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***Nothogreniera* new genus, for two species of Australian "*Paracnephia*" (Diptera: Simuliidae)**

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Abstract

Two species of Australian Simuliidae known only from adult females and currently assigned to "*Paracnephia*" are re-described, as are their now-known males and immature stages. Morphological character states of "*Paracnephia*" *fergusoni* (Tonnoir) and "*P.*" *fergusoni* var. (Mackerras & Mackerras) reveal that they are markedly distinct from all other Australian species, and are here assigned to the new genus—*Nothogreniera*—the most plesiomorphic Gondwanan Australian simuliid. Structural variation among populations of *N. fergusonii* suggests that this entity comprises a species complex.

Key words: Gondwana, Australia, New South Wales, Victoria, Western Australia, Simuliidae, *Paracnephia*, black flies.

Introduction

This is the third in a series of papers (Craig *et al.* 2017, 2018) revising the neglected and little-studied Gondwanan simuliids of Australia. Long referred to as "*Cnephia*" by Australian authors, and more recently as "*Paracnephia*", these species represent a heterogeneous assemblage of primitive-grade simuliids not assignable to either of the other two genera previously recognized from that region: *viz.* *Austrosimulium* and *Simulium s.l.* With two species of plesiomorphic Australian black flies recently assigned to *Paraustrosimulium* Wygodzinsky & Coscarón (Craig *et al.* 2017), and a third assigned to the monotypic genus *Bunyipellum* (Craig *et al.* 2018), with this work, the number of fully characterized Australian genera now stands at five.

The two plesiomorphic simuliids under consideration in the present study were previously known only from adult females. *Simulium fergusonii* Tonnoir (1925: 238), a well-known biter of livestock, was perhaps responsible for one of the earliest written accounts of problem black flies in Australia (Lea 1917, Tonnoir *loc. cit.*). At the time of its description *S. fergusonii* was unique among Australian black flies in having no indication whatsoever of a calypala. In a major reorganization of the Australian Simuliidae, Mackerras & Mackerras (1949) assigned a number of plesiomorphic species, including *S. fergusonii*, to *Cnephia* Enderlein—an otherwise exclusively northern hemisphere genus. Among those was a ‘variety’ of *S. fergusonii* originally dubbed “*Simulium fergusonii occidentalis*” in an unpublished manuscript by Tonnoir. Mackerras & Mackerras (*loc. cit.*) took authorship of that name by providing a partial description and diagnosis of females of that form as *Cnephia fergusonii* var.

Recently collected high-quality material of typical "*Paracnephia*" *fergusoni* and "*P.*" *fergusoni* var., provide the basis for a reevaluation of these entities. Females are redescribed, with males, pupae and larvae of both entities described for the first time. "*Paracnephia*" *fergusoni* var. is shown to be specifically distinct from "*P.*" *fergusoni* and is here accorded full species status. Character states of the two species differ markedly from those all other Gondwanan simuliids, warranting recognition of a new genus. Comparisons with other ‘*Cnephia*-grade’ genera are discussed, as are aspects of biogeography.

Material and methods

Preparation and examination of material from the Grampians National Park followed Craig *et al.* (2012: 49). For older (*e.g.* 1916) pinned adult paratype material made available from Australian National Insect Collection (ANIC), three specimens were examined in detail. Differential interference contrast (DIC) microscopy was used to show the annulations on the distal article of larval antennae.

Photography followed Craig *et al.* (2012). We use terms for structures following Adler *et al.* (2004) and Craig *et al.* (2017, 2018), in particular numbers to designate larval hypostomal teeth (*e.g.* Fig. 46). Terms for wing veins follow de Moor (2017). For convenience, we provide latitude and longitude coordinates of localities in degree decimal format. When reporting label data, square brackets "[]" indicate a label and a slash "/" the end of a line. An {M} or {F} is used to replace sex symbols. Also, since the Mackerras' literature for Australian simuliids is additive over a period of years, page numbers are provided for convenience. Codons for depositories of material are "ANIC" for Australian National Insect Collection, CSIRO, Canberra and "UASM" for University of Alberta, Strickland Museum, Edmonton.

Nothogreniera gen. nov. Craig, Currie & Moulton

Type species: *Simulium fergusonii* Tonnoir 1925

Cnephia fergusonii. Mackerras & Mackerras (1949: 386). Generic reassignment.

Paracnephia fergusonii. Crosskey & Howard (1997: 18). Generic reassignment.

Diagnosis. *Adults*: darkly pigmented. Antenna with nine flagellomeres, extended well beyond head margins; mandible of female with numerous distinct teeth on both sides. Wing relatively long in relation to width; small but distinct basal cell; basal radial cell elongated (a/b ratio 1.0:2.6); costa with hair-like setae only; Rs not forked and no evidence of terminal expansion, hairs only; M1 apparently double (produced by parallel fold with concentration of microtrichia); CuA markedly sinuous. Anepisternal (pleural) membrane lacking hairs; anteprenotal lobe and proepisternum haired; katepisternal sulcus poorly expressed. Hind basitarsus with ventral row of spines; calcipala absent to poorly developed, aggregation of stout spines in that position; pedisulcus absent; tarsomere II elongate; claws of female with tooth absent, or if present, minute, rounded heel well developed. Hypogynial valves well strengthened along medial edges; genital fork anterior arm thin, distinct, lateral arms lacking anterior pointing apodemes; spermatheca spherical, surface smooth, sparse inner acanthae, duct junction sculpted, clear area small. Male markedly hirsute; ventral plate of genitalia hirsute, broad and flattened apically with slight lip, medial carina poor-to-well expressed, basal arms substantial as are paramere connectors, parameres as flattened plates thickened along one edge, spines absent, adeagal membrane with concentration of small spines centrally; gonostyli broad, two substantial short terminal spines. *Pupa*: gill with 15 or 16 fine unbranched filaments; abdomen with anterior small spine combs on tergites VI–IX, lightly expressed on tergite V; moderate pleurite on segment V, smaller pleurites on segments VI and VII; segment IX with two short substantial terminal spines plus grapnel hooks. *Cocoon*: shapeless, fabric of coarse fibres, covering only posterior portion of abdomen, often with extraneous material. *Larva*: overall dark brown or yellowish, labral fans normal to enlarged; antenna subequal to, or longer than fan stem, basal and medial antennomeres subequal in length, together subequal to distal antennomere; apical antennomere with fine banding pattern observable at high magnification; cephalic setae not exacerbated; hypostoma with teeth in three distinct groups, one main hypostomal seta per side; mandible with enlarged proximal preapical tooth, serration and sensillum well developed; genal cleft markedly shallow V-shaped to deeper, poorly expressed; cervical sclerites fused to postocciput; lateral sclerite of anterior proleg D-shaped; ventral tubercles absent to poorly expressed; anal sclerite of posterior proleg X-shaped, not markedly expressed, interarm struts absent; rectal scales absent; circlet of hooks with small number of rows and hooks.

Etymology. From Latin *nothus* (= false or bastard).

Constituents. *Nothogreniera fergusonii* (Tonnoir, 1925) (type species), *N. occidentalis* (Mackerras & Mackerras, 1949).

***Nothogreniera fergusonii* (Tonnoir), 1925. New combination**

(Figs. 1–49)

Simulium fergusonii Tonnoir 1925: 238. Original description, female only.

Simulium fergusonii. Smart 1945: 505. Overview of Simuliidae. (As Sharp[*sic*] in Mackerras & Mackerras 1949: 386).

?Unidentified simuliid. Wharton 1949: 411. Larvae—probably *fergusonii*.

Cnephia fergusonii (Tonnoir). Mackerras & Mackerras, 1949: 386. New combination; *terebrans*-species group.

Cnephia fergusonii (Tonnoir). Grenier, 1960: 739.

(*Cnephia* of authors) *fergusonii*. Crosskey, 1987: 443. Prosimuliini, undetermined genus.

Paracnephia fergusonii (Tonnoir). Crosskey & Howard, 1997: 18, 117. New combination, unplaced to subgenus.

Paracnephia fergusonii. Bugledich, 1999: 328. Compilation of data.

“*Cnephia*” ‘S. x. (east)’. Moulton, 2000: 98. 2003: 47.

Paracnephia fergusonii. Crosskey & Howard, 2004: 10. Unplaced to subgenus. Adler & Crosskey, 2008: 26. Unplaced to subgenus, transferred to Simuliini: 16. Adler & Crosskey, 2018: 30.

Nothogreniera fergusonii (Tonnoir). New combination, this paper.

Description. *Adult female* (based on three paratypes and two paratype specimens). *Body*: head and thorax dark, markedly pollinose in some lighting, producing greyish-silvery appearance (Figs. 1, 3—in alcohol), with dark brown and yellowish abdomen; total length *ca.* 1.5 mm. *Head* (Fig. 5): frons tapered only slightly towards antennae, narrowest just above antennae; width 0.71–0.79 mm; depth 0.59–0.63 mm; postocciput black, vestiture of sparse, long black hairs; frons, dark brown-black, vestiture of markedly sparse silvery hairs; frons/head ratio 1.0:5.5–1.0:4.7. *Eyes*: interocular distance 0.16–0.17 mm; ommatidia diameter 0.016 mm; *ca.* 37 rows across and 47 down at mid-eye. *Clypeus*: broad, width 0.25–0.28 mm; silvery, moderate vestiture of fine silvery hairs. *Antenna* (Fig. 6): total length 0.75–0.9 mm, extended more than half length beyond head margin; scape small, pedicel broader distally, nine flagellomeres, first broad, remainder broader than long, distal flagellomere small, tapered, longer than broad; antenna overall slightly tapered. *Mouthparts*: *ca.* 0.5x length of head depth; cibarium (Fig. 9) cornuae broadly flared and moderately sclerotized, median depression flat-bottomed; mandible (Fig. 8), pointed apically with *ca.* 16 outer and 41 inner teeth; lacinia with *ca.* 20 teeth on either side; maxillary palp (Fig. 7), total length 0.54 mm, palpomeres I and II small, III darker brown than remainder, only slightly extended beyond articulation with IV, that relatively short, V not remarkably elongate; proportional lengths of III–V palpomeres 1.0:0.7:1.1; sensory organ elongated, 0.5x length of palpomere III, opening 0.5x width of vesicle. *Thorax*: length 1.5 mm; width 0.9–1.2 mm; postpronotal lobe well developed, with dense fine hair longer than on scutum, that showing dense pollinosity in some lighting (Fig. 1), overall with even sparse fine small hairs; scutellar depression similar; scutellum slightly paler than scutum, vestiture of sparse fine yellowish hairs; postnotum concolourous with scutellum, vestiture similar; antepronotal lobe (aka propleuron) and proepisternum with long fine yellowish hairs; fore coxa haired; pleuron and anepisternal membrane lacking hairs (Fig. 10). *Wing* (Figs. 11, 12): length 3.0–3.3 mm; width 1.5–1.7 mm; small basal cell present; a/b ratio from 1.0:2.6 to 1.0:2.7. Costa lacking spine-like setae; Rs not branched, CuA markedly sinuous, M₁ appears double (distinct arrangement of microtrichia plus fold). *Haltere*: overall light brown. *Legs* (Fig. 13): evenly medium brown; hind basitarsus with ventral row of stout spines, clustered at posteroventral terminus of basitarsus; calcipala absent; distinct hirsute intersegmental plate ventrally between basitarsus and tarsomere II; pedisulcus absent; tarsomere II 4x longer than basal width; claws small (Fig. 14), talon only slightly curved, not obviously serrated, basal tooth poorly expressed, lateral of talon and variable even on same specimen, rounded heel moderately developed. *Abdomen* (Fig. 15): basal scale dark brown, vestiture of long dense yellow hairs; remaining segments dark brown, tergites yellowish brown, slightly shiny; tergite II broadly bowl-shaped, dark, tergites III–VI roundly rectangular, subequal in size; vestiture of markedly sparse, small silvery hairs increasing in length and density posteriorly, remaining tergites broader; pleurites moderately developed; sternites apparently absent. *Genitalia*: sternite VIII more-or-less evenly pigmented across full width, vestiture of rows of microtrichia, large strong hairs posterolaterally; hypogynial valves (Fig. 19), lightly pigmented, vestiture of triads of microtrichia, medial edges of valves convex, slightly strengthened; genital fork (Fig. 18) anterior arm narrowed, distinct, apex slightly expanded, membranous lateral areas, lateral arms well expressed, poorly sclerotized, apodeme barely obvious as raised ridge at junction of arm and posterolateral expansion, that rounded laterally, rectangular medially; cercus in lateral view broadly rounded apically with slight indentation, tending to flat along dorsal margin, anal lobe substantial (Fig. 20); spermatheca ovoid, externally smooth with internal fine spines (Fig. 16) not obvious in fully mature examples (Fig. 17), spine length *ca.* 7.1 μm,

width *ca.* 0.47 μ m, length to width ratio *ca.* 1:5, density 0.055/ μ m², region surrounding junction with spermathecal duct sculpted, not markedly clear.

Adult male (reared individuals and pharate specimens). *Body*: in ethanol, overall colour black; total length 3.8 mm. *Head* (Fig. 21): width 1.1 mm; depth 0.8 mm. *Eyes*: upper ommatidia dark reddish black, diameter 0.029 mm, *ca.* 30 across and 27 down; lower ommatidia black, markedly small, diameter 0.007 mm, *ca.* 35 across and 44 down; larger ommatidia overhang smaller ommatidia at junction. *Clypeus*: black; width 0.17 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 22): total length 0.79 mm; overall black, pedicel small, scape twice as long and rounded, antennomere I slightly narrower than scape, remaining antennomeres tapered slightly to small apical antennomere. *Mouthparts*: insubstantial; length 0.3x head depth; maxillary palpus (Fig. 23) 0.65 mm long, palpomeres I and II small, proportional lengths of III–V palpomeres 1.0:0.7:1.1, sensory vesicle of irregular spherical shape, occupying 0.45x width of palpomere III, opening 0.3x vesicle width. *Thorax*: length 1.4 mm; width 0.96 mm; postpronotal lobe, anteppronotal lobe and proepisternum haired; scutum evenly velvety black, vestiture of sparse short fine pale hairs, dense and long in scutellar depression; scutellum concolourous with scutum, bare medially with sparse long pale hairs laterally; postnotum concolourous with scutum; pleurae dark brown, anepisternal membrane lacking hairs. *Wing*: length 3.4 mm, width 1.6 mm, otherwise as for female. *Haltere*: base of stem black, knob dark tan. *Legs*: front leg black, femur with markedly long fine hairs; mid leg mainly black to blackish brown; hind leg with proximal segments hirsute, blackish brown, basitarsus dark brown as are tarsomeres; basitarsus with dense short spine-like hairs on proximal 2/3, ventral row of stout spines present, calcipala absent, however the small, hairy, ventral, intersegmental sclerite may appear as a poorly developed calcipala; pedisulcus absent; tarsal claw grappling pad of *ca.* 25 teeth. *Abdomen* (Fig. 24): overall black, basal scale hairs black, extended to posterior of segment IV, tergites velvety black, 3 to 4x as wide as long, tergites II–IV with long hairs laterally, remainder with more evenly arrayed vestiture; pleurites poorly developed; sternites present, but small. *Genitalia* (Figs. 25–29): heavily pigmented; gonocoxa broader basally than long, vestiture of sparse hairs, microtrichia in rows, hairs accentuated anterolaterally, and medially; gonostylus approximately 2.0x longer than basal width, flattened in lateral view, vestiture of short hairs except posterolateral longer grouping, two substantial short, blunt, apical spines (Fig. 26); ventral plate (Figs. 27–29) complex, 1.6x wider than length, posterior edge raised and rounded, broadly rounded laterally, broadly concave anteromedially; vestiture of coarse hairs; marked central carina, broadly cross-shaped apically in ventral view (Fig. 25); basal arms not markedly developed, but substantial, tapered smoothly to join with well developed paramere connectors; median sclerite well developed, distinct distal bifurcation expanded and flared ventrally (Figs. 27, 28)—not visible in ventral view; parameres blade-like, with marked articulations with the ventral plate paramere connectors and gonocoxal apodeme, medial edge well delimited, with body of paramere tapered smoothly to thin posterolateral extremity, posteromedially extended to intersect with end of median sclerite bifurcations and aggregation of small coarse spines (not part of the paramere) medially on the aedeagal membrane (Fig. 29); membrane with arrays of microtrichia; dorsal sclerite absent.

