



A new genus, *Protaustrosimulium*, for four species of Australian black flies (Diptera: Simuliidae)

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Abstract

Protaustrosimulium n. gen. is described for four species: two previously named species from southeastern Australia—*Paracnephia pilfreyi* (Davies & Györkös 1988) and *Paracnephia terebrans* (Tonnoir 1925)—plus two newly described ones from the southwestern-most corner of Western Australia—*Prot. amphorum* n. sp. and *Prot. opscorum* n. sp. Molecular and morphological data suggest a close relationship between members of the new genus and *Austrosimulium* Tonnoir 1925. Monophyly of *Protaustrosimulium* is supported mainly by characters of adult females, as two of the four species are known only in that life stage. Two species groups are recognized: the *pilfreyi*-group for *Prot. pilfreyi* and *Prot. amphorum*, and the *terebrans*-group for *Prot. terebrans* and *Prot. opscorum*. The constituent species in each group are distributed vicariously in southeastern and southwestern Australia—a common biogeographical pattern in Australian simuliids.

Key words: Gondwana, Australia, Diptera, Simuliidae, *Cnephia*, *Paracnephia*

Introduction

This paper treats two enigmatic and little-known nominal species of “*Paracnephia*” Rubtsov 1962 from southeastern Australia, plus two undescribed species from Western Australia. “*Paracnephia*” *terebrans* (Tonnoir 1925)—although formally described nearly a century ago—is still only known from adult females collected at just six localities in New South Wales, Australian Capital Territory and Victoria. The apparent scarcity of this species is puzzling because its females have markedly developed mouthparts and are known to bite humans. Anthropophilic species are generally among the best known simuliids; and consequently, they are typically disproportionately represented in collections. “*Paracnephia*” *pilfreyi* (Davies & Györkös 1988) is somewhat better known in that all life-stages were described by its authors; however, as noted by Craig (2011), the type material was not properly curated and much of it (including parts of the holotype) was lost. That species is currently known only from the original type series in the Australian Capital Territory, plus DNA sequence data from one other locality in Victoria (Moulton, 2000, 2003). With so little high-quality material available for study, the relationships of these two species have long intrigued specialists of the Simuliidae.

Davies & Györkös (1988) suggested that “*Paracnephia*” *pilfreyi* was most closely related to the “*terebrans*-group” of Mackerras and Mackerras (1949, 1952), which at the time was a heterogeneous assemblage that included “*P.*” *terebrans*, a closely related undescribed species from Western Australia dubbed “sp. A.”, plus two more-distantly related species—“*P.*” *fergusoni* (Tonnoir) and “*fergusoni* var.” These latter two entities are now recognized as valid species in the recently described genus *Nothogreniera* Craig, Currie & Moulton 2018. Nonetheless, Davies & Györkös (1988) hypothesis of a close relationship between *pilfreyi* and *terebrans* is supported by unpublished molecular data of J.K.M.

Some authors have speculated about the broader relationships of the species under consideration. Mackerras

and Mackerras (1949), for example, noted the resemblance of their “*terebrans* group” to *Austrosimulium* Tonnoir 1925, based on the small size, dark colour and similarities in palpal and abdominal characters of the female. Moulton (2003) similarly noted morphological similarities between “*Paracnephia*” *pilfreyi* and *Austrosimulium*, although without mention of particular character states.

In this paper we describe the new genus *Protaustrosimulium* to accommodate “*Paracnephia*” *terebrans* and “*P*”. *pilfreyi* from southeastern Australia, plus two new species from Western Australia—each the vicariant sister species of one of the nominal eastern species. One of the new species corresponds with “*Cnephia* sp. A.” of Mackerras and Mackerras (1949: 385). The relationships of these species to each other are discussed, as are the relationships of *Protaustrosimulium* with other genera. This is the fifth in a series of papers (*i.e.*, Craig *et al.*, 2017, Craig *et al.*, 2018a, b, Moulton *et al.*, 2018) that revises the neglected and little studied Australian Simuliidae of Gondwanan provenance. With the description herein of a new genus, the number of recognized Australian genera now stands at eight: *Austrosimulium*, *Bunyipellum* Craig, Currie & Moulton 2018, *Ectemnoides* Moulton, Currie & Craig 2018, *Nothogreniera*, *Paracnephia* *s. lat.*, Rubtsov 1962, *Paraustrosimulium* Wygodzinsky & Coscarón 1962, *Protaustrosimulium* and *Simulium* *s. lat.* Latreille 1802.

Material and methods

Material for “*Paracnephia*” *terebrans* and “*Paracnephia*” sp. A, was from the Australian National Insect Collection (ANIC). Most of the original material for “*Paracnephia*” *pilfreyi* was lost, as described by Craig (2011: 4). In short, that material was never deposited in ANIC as stated by Davies & Györkös (1988: 107) and when recovered was in a poor state. Therefore, we rely heavily on the original description and illustrations. Details of the larva of “*P*”. *pilfreyi* are based in large part on new material from the Grampians National Park, Victoria.

