition is also seen in *Paracnephia fergusoni* (Tonnoir 1925: 221) and other now-known Australian simuliids. Moulton *et al*. (2004: 1, 4) describe the calcipala as 'large'; however, as noted above, other simuliids possessing a poorly expressed or small calcipala have a similar clump of spines to *B. gladiator*, so we consider that its calcipala to be small, albeit distinct—it is less than quarter the length of the second tarsomere and 0.4x the width of the basitarsus apex. The calcipala (Fig. 22) is, however, of similar development to those of *Araucnephia* and *Araucnephoides*, but no mention in descriptions is made of presence or absence of a ventral row of hind basitarsus spines (Wygodzinsky & Coscarón 1973). *Araucnephia*, *Araucnephoides* and *Bunyipellum* all lack a pedisulcus. Absence or poorly expressed claw basal tooth in female *Bunyipellum* (Fig. 10) is now also known for some Australian Gondwanan simuliids, whereas *Araucnephia* and *Araucnephoides* possess a moderately-sized basal tooth. The cerci and anal lobe of the female are markedly protruded ventrally (Fig. 1), yellowish and distinct. Moulton *et al*. (2004) noted that the median sclerite of male genitalia of *B. gladiator* was similar to that of *Araucephia montana* Wygodzinsky & Coscarón, but made no other comparisons regarding the genitalia. Overall, however, the genitalia are markedly congruent, with similarities in the narrowed gonostylus and two terminal spines, ventral plate, paramere connector, paramere and spines (Wygodzinsky & Coscarón *loc cit*.: 169). In *Bunyipellum gladiator*, the narrow gonostylus with two terminal spines is unique for Australian Gondwanan simuliids and, in general, at considerable variance to males of *Austrosimulium* (Craig *et al*. 2012). The paramere and parameral spines (less so the paramere connector), are of similar expression to those in *Paraustrosimulium* (Craig *et al.* 2017).

The pupa and cocoon structure of *B. gladiator* suggest adaptation for high velocity flow and are, therefore, something of a conundrum. Pupae occur in shallow riffles of small streams where water velocity, albeit relatively high in some instances, does not exert marked force. The terminal spines on the pupal abdomen are moderately long and sharply pointed (Figs. 27, 28) with the probable function of holding the pupa within the cocoon. Indeed,



FIGURES 31–36. *Bunyipellum gladiator* larva. (31) Antenna. Scale bar = 0.1 mm. (32) Mandible. Scale bar = 0.2 mm. (33) Mandible apex. Scale bar = 0.05 mm. (34) Maxilla. Scale bar = 0.1mm. (35) Postgenal cleft. Scale bar = 0.2 mm. (36) Hypostoma. Scale bar = 0.05 mm.



FIGURES 37–42. *Bunyipellum gladiator* larva. (37) Lateral thorax showing pupal gill histoblast. Scale bar = 0.2 mm. (38) Pharate pupal gill. Scale bar = 0.2 mm. (39) Gill structure. Scale bar = 0.05 mm. (40) Anterior proleg. Scale bar = 0.05 mm. (41) Abdominal cuticle (phase contrast). Scale bar = 0.05 mm. (42) Anal sclerite and circlet of hooks. Scale bar = 0.2 mm.

the terminal spines can be seen protruding through the cocoon (Fig. 24). The raised ridges with fine armature on some of the tergites (Fig. 27) also suggest a similar adaptation. However, the spine-like setae on the thorax (Fig. 24) and head capsule (unique among the Australian Simuliidae) (Figs. 25, 26) are not always covered by the cocoon and are, perhaps, protective devices for the gill, or against predators. The pupae of *Araucnephia* and *Araucnephoides* have little in common with that of *B. gladiator*, lacking the major thoracic spines, raised abdominal tergite ridges and large terminal spines. Notwithstanding, all three genera lack well developed grapnel hooks on the IX segment, with the homologs either straight in *Bunyipellum* (Figs. 27, 28) or slightly curled in *Araucnephia*. *Bunyipellum* has many more pupal gill filaments than either of the two South American genera.