Pupa (based on numbers of exuviae and pharate adults). *Body*: length, female 3.6–4.0 mm (Fig. 30), male 3.5–3.6 mm (Fig. 31), dark brown, shiny. *Head*: frons of female bluntly shaped with ratio of frons width to vertex width 1.0:1.2 (Fig. 34), that of male more rounded; ratio 1.0:1.9 (Fig. 35); both lacking cephalic depression; apparently smooth, but covered with barely visible minute tubercles; muscle scars positive; frontal setae absent, facial setae present, epicranial setae present, but not obvious (obscured by antennal sheaths), in male well lateral; postorbital spine absent, but clear area on ocular shield in that position; antennal sheath of female extended to edge of ocular shield, that of male not so (*cf.* Figs. 33, 34). *Thorax*: anterior dorsal shield with minute densely packed tubercles, more distinct and larger posteroventral of gill base (Fig. 37). *Gill* (Fig. 33): 15 or 16 long thin filaments arising from 5 or 6 short basal trunks, some bifurcating near base, others more distally; total length 2.5–2.7 mm; shorter than pupa. Surface finely annulated, unremarkable (Fig. 33; insert). *Abdomen* (Fig. 36): overall, cuticle covered with minute tubercles; armature minimal; tergite II lacking stiff sharp hairs; tergite III similar; tergite IV with four posterior stiff sharp hairs directed anteriorly, two fine hairs laterally, tergite extended laterally to incorporate much of the pleural region and one fine hair; tergite V with four hairs with spine comb sparse; tergite VI similar, but with three hairs per side; tergite VII with a posterior pair of fine hairs on each side and poorly developed spine comb anteriorly; tergite VIII with small comb of fine spines anteriorly and two fine hairs posteriorly on each side; two terminal spines on tergite IX not markedly developed, but substantial and sharply tapered, not markedly curved, grapple hooks difficult to see, a single hair and minute spicules on either side (Fig.

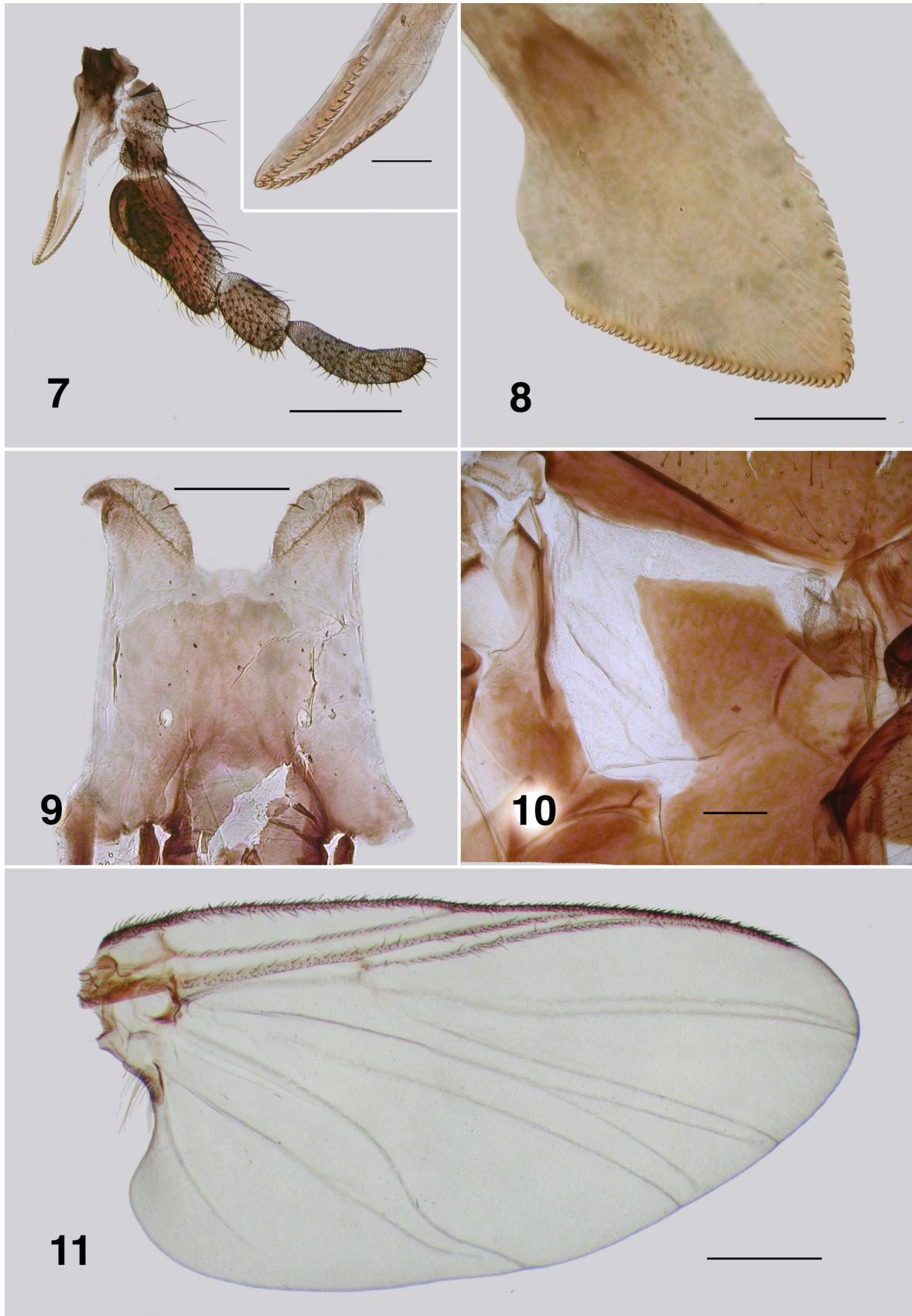
38); sternites III & IV lacking hook, replaced by homolog hair, other hair and spicules as before: pleurites V–VII as small plates with fine hairs; sternite V continuous medially with hook, hair and spinules as before; sternites VI and VII separated medially, each plate with a posterior single hook directed anteriorly, array of minute spicules anteriorly and single small hair anterolaterally; sternite VIII as a single plate with median junction, with array of minute spicules anteriorly and a single hair on each side; sternite IX below the terminal spines formed of two lobes, upper one with two single hairs and the grapnel hooks on either side, the other lobe essentially devoid of armature. *Cocoon* (Figs. 30, 31). Poorly woven shapeless bag covering posterior of abdomen, occasionally reaching thorax; silk fibers thick; extraneous material from substrate often incorporated (Fig. 32).

Larva (based on numerous last instar larvae). *Body* (Fig. 39): total length 6.4–6.6 mm, evenly yellowish grey. *Head* (Fig. 40): evenly medium brown with darker regions; anterior apotome paler and along ecdysial line to posterior of head; length 1.18–1.23 mm, width 0.86–0.88 mm; distance between antennal bases 0.55–0.57 mm; anterior margins of head parallel, convex posterior of stemmata; head spot pattern markedly positive; ecdysial lines well visible, divergent and straight (or slightly concave) until near posterior of head, then markedly bent; cervical sclerites not fused to postocciput; genae anterior of stemmata markedly dark brown. *Antenna* (Fig. 41): not extended beyond labral fan stem; total length 0.48 mm; basal and medial antennomere dark brown, apical antennomere paler (diameter 0.007 mm); basal (diameter 0.04 mm) and medial (diameter 0.023 mm) antennomeres subequal in length, together subequal to apical antennomere; proportional lengths of the three antennomeres 1.0:0.8:1.7; proximal half of basal antennomere with thickened wall, distal antennomere with closely packed bands (Fig. 41; insert). *Labral fan*: stalk light brown, ca. 66 rays, 7 posterior rays finer than remainder, length 0.65 mm, mid-ray width 0.014 mm; distinct pattern of microtrichia, longer microtrichia interspersed with 9 or 10 markedly smaller microtrichia. *Mandible* (Fig. 42, 43): overall darkly pigmented; outer teeth short, broad, poorly developed; apical tooth elongate and substantial; preapical teeth, 2 small and equal in length, proximal tooth well developed; ca. 8 spinous teeth, sometimes apparently worn; sensillum and serration simple, well developed on raised base; blade region with 6 or 7 irregular small serrations sometimes apparently worn. *Maxilla* (Fig. 44): palpus 2.7x as long as wide, very dark, longer than maxillary lobe; distinct gap between lobe and palp; dense tuft of hair at base of palp. *Postgenal cleft* (Fig. 45): poorly developed, shallow V-shaped, well sclerotized with markedly irregular edges; posterior tentorial pits small; postgenal bridge evenly dark brown, concolourous with genae; elongated posteroventral muscles spots small. Ratio of hypostoma, postgena and cleft 1.0:1.5:0.5. *Hypostoma*: darkly pigmented; teeth in three distinct units, variable, (Serra Road, Fig. 45; insert)—tooth 0 (median) often worn and rounded apically, tooth 1 (first sublateral) markedly smaller and on base of tooth 0, tooth 2 minute and often not expressed on one side, tooth 3 well expressed and on base of tooth 4 (lateral), that markedly extended beyond tooth 0, tooth 5 (paralateral) barely expressed on side of tooth 4, tooth 6 small but distinct on base of tooth 4, tooth 7 expressed merely as lateral bump, tooth 8 absent, all well raised from curved base of hypostoma; irregular lateral serrations; (Zumstein Track, Fig. 46)—tooth 0 (median) well extended to half length of tooth 4 (lateral), tooth 1 (first sublateral) well expressed and flange-like on base of tooth 0, with tooth 2 minute and variable, often not expressed on one side, tooth 3 larger and inserted on base of tooth 4, tooth 5 poorly expressed on base of tooth 4, tooth 6 distinct, tooth 7 poorly expressed as mere bulge, tooth 8 absent, all as steep-sided unit above remainder of hypostoma; lateral serrations numerous but small, extended well along side of convex hypostoma; 2 or 3 hypostomal setae on each side; 3 or 4 other small setae randomly arrayed more basally. *Thorax* (Fig. 47): prothorax dark brown, remainder of thorax lighter; the mature pupal gill histoblast poorly L-shaped, filaments directed ventrally then broadly posteriorly to recurved dorsally then partially anteriorly and then dorsally, recurved terminally at gill base; 3 or 4 basal thicker filaments showing and some bifurcations. *Anterior proleg* (Fig. 48): with distinct D-shaped lateral plates. *Abdomen*: evenly mottled medium yellowish brown. *Ventral tubercles*: absent or poorly expressed. *Rectal papillae*: three simple lobes. *Anal sclerite* (Fig. 49): simple X-shape, arms subequal in length; anterior arms not markedly flared apically, medial region well developed, interarm struts absent, posteroventral arms substantial, but tapered rapidly. *Posterior circling*: ca. 63 rows of hooks with 12 or 13 hooks per row (total ca. 780).

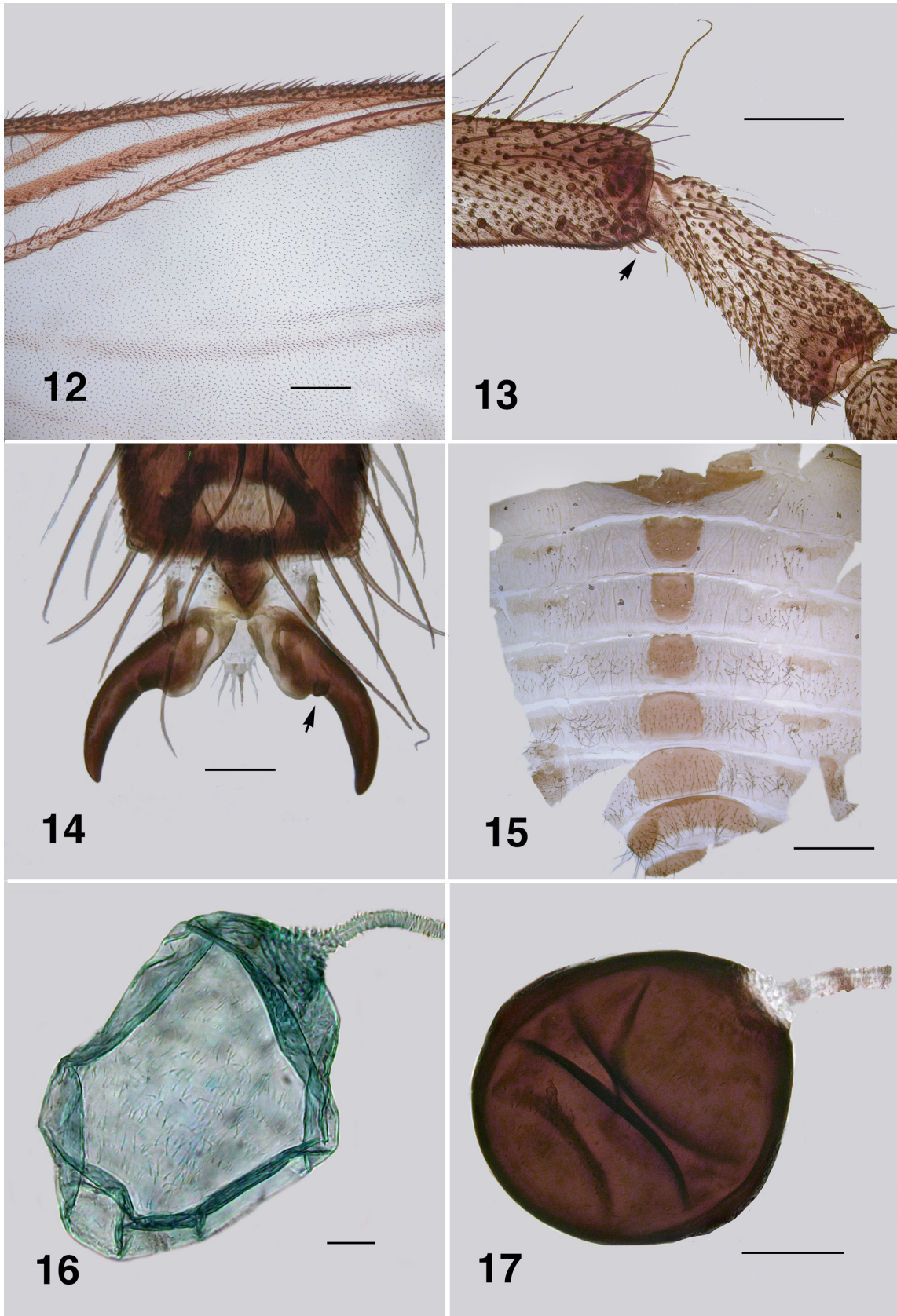
Etymology. Not specified by Tonnoir (1925), but named for Eustace William Ferguson, well known Australian entomologist and president of the Linnean and the Royal Zoological Societies of New South Wales, and who collected the type material. Ferguson was noted for his expertise in medical entomology and startling abilities as a collector in the field (Vallee 2012).