Methods, terms and codens follow those of Craig *et al.* (2012), Craig *et al.* (2017) and Craig *et al.* (2018a). For designation of wing veins (*e.g.*, Fig. 30) we follow Cumming and Wood (2017). All images are by DAC, unless otherwise indicated.

Protaustrosimulium n. gen. Currie, Craig & Moulton

Type species: *Cnephia pilfreyi* Davies & Györkös 1988: 107.

Members of the *Protaustrosimulium terebrans*-group, as defined below (*i.e.*, *Prot. terebrans* and *Prot. opscurum* n. sp.) are known only as adult females. Accordingly, the following diagnosis is confirmed just for that particular life stage. Character states of males, pupae and larvae apply definitely only to members of the *Prot. pilfreyi*-group; however, a subset of these states may eventually prove to be diagnostic of the genus as a whole.

Diagnosis. *Female*: small, darkly coloured flies. *Head*: antenna with nine flagellomeres. Lateral cervical sclerites well expressed. *Thorax*: not markedly domed; katepisternal sulcus well defined and more or less complete anteriorly; katepisternum and anepisternal membrane bare. *Wing*: rather fumose, especially apically, with darkly pigmented veins; basal medial (bm) cell present, but minute (absent in male of *Prot. pilfreyi*); membrane surrounding r-m junction not markedly pigmented; a:b ratio *ca.* 1.0:2.8; Costa with short spinules interspersed among typical setae on apical half; vein Rs unbranched; R₁ and R_s closely approximated distally, confluent before junction with C; basal section of R haired; M₁ appears doubled distally; CuA slightly sinuous. *Legs*: basitarsus without row of stout spines ventrally; calcipala well developed, with base one-third to one-half width of hind basitarsus apex; pedisulcus present but variously expressed; tarsal claws smoothly and shallowly curved, with small basal tooth arising from medial side of claw, heel small to well expressed. *Genitalia*: spermatheca with pigmentation extended markedly onto apex of spermathecal duct (condition unknown in *Prot. opscurum*). *Male*: details of head, thorax and wing as described for females. *Genitalia*: gonostylus slightly shorter than gonocoxite, with three to five short apical spines; ventral plate trapezoidal shaped, with distinct median keel; paramere plate-like, subtriangular, with four long apical spines; aedeagal membrane with microtrichia; median sclerite deeply forked. *Pupa*: gill thin-walled and transparent, consisting of 6–10 short finger-like filaments; thoracic notum smooth, with typical array of setae; abdominal cuticle thin and lightly pigmented; pleurites absent; abdominal

armature sparse, with hooks present only on tergites V and VI; spine combs minute, present on tergites VI–IX; anchor-shaped hooks present on pleura of terminal abdominal segments; terminal spines minute. *Cocoon*: shoe-shaped or slipper-shaped, without anterior rim, constructed of fine loosely woven silk covering most of pupa. *Larva*: antenna extended well beyond apex of labral fan base; article length ratio (basal:medial:distal) *ca.* 3:1:7; basal and medial articles relatively thick and brown, distal article relatively thin (*ca.* one-third width of other articles) and hyaline; cervical sclerites not fused to postocciptus; hypostoma with apical teeth not arranged on prominent lobes; teeth partially covered by ventral wall of hypostoma; tooth 0 and 4 most prominent; lateral serrations absent; postgenal cleft virtually absent, represented at most by narrow inverted-V shaped notch; abdomen with ventral tubercles well expressed; anal sclerite X-shaped, interarm struts absent; accessory and semicircular sclerites present; rectal papillae of three simple lobes.

Distribution. Australia; with species distributed vicariously in New South Wales, the Australian Capital Region and Victoria in the southeast, and Western Australia in the west.

Etymology. In reference to the apparent close relationship between the species under consideration to *Austrosimulium*, *Paraustrosimulium* and *Cnesiamima* Wygodzinsky & Coscarón 1973.

Constituents. *Protaustrosimulium pilfreyi* (Davies & Györkös) **n. comb.** *Prot. amphorum* **n. sp.**, *Prot. terebrans* (Tonnoir) **n. comb.**, and *Prot. opscurum* **n. sp.**