The larvae of *Bunyipellum gladiator* are a puzzling mixture of character states. The substantial body and shape with the expanded posteroventral abdomen (Fig. 30) are found in other simuliid larvae that inhabit fast water, such as, for example, *Paracnephia strenua* (Mackerras & Mackerras), *Simulium* (*Inseliellum*) *tahitiense* Edwards and *Simulium* (*Gomphostilbia*) *palauense* Stone. An expanded abdomen appears to enable simuliid larvae to clump together to produce skimming flow, a common ploy to reduce drag forces (Nowell & Jumars 1984: 317), yet still remain sufficiently upright for the fans to be oriented into the flow. Larvae of *B. gladiator* are found in the riffles of small streams as described above for pupae. Although water velocity is sometimes moderate to high in such habitats, the shallow depth ensures that shear stresses are low.

The labral fans are unique for Australian simuliids (Fig. 29). The expression of the fan stalk, short and broad is not seen in others and the rays are heavily expressed and numerous. These do not fit the fan structure model proposed by Palmer & Craig (2000: 213) for simuliid larvae inhabiting higher velocities and what we assume as medium level seston.

The larval antenna, with its unusual short proximal article (Fig. 31), is unique among the Australian Simuliidae, but is markedly similar to those of the South American genera *Araucnephia* and *Araucnephoides* larvae. This possibly represents a synapomorphy of these three genera. Antennae subequal in length to, or shorter than the labral fan stem are commonly expressed in simuliid larvae that inhabit fast flowing water (Crosskey 1990: 108, Adler *et al*. 2004: 153), again somewhat paradoxical in *Bunyipellum* given the known habitats of larvae. Long antennae are seen in aquatic insects in slow-flow habitats and are so expressed to penetrate the attached boundary layer (Craig 1990: 349).

No comment was made by Moulton *et al*. (2004) about the unusual concave configuration of the larval hypostoma (Fig. 36). A similar arrangement is found in the larvae of the *Ectemnia* Enderlein, which attach themselves to a silk stalk (Moulton & Adler 1997). Details of the attachment behaviour of *B. gladiator* larvae remain unknown; however, it seems unlikely that *Bunyipellum* and *Ectemnia*—a northern hemisphere genus—share an immediate common ancestry. The hypostomal teeth of *Bunyipellum* differ markedly from those of *Araucnephia* and *Araucnephoides* in that the former are uniformly small (Fig. 36), contrasting markedly with the well expressed teeth in the latter two genera. The postgenal cleft of *Araucnephia montana* can be angulate, similar to that of *B. gladiator* (Fig. 35), albeit shallower.

The anterior thoracic proleg circlet of hooks is uniquely small for Australian simuliids. This proleg is used by simuliid larvae to grasp a pad of salivary silk when moving position and before the posterior proleg hooks are attached (Barr 1984). The small size is suggestive of adaptation to habitats with low velocity. A similar pattern is seen in the circlet of hooks of the posterior proleg. With only *ca*. 440 hooks, the posterior proleg conforms to other simuliids that inhabit slow-flow habitats (Palmer & Craig 2000: 204, and others). The hooks are, however, enlarged and markedly sclerotized (Fig. 42). The anal sclerite is delicately expressed, similar to certain other low-flow-inhabiting Australian simuliids, such as *Paracnephia umbratora* (Tonnoir). In that species, however, reduction is different and related to the habit of attaching to a thread (Moulton & Adler 1997: 1907). These morphological expressions of structures of larval *B. gladiator* are suggestive of finer-scale behaviours that warrant further study.