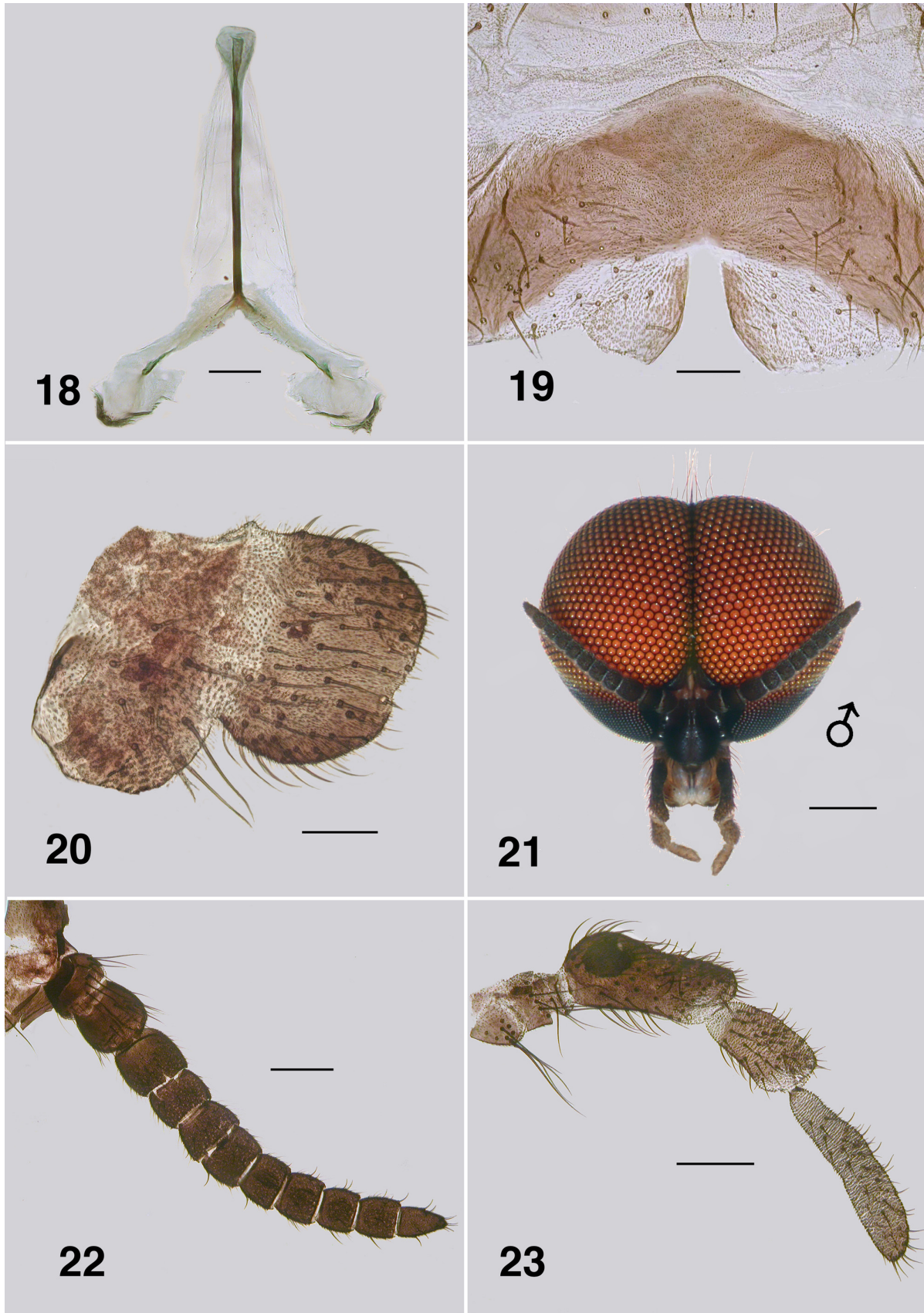
FIGURES 1–6. *Nothogreniera fergusonii* adult female. (1) Habitus of holotype (Bumberry, 1916). Scale bar = 1.0 mm. (Image courtesy of Russell Cox, Australian Museum, Sydney). (2) Holotype labels. (Image courtesy of Melissa Graf, Australian Museum, Sydney). (3) Habitus of female. In ethanol (Grampians National Park, 2014). Scale bar = 1.0 mm. (4) Paratype labels. (Australian National Insect Collection, Canberra). (5) Frontal view of head. (Grampians National Park). Distal palpomere foreshortened. Scale bar = 0.2 mm. (6) Antenna, paratype (ANIC No. 29 029396. Bumberry). Scale bar = 0.2 mm.



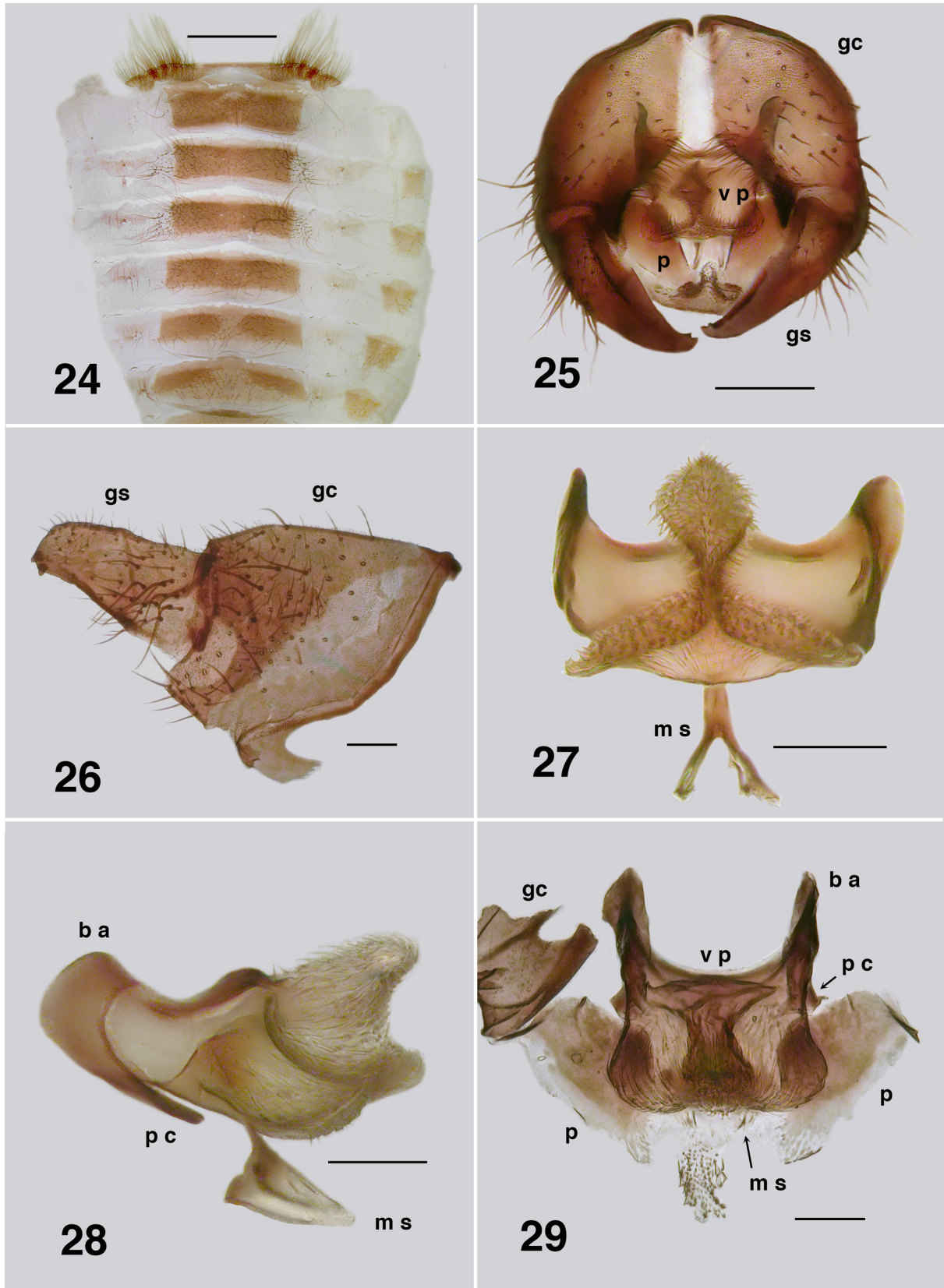
FIGURES 7–11. *Nothogreniera fergusonii* adult female. (7) Maxillary palpus, lacinia. Scale bar = 0.2 mm. Insert, lacinia tip. Scale bar = 0.05 mm. (8) Mandible tip. Scale bar = 0.05 mm. (9) Cibarium, paratype (ANIC No. 29 029396. Bumberry). Scale bar = 0.1 mm. (10) Anepisternal membrane, paratype. (As for Fig. 9). Scale bar = 0.1 mm. (11) Wing, paratype. (As for Fig. 9). Scale bar = 0.5 mm.



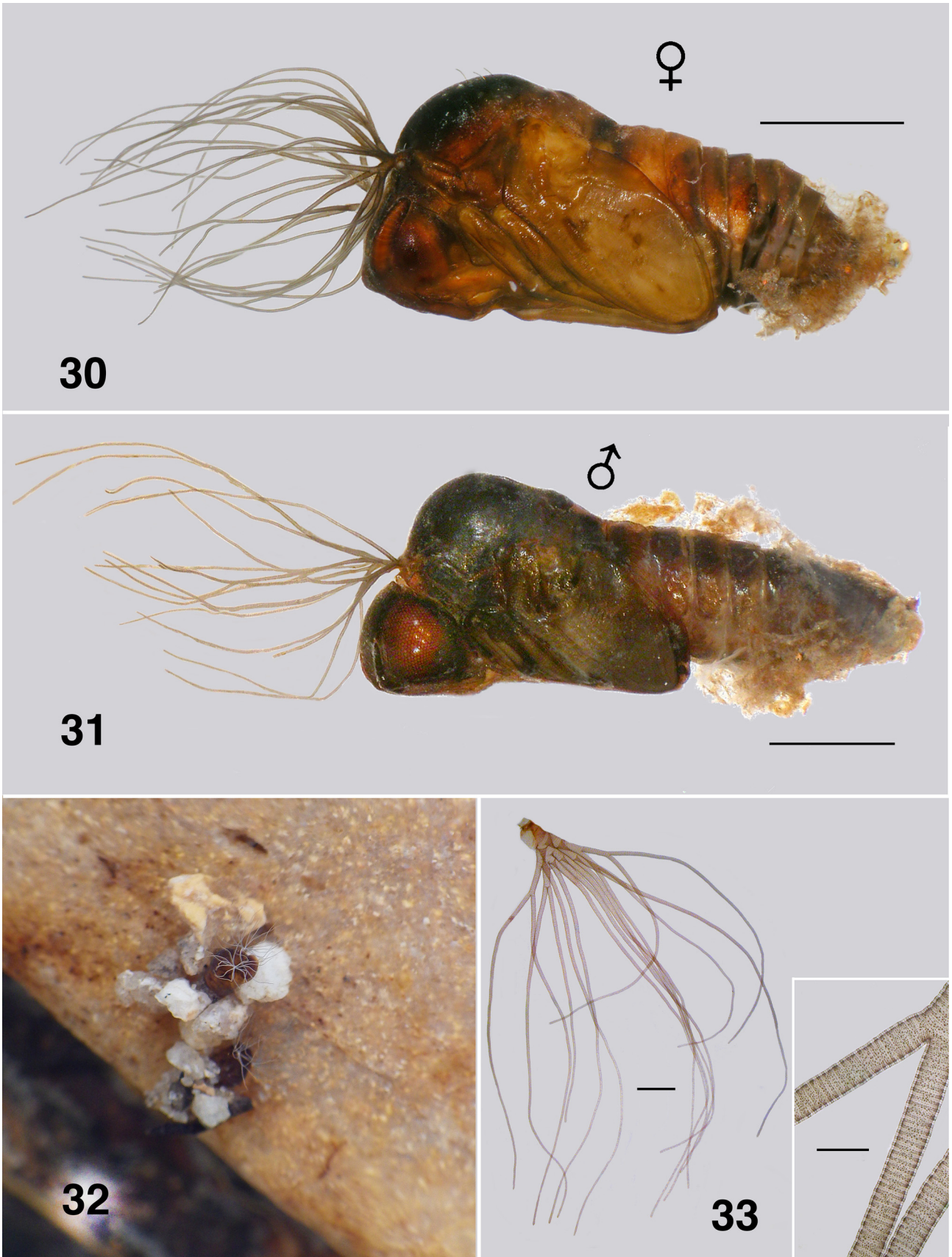
FIGURES 12–17. *Nothogreniera fergusonii* adult female. (12) Higher magnification of costal vein showing hair-like setae. Scale bar = 0.1 mm. (13) Hind basitarsus. Arrow points to concentration of spines at position of absent calcipala. Scale bar = 0.1 mm. (14) Claw. Arrow indicates minute tooth. Scale bar = 0.02 mm. (15) Abdominal tergites. Scale bar = 0.5 mm. (16) Pharate spermatheca, showing internal acanthae and sculpted junction of spermathecal duct. Stained with Chlorazol Black. Scale bar = 0.02 mm. (17) Spermatheca, fully developed, paratype. (As for Fig. 9). Scale bar = 0.05 mm.



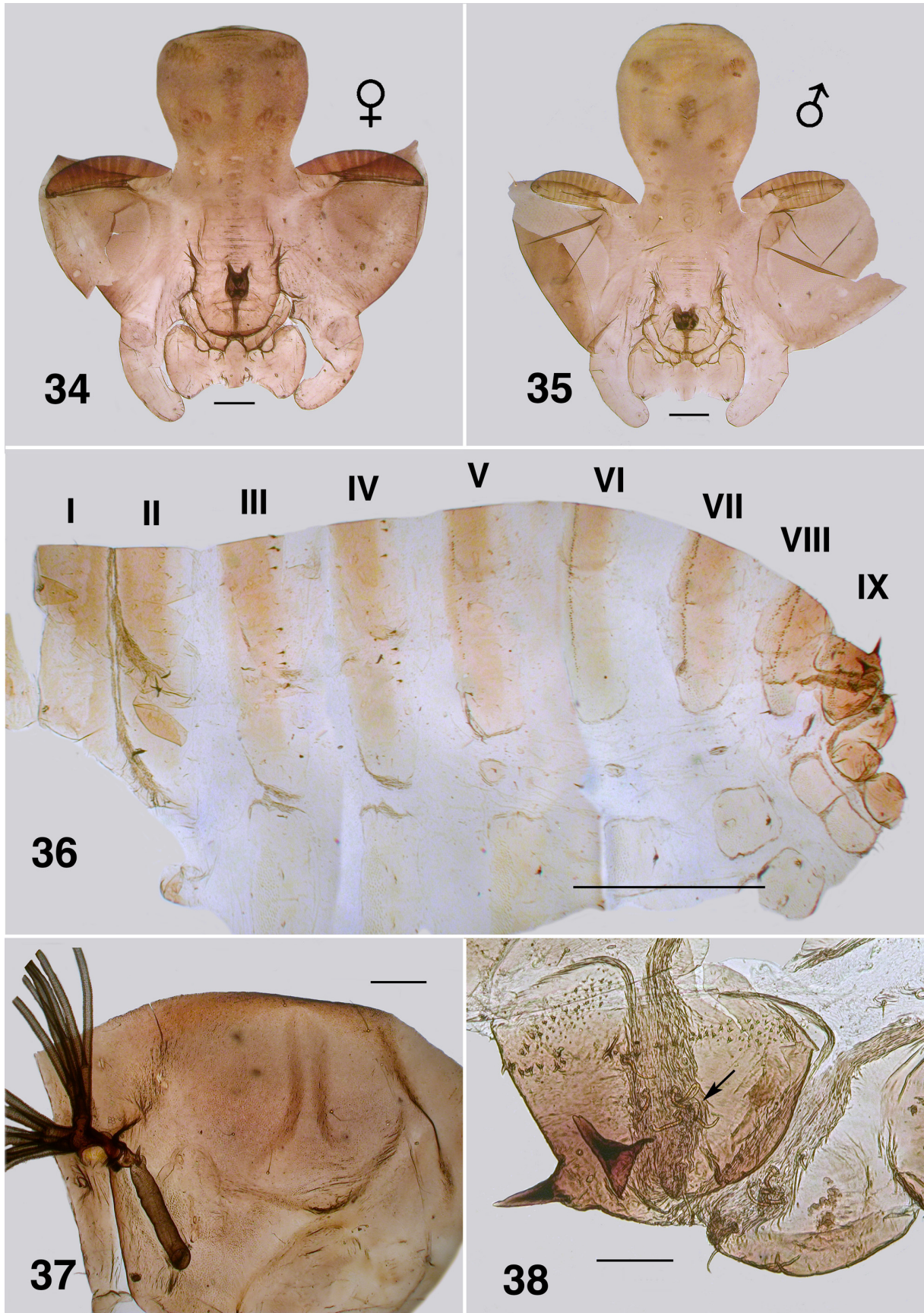
FIGURES 18–20. *Nothogreniera fergusonii*, adult female. **FIGURES 21–23.** Male. (18) Genital fork, paratype (As for Fig. 9). Scale bar = 0.05 mm. (19) Hypogynial valves, paratype (as for Fig. 9). Scale bar = 0.05 mm. (20) Anal lobe and cercus, paratype (as for Fig. 9). Scale bar = 0.05 mm. (21) Frontal view, head, reared (Grampians National Park). Scale bar = 0.25 mm. (22) Antenna. Scale bar = 0.1 mm. (23) Maxillary palpus. Scale bar = 0.1 mm.



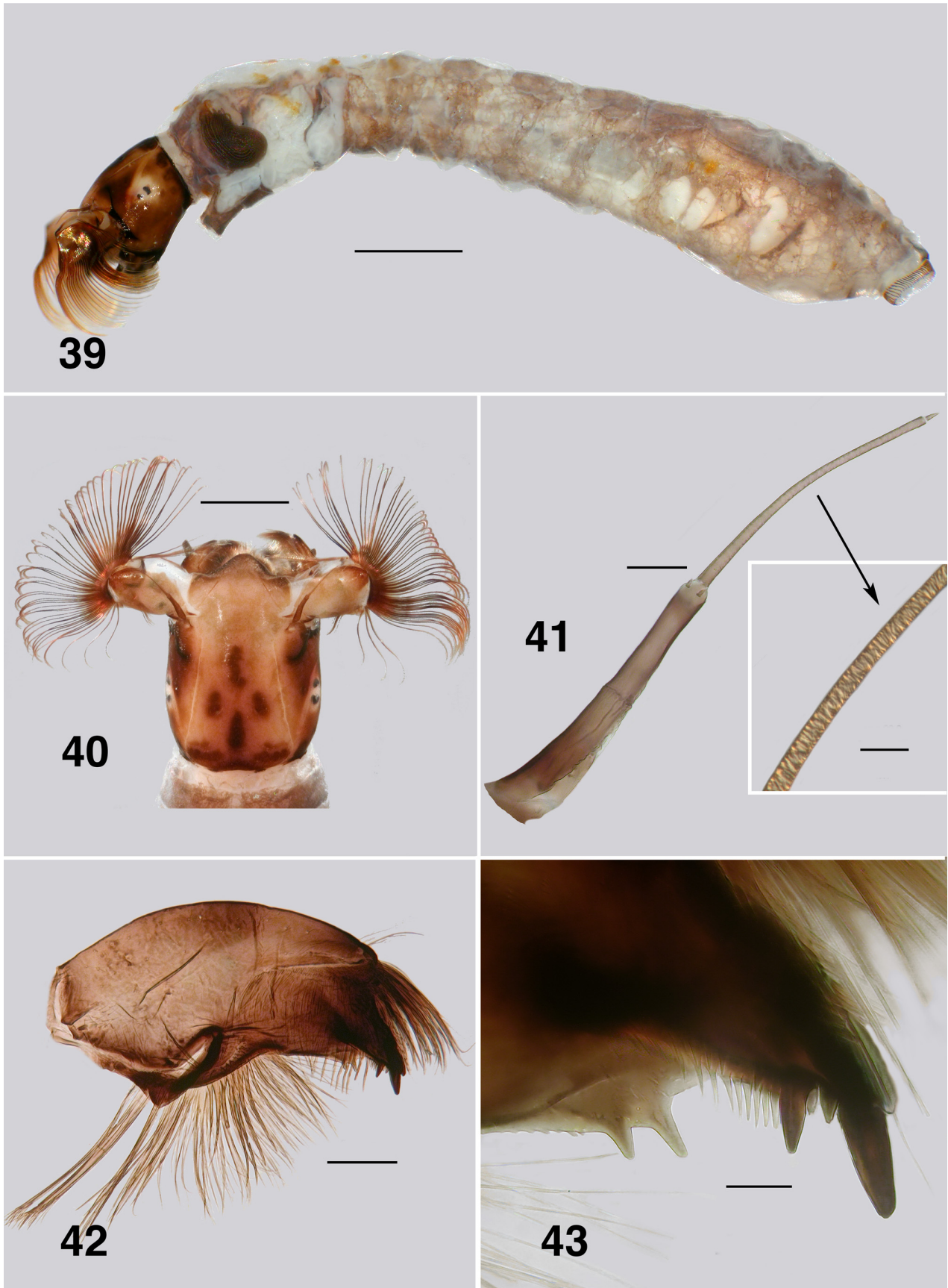
FIGURES 24–29. *Nothogreniera fergusonii*, male. (24) Abdominal tergites, reared. Scale bar = 0.5 mm. (25) Ventral view, genitalia, reared. gc—gonocoxa; gs—gonostylus; p—paramere; vp—ventral plate. Scale bar = 0.1 mm. (26) Gonostylus—gs & gonocoxa—gc. Scale bar = 0.05 mm. (27) Ventral plate. Posterior view. ms—median sclerite. Scale bar = 0.05 mm. (28) Ventral plate, lateral view. ba—basal arm; ms—median sclerite; pc—paramere connection. Scale bar = 0.05 mm. (29) Genitalia, slide mounted. ba—basal arm; gc—gonocoxa; ms—median sclerite; p—paramere; pc—paramere connection; vp—ventral plate. Scale bar = 0.05 mm.



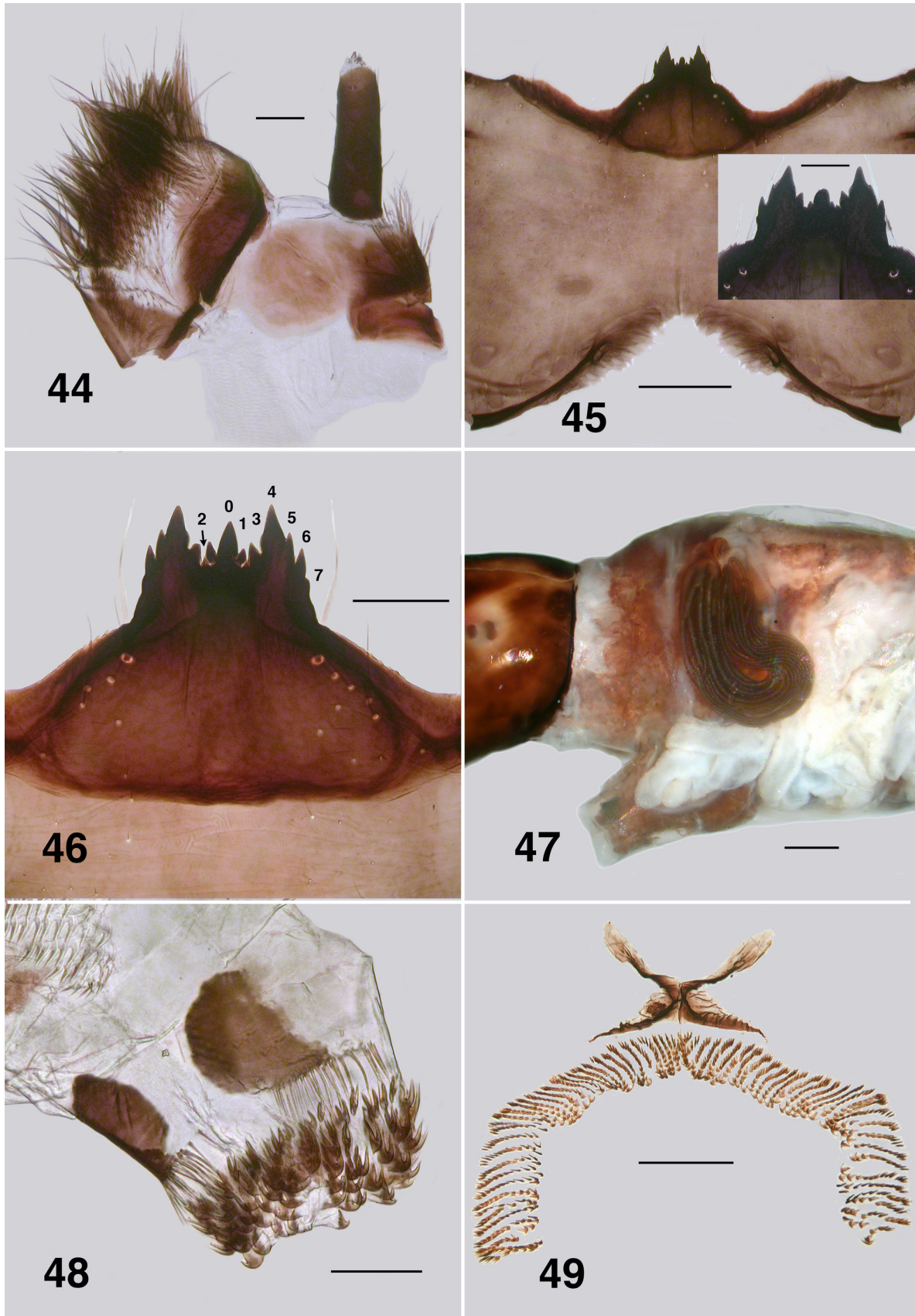
FIGURES 30–33. *Nothogreniera fergusonii*, pupae. (30) Habitus (female). Scale bar = 1.0 mm. (31) Habitus (male). Scale bar = 1.0 mm. (32) Pupae, in situ. (Zumstein Track Stream, see Fig. 52). (33) Pupal gill. Scale bar = 0.5 mm. Insert: Surface of gill filament. Scale bar = 0.05 mm.



FIGURES 34–38. *Nothogreniera fergusonii*, pupae (exuviae). (34) Cephalic capsule, female. Scale bar = 0.2 mm. (35) Cephalic capsule, male. Scale bar = 0.2 mm. (36) Abdomen, slide mount. Scale bar = 1.0 mm. (37) Thoracic cuticle. Scale bar = 0.2 mm. (38) Segment IX, showing terminal spines. Arrow indicates grapple hooks. Scale bar = 0.1 mm.



FIGURES 39–43. *Nothogreniera fergusonii*, last instar larva. (39) Habitus. Scale bar = 1.0 mm. (40) Dorsal head. Scale bar = 0.5mm. (41) Antenna. Scale bar = 0.05 mm. Insert: high magnification DIC of apical antennal article. Scale bar = 0.02 mm. (42) Mandible of last instar. Scale bar = 0.1 mm (43) Mandible tip. Scale bar = 0.02 mm.



FIGURES 44–49. *Nothogreniera fergusonii*, last instar larva. (44) Maxilla, palpus. Scale bar = 0.05 mm. (45) Postgenal cleft, hypostoma. (Serra Road). Scale bar = 0.2 mm. Insert. Hypostomal teeth. Scale bar = 0.05 mm. (46) Hypostoma. (Zumstein). Scale bar = 0.1 mm. (47) Lateral view of thorax, showing gill histoblast. Scale bar = 0.2 mm. (48) Anterior proleg. Penultimate instar. Scale bar = 0.05 mm. (49) Anal sclerite & circlet of hooks. Scale bar = 0.2 mm.

Types. *Holotype.* Mackerras & Mackerras (1949: 286) commented that whereabouts of the type of *fergusoni* was not known, but that paratypes were in the School of Public Health and Tropical Medicine, Sydney. The paratypes are now in ANIC, CSIRO, Canberra. Bugledich (1999) too noted the holotype was missing. It is, however, listed in Daniels (1978: 416) as in the Australian National Museum, Sydney. Details and images (e.g. Figs. 1, 2) are available on the "Atlas of Living Australia" <<https://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.taxon:ed160f9b-a369-4d87-9edd-f5b1b298c009>> (accessed 4 May 2018). Label data (Fig. 2):- [Bumberry NSW./ Biting Man/ 1/10/16] [S./ fergusoni/ Tonn./ det. A. Tonnoir 1923] [TYPE] [K48711], in Tonnoir's handwriting. The specimen is in good condition, albeit it appears that the left middle leg is absent, otherwise the remainder of the body is well preserved. Not examined beyond supplied images.

Paratypes. Of the eleven pinned female paratypes designated by Tonnoir (1925: 239), Bugledich (1999: 328) found 10 in ANIC. As of 2014, (DAC pers. obs.) seven were available and three of those were examined in detail. Label data as for holotype, but with:- [ANIC Database No./ 29 029396]—now mounted on slide. As above, but with:- [ANIC Database No./ 29 029394] [Aust. Nat./ Ins. Coll.]—now cleared and parts in genitalic vial on the pin. As above, but with [ANIC Database No./ 29 029398]—pinned.

Based on label data (cf. Fig. 2 & 4) and similarity of handwriting on paratypes and holotype labels, all are those described by Tonnoir (1925: 258).

Additional material. Apart from the paratypes noted above, large numbers of final instar larvae, pupae, pupal exuviae, reared and netted females, and reared males, from Grampians National Park, namely Serra Road, plus Zumstein Track and picnic area at Mackenzie Falls were available for study. Rearing allowed firm association of the earlier pinned females of Tonnoir to the newer adults and immature stages. There are seven pinned females from Colo Vale in ANIC; we examined two. Label data [Colo Vale/ 3. 3. 56/ Station No 2. Man/ E. O'Sullivan] [Paracnephia/ fergusoni/ (Tonnoir)] [Colo Vale/ 6. 3. 56/ Station 4. To man/ 1715-1745 J. Citowisch] [Paracnephia/ fergusoni/ (Tonnoir)].

Representative material in ETOH from the Grampians National Park is deposited in the ANIC, (ANIC Database No. 29 026650). Similar ETOH samples (UASM# 353360–353362) and slide mounts (UASM# 353363, 353364, 353146–353150, 353211–353225, 353463–353470), are deposited in the Strickland Museum, University of Alberta <www.biology.museums.ualberta.ca/en/EHStricklandEntomologicalMuseum.aspx>.