Moulton *et al*. (2004: 3) and Adler & Crosskey (2015: 31) both included "*Cnephia* B" of Bedo in Rothfels (1979: 522) in their synonymical list of *P. gladiator*. We have confirmed (Bedo, pers. comm. 2017) that this informal cytological designation indeed refers to *Bunyipellum gladiator*. The chromosomes have distinct centromere bands, an expanded region in CI, undifferentiated sex chromosomes (Xo Yo) and no inversion polymorphism.

With its suite of unique morphological characteristics and lack of congruence with other Australian simuliids, we consider these to be sufficient grounds to assign *B. gladiator* to its own monospecific genus, with possible relationship to South American *Araucnephia* and *Araucnephoides*.

Concluding comments. Most other Gondwanan Simuliidae of Australia have east-west sibling species or segregates separated by the Nullarbor desert region; a common situation for Australian biota. *Bunyipellum* is so far known exclusively from southwestern Australia—a pattern confirmed from our own wide-ranging collections (*e.g.* Craig *et al*. 2017), and those of earlier specialists (*e.g*. Mackerras & Mackerras 1952, Colbo 1974, and others). Known localities for *B. gladiator* are from a region along the Darling Escarpment in what is referred to as the Jarrah Forest Bioregion on the western edge of the ancient Yilgarn Craton. The collection by A. Zwick, 2003, was to the far southwest in the Warren Bioregion (Fig. 43).