Distribution (Fig. 84). *New South Wales:* Bumberry, S33.1630° E148.5240°, elev. 600m., 1-x-1916 (Tonnoir 1925); Engineers Cascade, Mount Victoria, S33.5985° E150.2512°, elev. 1043m., January (Wharton 1948); Colo Vale, S34.3779° E150.4462°, elev. 700m., March (Lee *et al.* 1957).

Victoria: Cohuna, S35.8100° E144.2200°, elev. 88m., September (Mackerras & Mackerras 1955); Grampians National Park, Serra Road, S37.2966° E142.4371°, elev. 270m., 8-ix-2011, DAC; Zumstein Picnic Area, S37.0929° E142.3851°, elev. 250m., 28-ix-1996, JKM; Zumstein Track, S37.0946° E142.3821°, elev. 250m., 12-ix-2014, DAC, JKM, DCC; Mackenzie Falls Picnic Area, S37.1096° E142.4124°, elev. 435m., 13-ix-2014, JKM. There is a probable error with the locality of "Turret Falls, Marysville, NSW" in Mackerras & Mackerras (1955: 105). There is no such named waterfall in the area, but rather a Steavenson Falls (S37.5327° E145.7737°, elev. 630m). A Turret Falls (S37.1584° E142.4979°, elev. 540m.) is near Halls Gap, Grampians National Park, Victoria. This is a much more likely locality since there are thin films of water and flow is intermittent (DAC pers. obs., 2014). We are of the opinion that the location at Marysville is in error.

South Australia: Lucindale, S36.9700° E140.3700°, elev. 30m. (Mackerras & Mackerras 1949: 386).

Bionomics. Tonnoir (1925: 239) noted that type material of females (e.g. Fig. 1) had been collected while flying around and biting people (Figs. 2, 4), in association with *Austrosimulium furiosum* (Skuse). Label data on material from Lucindale, South Australia, indicates that *N. fergusoni* seriously injured horses and cattle, indeed, Mackerras & Mackerras (1949: 386) noted that this was probably the basis of the early report by Lea (1917) regarding injurious simuliids.

Biting behaviour would be in keeping with the well-developed mandibles and the enlarged sensory vesicle on the maxillary palpomere III, generally assumed to be a carbon dioxide receptor (McIver & Charlton 1970). Smaller abdominal tergites (Fig. 15) point, as well, to blood-feeding behavior (e.g., Adler *et al.* 2004; Craig *et al.* 2012). Numbers of female adults were collected flying around the authors at the picnic area at Mackenzie Falls, Grampians National Park, September, 2014; none landed or attempted to feed.

Larvae, pupae and reared adults are from three localities in the Grampians National Park. JKM collected material from near Zumstein Picnic Area (S37.0929° E142.3852°, elev. 250m.) in September, 1996. On 8th

September, 2011, DAC collected from the downstream side of a culvert on Serra Road (S37.2966° E142.4371°, elev. 270m.) (Fig. 50). Large numbers of larvae and pupae were on the lip of the culvert pipe and on hard surfaces a few metres downstream. Larvae formed typical spaced arrays (Fig. 51). At 13:00 hrs, air temperature was 14.1°C, water 11.0°C, conductivity 120µS/cm, pH 7.7, velocity *ca.* 0.62 m/s and the water slightly turbid. Larvae were mainly in shallow even flow and not found on stones or vegetation where flow was markedly turbulent. This site was dry in September, 2014, and clearly had not had running water since 2011, a year with serious flooding in the Grampians.

A third site was a small stream on Zumstein Shortcut (S37.0946° E142.3821°, elev. 250m.) (Fig. 52). On 12 September 2014, temperatures were—air 17.5°C, water 16.6°C, velocity 0.7 m/s in the small riffles. Larvae were on top and under stones with pupae under stones (Fig. 32). Female adults were netted and both sexes reared from pupae. Of note is that the area had been intensely burned some months before the collection and considerable ash was drifting in the water. This stream was revisited in November, 2014 and while expected to be dry, there was a small base flow. There was no evidence that *N. fergusonii* had ever been present. The only simuliid present was *Simulium ornatipes* Skuse, with large numbers of larvae and pupae.

Of note for the September collection of *N. fergusonii* pupae from Zumstein Shortcut was that the cocoons were heavily covered with small stone particles from the substrate (Fig. 32). Such was not seen at the Serra Road culvert site. With such substrate lacking, cocoons there had only algal strands incorporated into the rudimentary cocoon.

Our dates of collecting are in good agreement with Tonnoir's original sample of *N. fergusonii* females taken 1st October, 1916. Mackerras & Mackerras (1952: 105) commented that they had searched extensively for immatures of *N. fergusonii* at Bumberry, NSW, but were unsuccessful.

The three Grampian localities give clear evidence that *N. fergusonii* is a univoltine Austral spring species that inhabits intermittent streams. The wide ranging females, as netted at the McKenzie Falls Picnic Area, are probably looking for a blood meal and/or suitable sites to lay eggs. There is, though, no information on oviposition.

The Colo Vale specimens were taken during a preliminary investigation into control of rabbits with the myxoma virus (Lee *et al.* 1957). The adults were collected in March—at considerable variance to the collection dates from the Grampians. However, elevation at the Colo Vale locality is some 700m., so cold water would occur later into the year.

The low number (*ca.* 780) of hooks (Fig. 49) comprising the circlet of hooks is in good agreement with the velocities recorded (~0.62 m/sec.). Palmer & Craig (2000), Craig *et al.* (2012), Konurbaev (1973) and others, have shown close correlation between number of such hooks and general velocity of flow in the habitat.

Bugledich (1999) indicated that Hunter & Moorehouse (1976) dealt with biology of *N. fergusonii*, but this is in error.

Remarks. In the synonymy given by Mackerras & Mackerras (1949: 386) for *Simulium fergusonii*, Sharp [*sic*] (1945: 505) is in error and it should be 'Smart'.

As Tonnoir (1925) noted, *N. fergusonii* adult females could at that time be separated from other Australian simuliids by complete lack of calcipala and pedisulcus, a short palpomere IV and small apical antennomere. This generally also applies to *N. occidentalis* (see below). Absence of a calcipala was then unique among Australian simuliids, but examples of a small or absent calcipala are now known (Craig *et al.* 2018) for Western Australia *Bunyipellum gladiator* (Moulton & Adler) and undescribed species related to eastern Australia "*Paracnephia umbrator*" (Tonnoir).

The function of the calcipala in simuliid adults remains unclear, although it is believed to play a role in grooming the wing or the body (Crosskey 1990: 345; Adler *et al.* 2004: 41). The row of stout spines along the ventral surface of the hind basitarsus is distinct in *N. fergusonii* and, in particular, there is a concentration, or clump, of spines where the base of a calcipala would occur (Fig. 13). This was illustrated by Tonnoir (1925: 221; his fig. 2 F, G, H), including the elongated tarsomere II—unusually long for Australian simuliids. Such an aggregation of spines also occurs in *N. occidentalis* on a very small calcipala. That condition in *N. occidentalis* is not unique within Australian simuliids, being present in *Bunyipellum gladiator* (Moulton & Adler) (Craig *et al.* 2018) and as yet undescribed Australian species related to *Paracnephia umbrator*. Aggregation of spines suggests that they perhaps perform the function of the calcipala when the latter is small or absent.

The pupae of both species are similar, with gills of *N. occidentalis* longer than those of *N. fergusonii*. Larvae of *N. fergusonii* are darker in colour than *N. occidentalis* and the latter has larger labral fans. Expression of larval hypostomal teeth in *Nothogreniera* is unique for Australian simuliids. The markedly trilobed arrangement of teeth

(e.g., Fig. 46) is similar to those in *Greniera* and *Tlalocomyia* (Adler *et al.* 2004: e.g. 564). While trilobed arrangements are known for larvae of "*Paracnephia*" *fuscoflava*" (Mackerras & Mackerras) and "*P.*" *tonnoiri*" (Drummond), the lobes are not as strongly developed.

There are discrepancies between the type (Fig. 1) and newer material from the Grampians (Fig. 3); namely, the darker colouration of the type and density of the vestiture on the scutum. These and other differences suggest that *N. fergusonii* is a species complex. Unfortunately, efforts by Mackerras & Mackerras (1952: 105) to collect immature stages from the type locality (Bumberry, Victoria) proved unsuccessful. Indication of a species complex is further suggested by differences in the hypostomal teeth of last instar larvae between two populations from the Grampians; namely Serra Road and Zumstein track (*cf.* Figs. 45, 46). The latter has a hypostoma that is markedly similar in appearance to those of *Greniera* (Adler *et al.* 2004: 563). Given that the distance between the two sites is a mere 24 km, perhaps the female adults are not as vagile as we suggest above. Or, could such differences be environmentally dictated?



FIGURES 50–52. *Nothogreniera fergusonii*, habitats of immatures. (50) Serra Road, culvert, Grampians National Park, Victoria. (September 2011). (51) Late instar larvae. Arrow indicates direction of flow. (52) Zumstein Track Stream, Grampians National Park, Victoria. (September 2014).

The unidentified larvae reported and illustrated by Wharton (1949: 411, his figs 17-21) from Engineers Cascade, Mount Victoria, NSW, are referable to *N. fergusonii*, as here defined, despite minor discrepancies (*e.g.*, pupal gill) from the material reported here. Further studies including cytological and molecular data are needed to ascertain the status of these widely dispersed populations.

***Nothogreniera occidentalis* (Mackerras & Mackerras 1949, attrib. Tonnoir).**

New status and new combination

(Figs. 53–83)

'*Simulium fergusonii occidentalis*' Tonnoir. Unpublished manuscript name (*nec Simulium occidentale* Townsend 1891: 106; Smart 1945: 510). *Nomen nudum*.

Cnephia fergusonii (Tonnoir) var. Mackerras & Mackerras 1949: 386. (Type missing).

"*Cnephia*" 'S. x. (west)'. Moulton 2000: 98. 2003: 43. Molecular examination.

Nothogreniera occidentalis (Mackerras & Mackerras). New status and combination. The authors are following the precedent set by Crosskey & Howard (1997), who recognized Mackerras & Mackerras, 1949 as the authors of *occidentalis*. Curiously, Crosskey & Howard (*loc cit.*) did not comment on this muddy nomenclature.

Description. *Adult female*: (based on four pinned paratypes, one slide mount (Fig. 54) and a pharate specimen). *Body* (Fig. 53): total length 2.1–2.8 mm; markedly blackish grey with pollinosity on thorax, legs brown. *Head* (Fig. 55): overall black, pollinose in some lighting, frons tapered only slightly towards antennae, narrowest just above antennae; width 0.6–1.1 mm; depth 0.50–0.86 mm; postocciput vestiture of sparse, short black hairs; frons blackish brown; frons/head width ratio 1.0:3.8–4.6. *Eyes*: interocular distance 0.09–0.14 mm; ommatidia diameter 0.017 mm; *ca.* 27 rows across and 35 down at mid-eye. *Clypeus*: width 0.25–0.27 mm; dark brown, pollinose; vestiture of sparse pale hairs. *Antenna* (Fig. 56): total length 0.6–0.9 mm; nine antennomeres; tapered; scape small, pedicel marginally broader than antennomere I, that as broad as long, remainder gradually increasing in length, occasional antennomere malformed and fused to another, distal antennomere short, but longer than broad. *Mouthparts*: substantial, *ca.* 0.6x length of head depth; cibarium median depression shallow, smooth with irregular pigmentation, cornuae short, substantially sclerotised (Fig. 57); mandible markedly expanded distally, *ca.* 16 outer and 40 inner teeth, small, decreased in size proximally; lacinia with 16–18 and 17–19 teeth on inner and outer sides respectively (Fig. 59); maxillary palp (Fig. 58), total length 0.66–0.69 mm, palpomeres I and II small, III darker brown than remainder, slightly extended beyond articulation with IV, which is light brown and short, V (distal) pale and moderately long; proportional lengths III–V palpomeres 1.0:0.5:0.9; sensory organ not markedly elongated, irregular or oval (variable), 0.3–0.4x length of palpomere III, opening 0.4x vesicle width. *Thorax*: length 1.1–1.4 mm; width 0.9 mm; postpronotal lobe concolourous with scutum, markedly hirsute with fine hair longer than that on scutum, scutum overall black with even sparse fine golden hairs; scutellar depression concolourous, but pollinose with longer sparse golden hairs; scutellum concolourous with scutum, vestiture of sparse markedly long fine golden hairs; antepronotal lobe with dense long greyish hairs; proepisternum with dense long pale hairs; fore coxa haired; pleuron and anepisternal membrane dark brown, lacking hairs; katepisternal sulcus well expressed; metathoracic furcasternum lateral flanges not markedly developed (as for *N. fergusonii*, Fig. 8). *Wing*: (Fig. 63) length 3.1–3.5 mm; width 1.3–1.5 mm; costa lacking spiniform setae, hairlike setae only, R_s with hairlike setae only; basal radial cell well developed; a/b ratio 1.0:2.7; M_1 vein double. *Haltere*: dark yellowish to blackish brown. *Legs* (Fig. 60): evenly dark brown; hind basitarsus with row of widely spaced stout spines; calcipala markedly poorly developed, with a few stout spines concentrated in that position, distinct intersegmental plate ventrally between basitarsus and tarsomere II, hirsute, also between tarsomeres II & III; pedisulcus absent; claws small, thumblike lobe markedly small to essentially absent—variable, small rounded heel (Fig. 61). *Abdomen* (Fig. 62): abdominal scale dark brown, dull yellowish medially with long creamy-yellow hairs extended to abdominal segment III; remaining segments evenly dark brown, with mottled yellowish areas dorsally; tergite II broad, 3.3x broad as long, tergite III quadratic with rounded corners, tergite IV smaller and quadratic, tergite V the smallest, VI larger and tergite VII broad, vestiture essentially absent on anterior tergites, increased posteriorly; pleurites poorly developed; sternites absent. *Genitalia*: sternite VIII evenly pigmented vestiture of microtrichia and sparse substantial setae; hypogynial valves with medial edges strengthened and straight, gap slightly tapered anteriorly, vestiture of microtrichia and sparse setae (Fig. 64); genital fork with anterior arm narrowed and curved dorsally (distorted in image), anterior apex barely expanded, lateral arms poorly sclerotized, apodeme apparent, but well

lateral, posterolateral expansions rounded (Fig. 65); cerci bluntly rounded, straight dorsal margin, anal lobe poorly developed (Fig. 67); spermatheca ovoid, dark brown, externally smooth, internal fine spines (aka acanthae) sparse and not easily apparent even at high magnification, clear region surrounding junction with spermathecal duct barely evident, poorly developed sculpting (Fig. 66).

Adult male (reared specimen in poor condition and two pharate specimens). *Body*: in ethanol, overall colour black; total length 3.7–3.9 mm. *Head*: width 0.97 mm; depth 0.92 mm. *Eyes*: upper ommatidia, diameter 0.030 mm, ca. 19 across and 22 down; lower ommatidia small, diameter 0.015 mm. *Antenna*: markedly narrowed, total length 0.76 mm; overall black, pedicel small, scape twice as long and rounded, antennomere I slightly narrower than scape, remainder tapered smoothly to small apical antennomere. *Mouthparts*: markedly insubstantial; length 0.26x head depth; maxillary palp 0.74 mm long, palpomeres I and II small, palpomere III extended slightly past junction with palpomere IV; proportional lengths of III–V palpomeres 1.0:0.6:0.7, sensory vesicle irregular spherical shape, occupying 0.3x width of palpomere III. *Thorax*: only moderately domed, length 1.4 mm; width 1.0 mm; pronotal lobe, anteprenotal lobe and proepisternum haired; scutum evenly velvety black, vestiture of sparse short fine pale hairs, dense and long in scutellar depression; dense and longer on postpronotal lobe; scutellum concolourous with scutum, bare medially, with sparse long pale hairs laterally; postnotum concolourous with scutum; pleurae dark brown, membrane lacking hairs. *Wing*: details not available. *Haltere*: base of stem black, knob dark tan. *Legs*: details not available. *Abdomen*: details not available. *Genitalia*: heavily pigmented; gonocoxa wider than long, vestiture of sparse hairs; gonostylus broad, curved on outer edge, two substantial short, blunt, apical spines (Fig. 68); ventral plate complex (Fig. 69), 1.3x wider than length, broadly rounded posteriorly and expanded, narrowed medially, vestiture of distinct hairs; small central carina; basal arms broad, paramere connector well developed; median sclerite apparently not markedly developed; paramere blade-like, lightly strengthened along medial edge, articulation with the ventral plate basal arm extension not distinct, but is so with the gonocoxal apodeme, no apparent terminal spines; aedeagal membrane with small spines.

Pupa (based on three immature specimens and one exuvia). Body length ca. 3.0 mm (Fig. 70). Cuticle colourless and thin. Female head cuticle broad basally, length 1.5x basal width. Setae not apparent (Fig. 72). Male head cuticle, unknown. Thoracic cuticle smooth to slightly rugose (Fig. 71), thoracic dorsocentral setae elongate, with slightly curled tips. Gill: with short base, branching into three; dorsal and median branches substantial with multiple branching points, 15 long, light brown, markedly fine filaments, length ca. 3.8 mm, subequal to pupal length. Surface structure finely pseudoannulated. Abdominal armature and pleurites as for *N. fergusonii* (see Fig. 36); armature even less well developed. *Cocoon*. Apparently just a few threads of silk over the posterior of the pupal abdomen.

Larva (based on five last instar larvae). *Body* (Fig. 73): length 5.8–6.7 mm. *Head* (Fig. 74): length 0.8 mm, width 0.6 mm, colour light yellow and brown, variable, sometimes colourless; head spots positive. Earlier instar head medium brown. Anteromedian and posteromedial head spots positive and distinct, lateral spots less so; ecdysial lines sinuous; cervical sclerites attached laterally to postoccipt. *Antenna* (Fig. 75): extended beyond fan stem, 0.6 mm long, distal antennomere elongated and subequal to median plus basal antennomere, proportions 1.0:0.7:1.6. Distal antennomere with markedly fine sclerotized bands (Fig. 75; insert). *Labral fan*: stems colourless, fans markedly developed, ca. 70 fine rays, 0.75–0.90 mm long, mid width ca. 0.006 mm, long microtrichia subequal to ray width, interspersed with 4 or 5 smaller. *Maxilla* (Fig. 76): not heavily pigmented. *Mandible* (Fig. 77): elegantly curved and elongate, not markedly pigmented, anterior brush well expressed, apical tooth well expressed and protruded, preapical tooth half size of apical tooth, spinous teeth markedly fine and elongated, serrations and sensillum distinct and well expressed, blade region flat (Fig. 78). *Postgenal cleft* (Fig. 79): poorly expressed, shallow V-shape with irregular anterior apex, distinctly and broadly pigmented along edge, postgena essentially colourless, proportions of hypostoma to genae and cleft 1.0:1.8:0.4. *Hypostoma*: teeth markedly pigmented, in three units, teeth 0, 1, 2 markedly variable, tooth 0 either not protruded or directed dorsally (appears rounded and foreshortened in ventral view, e.g. Fig. 79) with teeth 1 and 2 small, subequal in size, or (Fig. 80), tooth 0 distinct with tooth 1 lateral on base, tooth 3 small on base of enlarged and protruding tooth 4, teeth 5 & 6 laterally on base of tooth 4, variable and occasionally poorly expressed, tooth 7 small, tooth 8 either not expressed, or poorly so on one side only; lateral serrations down convex sloped sides of hypostoma small, but distinct. Only one substantial hypostomal seta with two poorly expressed other setae more proximally, variable. *Anterior proleg* (Fig. 81): hooks markedly few, lateral sclerite poorly sclerotized and D-shaped. *Thorax* (Fig. 82): pharate pupal gill histoblast with filament bases curved ventrally, turning smoothly posteriorly and then dorsally almost to dorsal origin of gill, then bending rapidly ventrally to recurved dorsally again. *Abdomen*: mottled greyish yellow, lighter

posteriorly; sometimes with dorsal spot pairs dorsally on segments V–VII, expanded slightly to segments V–VII then decreased smoothly to posterior proleg. *Ventral tubercles*: absent or poorly expressed. *Rectal papillae*: three simple lobes. *Anal sclerite* (Fig. 83): with dorsal and ventral arms subequal in length, median region not markedly developed. *Posterior circlet*: 50–54 rows of hooks, 10 or 11 hooks per row (total *ca.* 550).

Types. The taxonomic history of *N. occidentalis* is somewhat murky. According to Mackerras & Mackerras (1949: 386), Tonnoir intended to describe this entity as "*Simulium fergusonii occidentalis*", even designating a holotype that supposedly was deposited in the School of Public Health and Tropical Medicine, Sydney. Tonnoir died in 1940 (Miller 1940: 37) and this description was never formally published. The putative 'holotype' is missing and considerable attempts by DAC to locate it have proven unsuccessful. However, 'paratypes', apparently labeled as such by Ian Mackerras, are now housed in ANIC, Canberra.

Nothogreniera occidentalis possessed sufficient morphological divergence from *N. fergusonii* to be considered a valid subspecies by Tonnoir—we concur, although at full species level.

Holotype. Whereabouts currently unknown, possibly lost; however, it may eventually be discovered in an Australian collection. Accordingly, at this time, we refrain from designating a neotype from one of the available paratypes.

Paratypes. Pinned females. Label data:- [One hind leg mounted between cover slips bits] [Bridgetown, W. A./ 29 Aug. 1926./ E. W. Ferguson] [PARATYPE. (printed)/ *Simulium/ fergusonii/ occidentalis/ Tonn* (blue, handwritten)] [*Cnephia/ fergusonii* var./ det. Mackerras] [ANIC Database No./29 029386] [AUST. NAT./ INS. COLL. (green)].

[Bridgetown W.A./ 29 Aug. 1926/ E. W. Ferguson] [PARATYPE/ *Simulium/ fergusonii/ occidentalis/ Tonn*] [ANIC Database No./ 29 029385] [Aust. Nat./ Ins. Coll.], plus No./ 29 029387 and No. 29 029382—now mounted on slide.

A pinned specimen (No. K67560), indicated as a paratype, is housed in the Australian National Museum, Sydney. Collected by E. W. Ferguson. Data given is, in part—"Paratype: *Simulium fergusonii occidentalis* Tonnoir, MSS name: Simuliidae: Diptera : Insecta:". The date of collection was 31-viii-1926, Tammin, WA (S31.6400° E117.4800°). It is not clear if this specimen is strictly a paratype. It is listed under "*Paracnephia fergusonii*" in the "Atlas of Living Australia" <https://biocache.ala.org.au/occurrences/search?q=lsid:urn:lsid:biodiversity.org.au:afd:taxon:ed160f9b-a369-4d87-9edd-f5b1b298c009#tab_recordsView>. Similarly, a specimen 'K179806', 30-viii-1926, Narrogin, WA (S32.9300° E117.1700°).

Additional material. Pinned females:- [3m. S. Mt. Cooke/ WA./ 30.viii.56/ O/L/ McIntosh] [*Cnephia/ fergusonii/ var.* (Tonn.)/ I. M. Mackerras det.] [Aust. Nat./ Ins. Coll.] and [Tammin/ 31 Aug '26/ Nicholson] [Western/ Australia] [*Cnephia/ fergusonii/ var.* det Mackerras] [Aust. Nat./ Ins. Coll.]. Slide material:- female [ANIC Database No/ 29 029359] [*Cnephia/ fergusonii* var./ {F}/ Bridgetown W.A./ 29/8/26. A.J.N]; on back of slide [Aust. Nat./ Ins. Coll.] (Fig. 54); female [*Nothogreniera/ occidentalis*] [Western Australia/ Dale River tributary/ S32° 21' 30"/ E 116° 27' 30"/ elev. 300m. 7-ix-1996/ Coll. JK Moulton] [ANIC Database No. 29 026653]. Last instar larva, as above [ANIC Database No. 29 026652]. All stages (UASM# 353138–353145). Alcohol material:- two larvae and a pupa. Label data:- [*Nothogreniera/ occidentalis*] [AUSTRALIA, WA/ Last stream on N. Metro Rd./ before X-ing with McCallum/ Rd. Trib. of Dale River/ S32° 21' 30"/ E 116° 27' 30"/ 7 September 1996/ Coll. J. K. Moulton] [ANIC Database No. 29 026651]. Larvae, pupae, reared male:- [Dale R. trib (11-5)/ 11-vii-81 JP (aka Jane Prince)] (UASM# 353367) and [AUSTRALIA, WA/ Last stream on N. Metro Rd./ before X-ing with McCallum/ Rd. Trib. of Dale River/ S32° 21' 30"/ E 116° 27' 30"/ 7 September 1996/ Coll. J. K. Moulton], (UASM# 353365, 353366). The pupae are of very early stage and suboptimal for description.

Etymology. Originally 'occidentalis' was an unpublished subspecies manuscript name by Tonnoir (Mackerras & Mackerras 1949: 386), albeit written on specimen labels. While not used by Mackerras & Mackerras (*loc. cit.*), we do so here for historical value.

Distribution (Fig. 84). *Southern Western Australia*: Mt. Cooke, S32.3500° E116.3300°, elev. 300m., 30-viii-1956 (ANIC); Bridgetown, S33.9700° E116.1400°, elev. 200m., August (Mackerras & Mackerras 1949); Narrogin, S32.9300° E117.1800°, elev. 360m., August (Mackerras & Mackerras 1949); Tammin, S31.6400° E117.4800°, elev. 240m., 31-viii-1926 (Mackerras & Mackerras 1949); Dale River tributary, S32.3586° E116.4583°, elev. 300m., 7-ix-1996 (JKM); Dale River tributary, S32.3500° E116.4500°, elev. 300m., 8-ix-1996 (JKM); Dryandra, S32.7200° E116.9300°, elev. 300m., 31-viii-1956 (ANIC); Donnybrook, S33.5900° E115.8200°, elev. 80m., 1-ix-1952 (ANIC).

Bionomics. All original female adults were collected in August. It can be assumed that they were netted while

attempting to bite the collector. Nothing else is known. The immature stages collected by JKM were taken from a small tributary of the Dale River on the Darling Escarpment, Western Australia in September. The locality was just a sandy ditch with low flow and a few substrates of sticks, leaf packs, and even rarer trailing grass—in full agreement with the physiognomy of the larvae. Large porous labral fans have been suggested (Palmer & Craig 2000; and others) as an adaptation to slow flow and high seston levels, and there is the well known correlation (*e.g.* Palmer & Craig *loc. cit.*; Konurbayev 1973; and again, others) between low velocity and small numbers of hooks in the posterior cirlet—for *N. occidentalis* some 550. While amongst the lowest numbers recorded by Crosskey (1990: 163) and Palmer & Craig (*loc. cit.*), "*Paracnephia*" *umbrator* larvae possess a mere 390 hooks. Similar low numbers are known for *Bunyipellum gladiator* and even lower for undescribed Western Australia species related to "*P.*" *umbrator*.

The long antennae on larvae of *N. occidentalis* and, less so those of *N. fergusonii*, point to adaptation to the slow flow of their known habitats. Both Crosskey (1990: 108) and Adler *et al.* (2004: 53) comment that longer antennae are common for simuliid larvae inhabiting slow flows. This agrees with a study by Craig (1990: 349) on the ephemeropteran *Cloeon dipterum* (Linnaeus), where long antennae are used to penetrate the boundary layer surrounding the body when the larva is moving slowly.

Dates of collection indicate that *N. occidentalis* is a univoltine Austral spring species, similar to *N. fergusonii*.

Remarks. As noted above, the *N. occidentalis* has a somewhat checkered taxonomic history. Tonnoir proposed the name in a manuscript, but it was never formally published. Thence the 'types' he designated and names on material still in existence, had no validity. However, Mackerras & Mackerras (1949: 386) had access to Tonnoir's 'paratypes' and described the species as "*Cnephia fergusonii* (Tonnoir) var." (*e.g.* Fig. 54). Prior to 1960, the ICZN allowed such as valid subspecies.

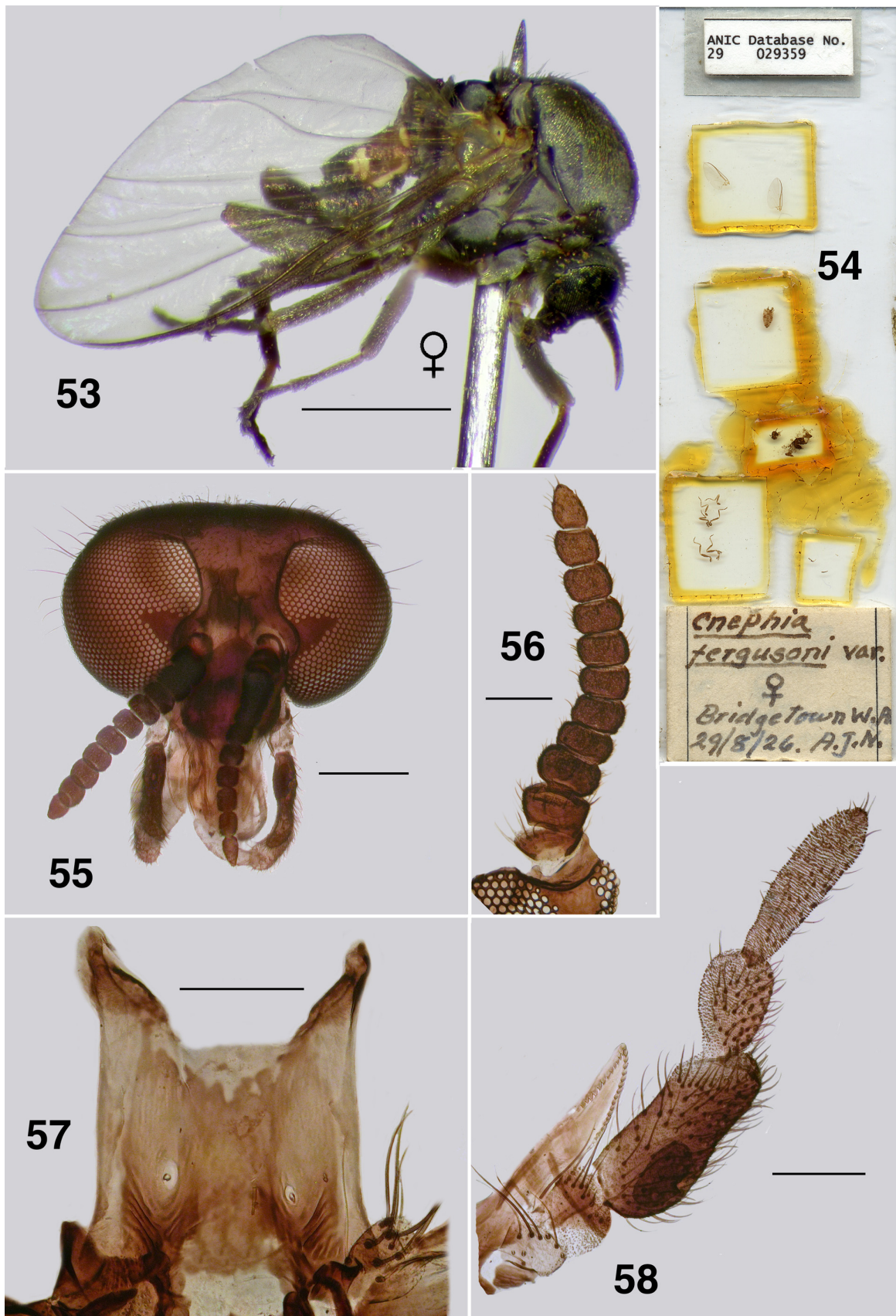
Here we formally raise that entity to species status and assign it to *Nothogreniera* as *N. occidentalis* (Mackerras & Mackerras). It is similar in many respects to *N. fergusonii*, with possession of a clump of stiff spines on the inner apical margin of the hind basitarsus (*i.e.*, in the vicinity of the calcipala, when present), minute tooth on the female claw, strengthened inner margins of the hypogynial valves, striations on the distal antennomere of the larval antenna and the markedly trilobed appearance of the hypostomal teeth. Adult *N. occidentalis* are overall distinctly more blackish in colour, with ashy reflections on thorax, with legs lighter brown (*cf.* Figs. 1, 2, 53). The larvae have large labral fans, longer antennae, a more acutely pointed postgenal cleft and more yellowish body colouration. Collectively, these differences are considered sufficiently distinct to warrant recognition of *N. occidentalis* as a valid species. Indeed, Moulton (2003: 50), in a molecular study, showed *N. fergusonii* and *N. occidentalis* (as "C." 'S.x. (East)' and "C." 'S.x. (West)' respectively) to be sister species with high support.