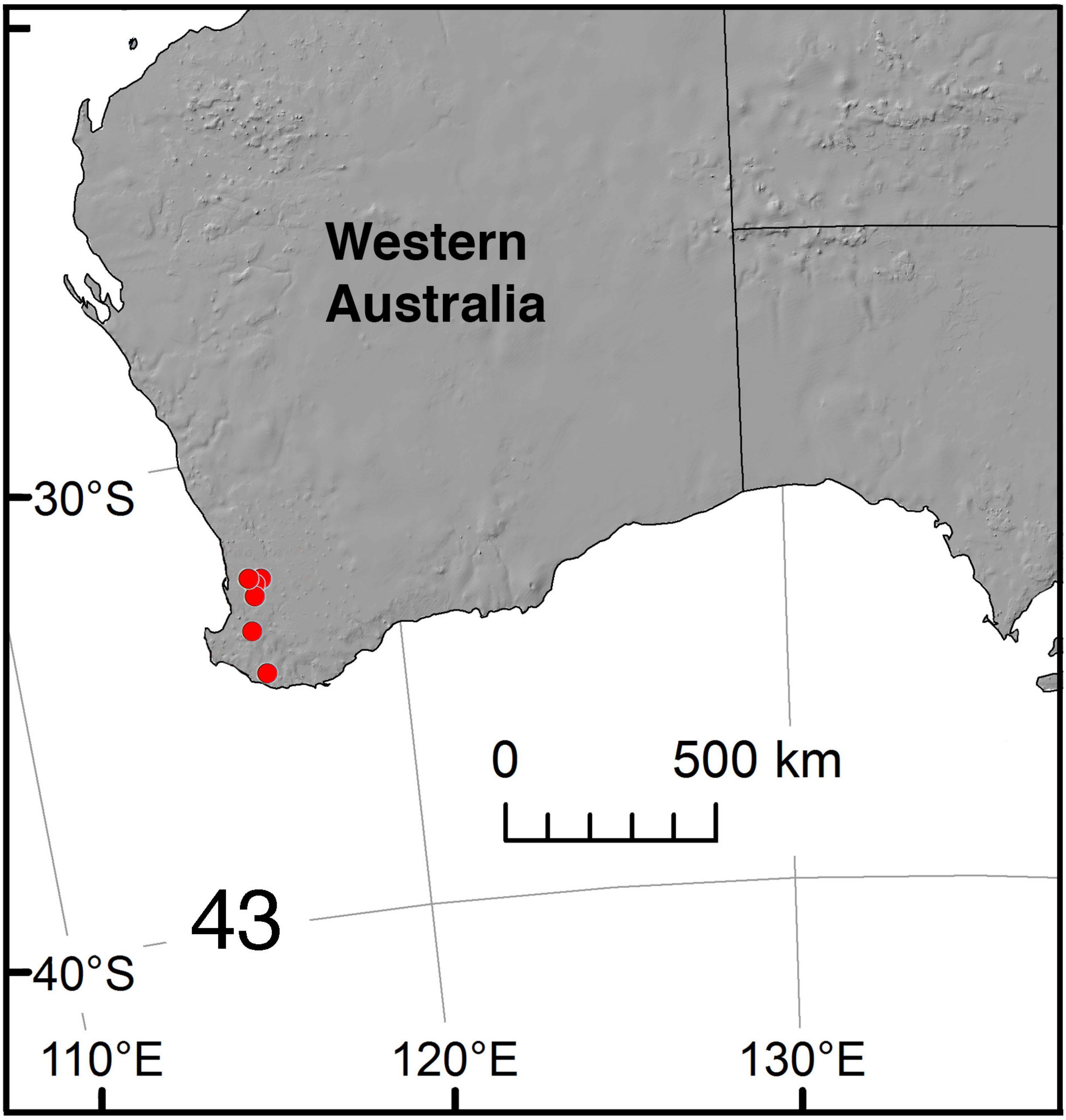


FIGURE 43. Western Australia, distribution of *Bunyipellum gladiator*.

A wide-ranging analysis of south-western Australian faunistic biogeography by Rix *et al*. (2015) lists key geographic and climatic events for this region and Australia as a whole. These include separation of southern Western Australia from Eastern Antarctica at *ca*. 96 mya (Cretaceous), complete separation of eastern Australia at *ca*. 32 mya (Early Oligocene) with commencement of aridification and of inundation of the south-central Australia Nullarbor region by the Eromanga Sea, with deposition of limestones at *ca*. 25 mya (Late Oligocene), such ending at *ca*. 14 mya (Mid Miocene) with the Nullarbor surface becoming exposed. Rix *et al*. (*loc. cit.*) used published, dated, molecular data sets to determine time of divergence of south-western Australian fauna from that of the south-east. What they refer to as "Tier 1 divergences" (their Fig. 5), fall mainly between the Early and Mid Miocene (*ca*. 24-6 mya). Of significance here, perhaps, is an older one (*ca*. 54-26 mya) suggested for the chironomid *Stictocladius* (Edwards) by Krosch & Cranston (2013).

Krosch & Cranston (*loc. cit.*) in their detailed examination of molecular phylogenetics, biogeography and evolutionary tempo of *Stictocladius*—a genus with Gondwanan distribution (Australia, New Zealand, South America)—concluded that divergence of the main lineages was Late Cretaceous (*ca*. 66 mya). Divergences of the Australian 'multiserialis' segregates were Late Eocene to Late Oligocene (*ca*. 45-26 mya). That for the 'sofour' lineages, may have been similar (*ca*. 45 mya), but apparently more recently in the Miocene (*ca*. 22-5 mya). Divergence of the east and west groups of 'multiserialis' appears to have been at *ca*. 40 mya (Mid Eocene), with further divergence of the eastern segregates continuing between the late Paleogene and early Neogene (36-11 mya).

Timing of later Tier 1 events of Rix *et al*. (*loc. cit.*), plus later divergences given above for *Stictocladius* segregates, might apply to presently known east-west distribution of Australian simuliid fauna (*e.g*., Mackerras & Mackerras 1952: 113, Craig *et al*. 2017). Given the unusual morphological character states of *Bunyipellum gladiator,* absence of any Australian sister group, plus possible relationship to South American *Araucnephia* and *Araucnephoides*, it seems possible that divergence of *Bunyipellum* was from a common precursor on Gondwana prior to separation of Australia and Antarctica, of possible similar ilk to *Stictocladius*—that is, Late Cretaceous or earlier. *Bunyipellum,* if not among the oldest lineages of Australian Gondwanan Simuliidae, is certainly one of the most unusual.

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