Discussion. With more stages now available, namely the immatures, it is clear the Australian so-called "*Paracnephia*" species do not belong in that African genus as assigned by Crosskey & Howard (1997).

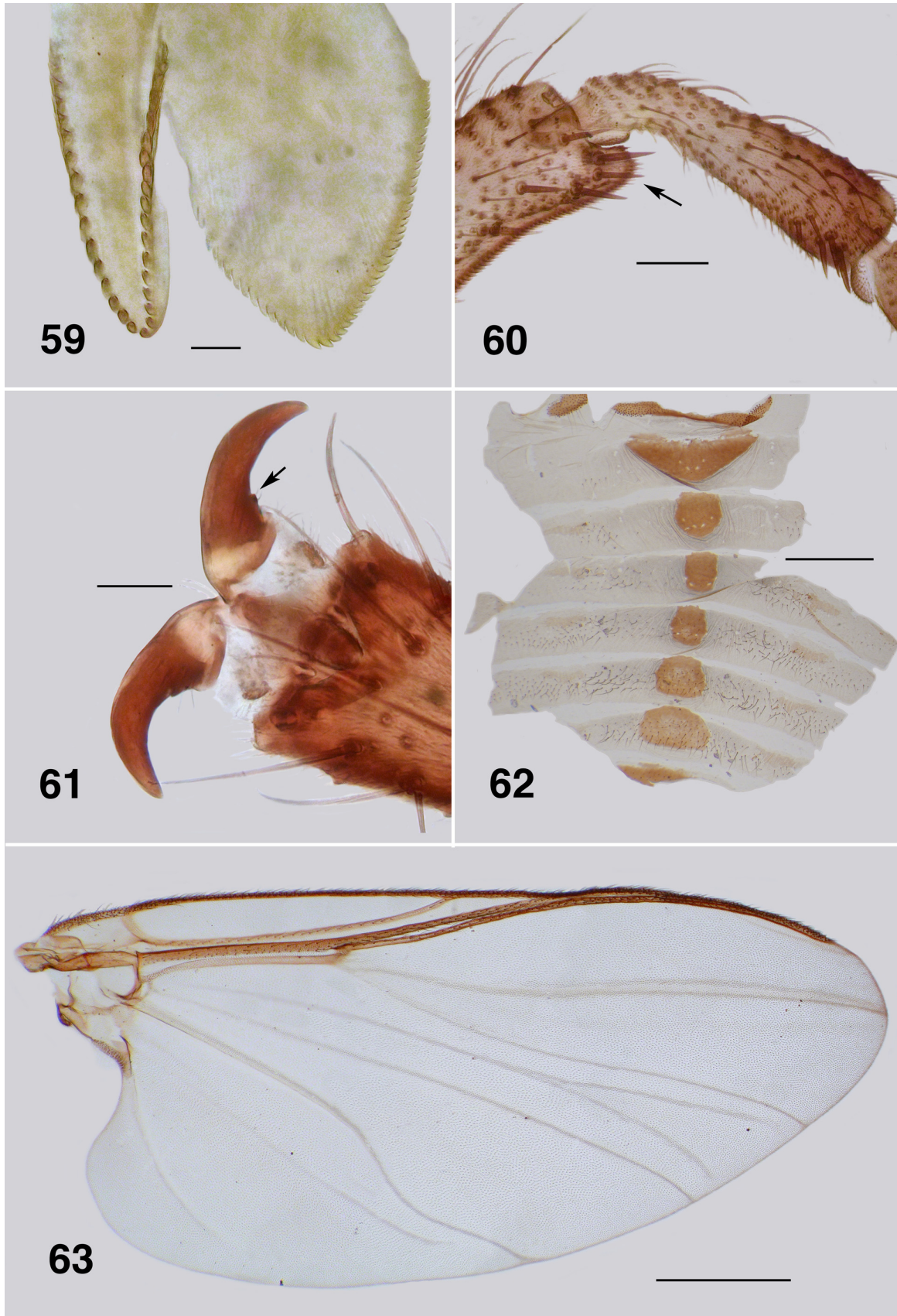
Nothogreniera, while sharing some character states with African *Paracnephia* (see de Moor 2017: 712), does not fit easily into any of the species-groups of that genus. The best fit would be in the *muspratti*-group (Crosskey 1969). Even there, however, at minimum, the terminal spines on the pupal abdomen of *Nothogreniera* are short and hooks are absent from sternite IV. No mention is made by Crosskey (*loc. cit.*) of extended antennae of larvae in any descriptions of *Paracnephia* species, or for that matter of any patterning on the distal antennomeres. That latter character state (Figs. 41, 75) is seen in segregates of *Greniera* (Adler *et al.* 2004: 280) and is certainly unique in Australian simuliids. Neither is there any mention for *Paracnephia s.s.* of the aggregation of stiff spines on the calcipala that Tonnoir (1925: 221, his Fig. 2 G), illustrated for *N. fergusonii*. This spine clump, at the time unique in Australian simuliids, is now known for *Bunyipellum gladiator* and also for undescribed species related to *Paracnephia umbrator*.

Further, in some species of the *muspratti*-group of *Paracnephia* the adult females lack teeth on the mandible—replaced with hairs, with males possessing an array of terminal spines on the gonostylus; character states markedly at variance to those in *Nothogreniera*.

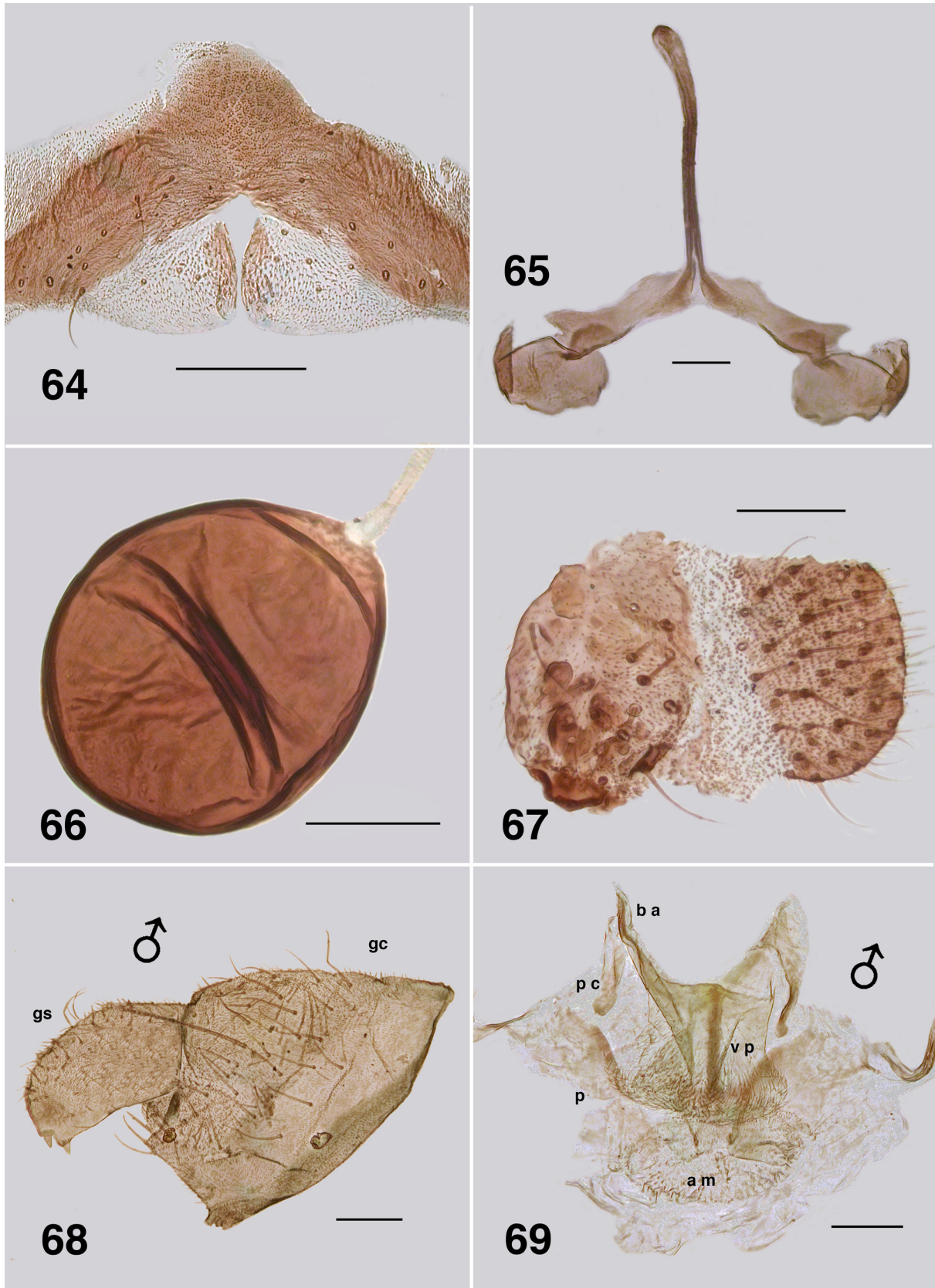
Nothogreniera is morphologically perhaps closer to South American *Araucnephia* or *Araucnephiodes* and is certainly of that grade of development. Nonetheless, *Nothogreniera* differs in a number of character states from those two genera, with *N. fergusonii* adults not keying out easily in those by of Wygodzinsky & Coscarón (1973: 141). Male genitalia match moderately well with those of *Araucnephia*, in particular the form the ventral plate and parameres (Wygodzinsky & Coscarón *loc. cit.*; Pessoa *et al.* 2012). Larvae have a similar arrangement of hypostomal teeth but differ in that *Nothogreniera* lacks rectal scales



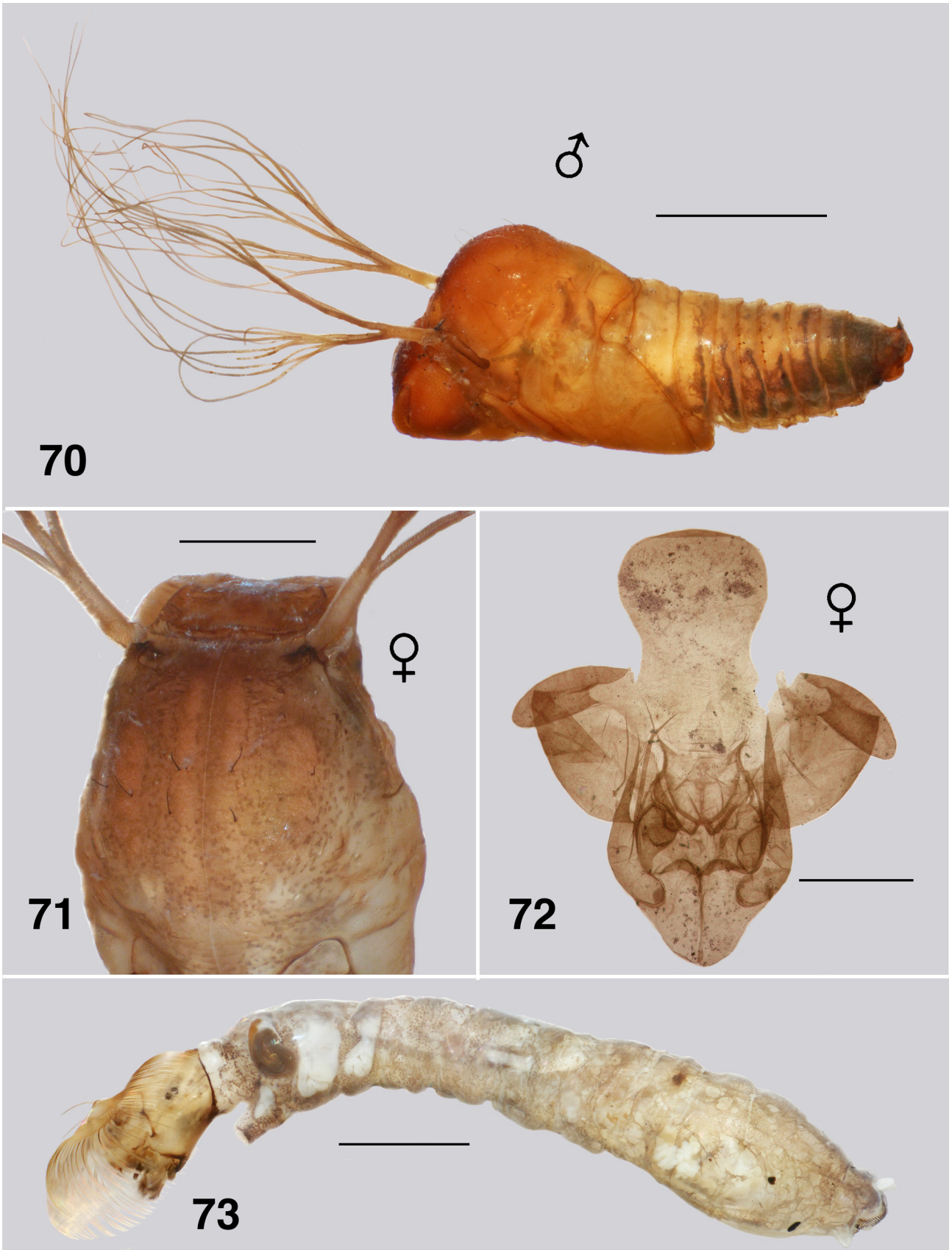
FIGURES 53–58. *Nothogreniera occidentalis* female. (53) Habitus. (Dryandra). Scale bar = 1.0 mm. (54) An original slide mount of *N. occidentalis* by Tonnoir. (55) Cleared head. (Dale River). Scale bar = 0.2 mm. (56) Antenna. (Dale River). Scale bar = 0.1 mm. (57) Cibarium (Dale River). Scale bar = 0.1 mm. (58) Maxillary palp & lacinia. (Dale River). Scale bar = 0.1 mm.



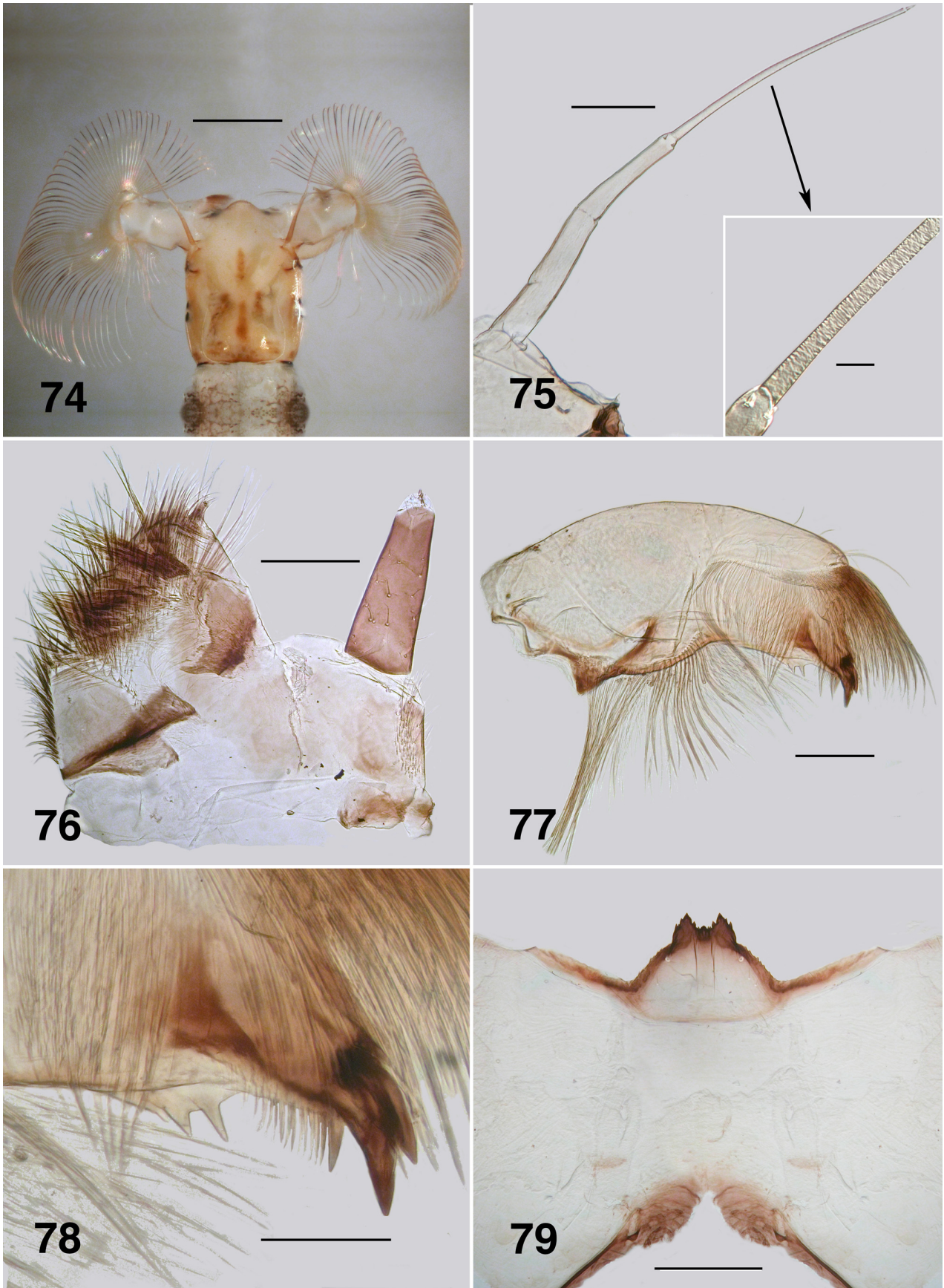
FIGURES 59–63. *Nothogreniera occidentalis* female. (59) Mandible & lacinia. Scale bar = 0.02 mm. (60) Hind basitarsus. (Dale River). Arrow indicates concentration of spines on minute calcipala. Scale bar = 0.05 mm. (61) Claw, paratype. Arrow indicates minute tooth. Scale bar = 0.02 mm. (62) Tergites. (Dale River). Scale bar = 0.5 mm. (63) Wing, paratype. Scale bar = 0.5 mm.



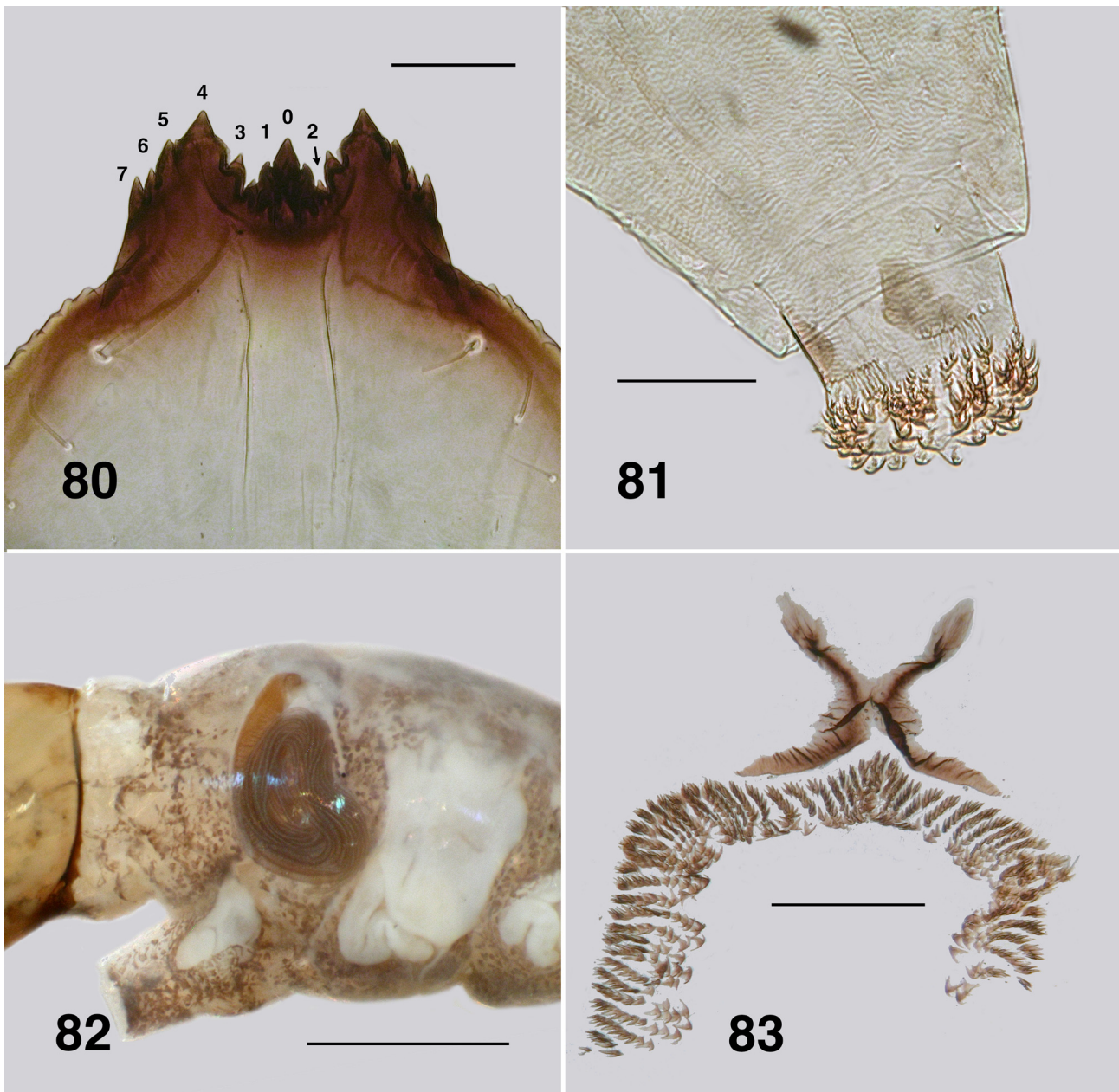
FIGURES 64–67. *Nothogreniera occidentalis* female. **FIGURES 68, 69.** Male. (64) Hypopygial valves. (Dale River). Scale bar = 0.1 mm. (65) Genital fork. (Dale River). Scale bar = 0.05 mm. (66) Spermatheca. (Bridgetown). Scale bar = 0.05 mm. (67) Anal lobe & cercus. (Bridgetown). Scale bar = 0.05 mm. (68) Gonocoxa & gonostylus. gc—gonocoxa; gs—gonostylus. Scale bar = 0.05 mm. (69) Genitalia, pharate specimen. Stained. a m—adeagal membrane; b a—basal arm; p—paramere; p c—paramere connector; v p—ventral plate. Scale bar = 0.05 mm.



FIGURES 70–72. *Nothogreniera occidentalis* pupa (Dale River). **FIGURES 73.** Larva. (70) Habitus of male pupa. Scale bar = 1.0 mm. (71) Dorsal view of thorax, showing dorsocentral setae. Scale bar = 0.5 mm. (72) Female cephalic capsule. Scale bar = 0.5 mm. (73) Habitus, last instar larva. Scale bar = 1.0 mm.



FIGURES 74–79. *Nothogreniera occidentalis*, last instar larva. (74) Head. Scale bar = 0.5 mm. (75) Antenna. Scale bar = 0.1 mm. Insert, DIC of distal article. Scale bar = 0.02 mm. (76) Maxilla. Scale bar = 0.1 mm. (77) Mandible. Scale bar = 0.1 mm (78) Mandible tip. Scale bar = 0.05 mm. (79) Postgenal cleft & hypostoma. Scale bar = 0.2 mm.



FIGURES 80–83. *Nothogreniera occidentalis* last instar larva. (80) Hypostoma. Scale bar = 0.05 mm. (81) Anterior proleg, penultimate larva. Scale bar = 0.1 mm. (82) Lateral view of thorax, showing gill histoblast. Scale bar = 0.5 mm (83) Anal sclerite & circle of hooks. Scale bar = 0.2 mm

Wygodzinsky & Coscarón (1973) compared *Araucnephia* to Australian “*Cnephia*”, namely *strenua* (Mackerras & Mackerras) and *tonnoiri* (Drummond) and concluded that they were not co-generic—we agree. Gil-Azevedo (2010) in a phylogenetic analysis using morphological character states, showed (his fig. 1, page 265) *N. fergusoni* + *N. occidentalis* as sister taxa, albeit unresolved to other Southern Hemisphere genera. Moulton (2003: 47) referred to these two *Nothogreniera* species as “*Cnephia*” ‘S. x (east)’ and “*Cnephia*” ‘S. x. (west)’ respectively. In his strict consensus analysis from the 28S gene, these are sister species, unresolved to other Southern Hemisphere simuliids, in agreement with Gil-Azevedo above. However, a neighbour joining analysis (his Fig. 2B) using the EF-1 α nucleotides showed the two species as sister to *Greniera denaria* + *Mayacnephia* (now *Tlalocomyia*). *Greniera* is a Northern Hemisphere genus, as is one segregate of *Tlalocomyia*, another in Central America (Adler & Crosskey 2017: 120). The putative close relationship between *Nothogreniera*, *Greniera* and *Tlalocomyia* is in agreement with the expression of the larval hypostomal teeth and details of the male genitalia (e.g., Adler *et al.* 2004).

The spermatheca is an underutilized source of characters in phylogenetic studies of simuliids. Evans & Adler (2000) surveyed variation in a number of character states throughout the family, including (among other features) the degree of sclerotization at the junction of the spermathecal duct and the main body of the spermatheca, and the presence or absence of internal spicules (acanthae). A spermatheca with an unpigmented ring surrounding the junction of the duct was hypothesized to be plesiomorphic—the condition found in *Nothogreniera*. Evolutionary patterns of internal spicules are somewhat more complex, with Evans and Adler (*loc. cit.*) hypothesizing the independent acquisition or loss of spicules in certain taxa. Nonetheless, the presence of internal spicules is arguably in the ground plan of the Simuliini based on the presence of that state in *Nothogreniera* and several other primitive-grade simuliine genera including *Araucnephia*, *Araucnephioides*, *Cnesia*, *Cnesiamima*, *Gigantodax*, *Lutzsimulium*, and *Paraustrosimulium*.

On balance, the combination of characters states indicates that *Nothogreniera* should be considered a separate genus. The degree of expression of numbers of such states (*e.g.*, wing venation, calcipala expression, larval hypostoma) indicates a plesiomorphic grade of development.

The east/west distribution of sister species is a common pattern in Australian biota (*e.g.*, Thompson & Stillwell, 2010) and well exemplified for simuliids (*e.g.*, Mackerras & Mackerras 1949: 380, Craig *et al.* 2017, Craig *et al.* 2018). Such points to a vicariant event of Gondwanan age—likely the southern extension of the inland Eromanga Sea that broke through central-south Australia in the Early Cretaceous (*ca.* 145 mya), when Australia was separating from Antarctica, and which led to the formation of the Nullabor Plains, a major arid barrier for Australia biota. Certainly, Simuliidae were in Australia then; fossil larvae of clear simuliid gestalt are known from the Cretaceous Aptian stage (116 mya) (Jell & Duncan, 1986, Jell 2004).

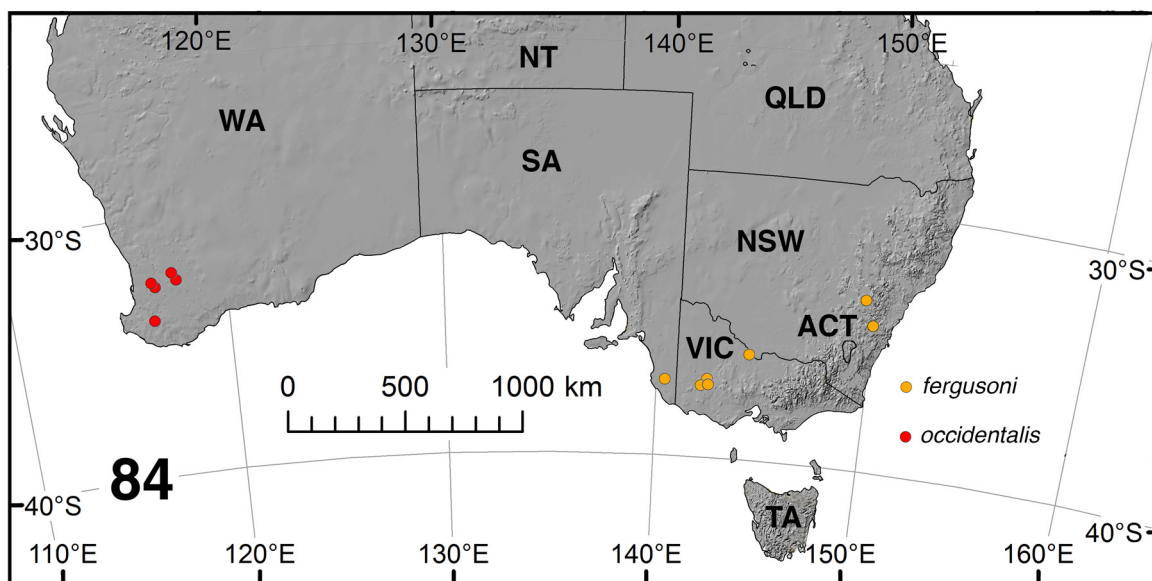


FIGURE 84. Map of southern part of Australia, showing distribution of *Nothogreniera*.

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