Discussion. *Protaustrosimulium* n. gen. is here established for four species of Australian black flies that share a close relationship with *Austrosimulium*, *Paraustrosimulium*, and *Cnesiamima*. They share with *Austrosimulium* a markedly similar wing venation, wherein R_1 and R_5 are closely approximated distally, becoming confluent before joining the costa. (*e.g.*, Figs. 29, 30). This state is clearly synapomorphic for members of these two genera, as R_1 and R_5 join the costa separately in *Paraustrosimulium*, *Cnesiamima* and all other simuliids. The wings of all four genera have a similar a:b ratio (*i.e.*, they all have a relatively short basal radial (br) cell that extends *ca.* one fourth length of wing as measured from cell base) and possess a small but distinct basal medial (bm) cell. Although the immature stages are unknown for members of the *terebrans*-group, larvae and pupae of the *pilfreyi*-group share a number of synapomorphic character-states with *Austrosimulium*, *Paraustrosimulium* and *Cnesiamima*. One such state is the elongate distal antennal article of larvae, which is two times or more the length of the basal and medial article combined. The hypostoma of the four genera are also similar in that their apical teeth are not grouped on prominent lobes and further are partially covered by the ventral wall of the hypostoma (*e.g.*, Fig. 16). Another character-state shared between *Protaustrosimulium* and *Austrosimulium* *s. str.* (but not by *Austrosimulium* (*Novaustrosimulium*), *Paraustrosimulium* and *Cnesiamima*) is presence of accessory and semicircular sclerites on the posterior proleg of larvae. Although similar structures occur elsewhere in the Simuliidae, such as in *Parasimulium crosskeyi* Peterson, *Gigantodax* Enderlein, *Simulium* (*Gomphostilbia*) *palauense* Stone (Takaoka & Craig, 1999) and *Crozetia* Davies (Craig *et al.*, 2003) they are likely to be independently evolved based on marked differences in their expression. As shown by Craig *et al.* (2012: 285), a clear ring of cuticle surrounds and supports the cirlet of hooks, and while parts of the ring may be darkly pigmented, as is the case in most *Austrosimulium* species and members of the *Prot. pilfreyi*-group (Figs. 21, 66), the structure is actually present in all simuliid larvae examined. The semicircular sclerite then, when expressed, is merely pigmentation of the ring. Accordingly, while this underlying cuticle is homologous across the Simuliidae, its expression, when sclerotized and pigmented, is subject to homoplasy. Nonetheless, the form of the accessory and semicircular sclerites is markedly similar in members of the *pilfreyi*-group and *Austrosimulium* *s. str.*, perhaps suggesting a common origin. Pupae of *Protaustrosimulium*, *Austrosimulium*, *Cnesiamima* and *Paraustrosimulium* are similar in that their abdominal armature is weakly expressed, the terminal spines are minute (Fig. 55), and the pleura of the terminal segments are endowed with anchor- or grapnel-shaped hooks. Finally, the hind basitarsus of female *Protaustrosimulium*, plus those of *A. australense* and members of the *A. unguatum* species-group, lack a row of stout setae that runs parallel to the comb in other simuliids (Craig *et al.*, 2012: 54). This character state either provides further evidence of a close relationship between *Protaustrosimulium* and *Austrosimulium*, or perhaps represents a synapomorphy (albeit a homoplasious one) of the new genus.

Although *Protaustrosimulium* shares many of the above-mentioned features with *Austrosimulium* and *Paraustrosimulium*, it lacks synapomorphies that link those latter two genera together. For example, *Protaustrosimulium* has nine (as opposed to eight) antennal flagellomeres, and lacks (as does *Cnesiamima*) interarm struts on the anal sclerite. *Protaustrosimulium* can be further distinguished from *Austrosimulium* in lacking the following autapomorphies of that genus; namely, *Protaustrosimulium* females have serrations on both

sides of the mandible (as opposed to just on the inner side), and their pupae have spine combs on abdominal tergites VI–VIII (as opposed to lacking spine combs altogether). In summary, the character state distribution in *Protaustrosimulium* is muddled, with different sets of relationships suggested depending on how characters are interpreted. Arbitrary assignment of the species in question to either *Austrosimulium* or *Paraustrosimulium* would render diagnosis of those genera difficult. We therefore prefer to recognize a new genus in order to maintain current generic concepts as far as possible. An alternative approach would be to recognize just a single Austral genus—*Austrosimulium s. lat.*—with five subgenera, viz., *Austrosimulium s. str.*, *Novaustrosimulium*, *Paraustrosimulium*, *Cnesiamima* and *Protaustrosimulium*. However, as noted above, marked structural disparity among included taxa would make generic diagnosis difficult.

While it is clear that *Protaustrosimulium* shares an immediate common ancestry with *Austrosimulium*, *Paraustrosimulium*, and *Cnesiamima*, monophyly of the new genus is less certain—mainly because adult females are the only life stage known for all four species. One possible synapomorphy is a spermatheca with pigmentation extended markedly into the apex of the spermathecal duct. Unfortunately, however, the spermatheca of *Prot. opscurum* is unknown, and this particular state is variously expressed in other simuliids, including *Cnesiamima* and *Paraustrosimulium*. Males and immature stages of the *terebrans*-group are needed to more fully assess monophyly of *Protaustrosimulium* as here defined.

The distribution of *Protaustrosimulium* (Fig. 99), with sister species split between southern Western Australia and the southeastern States, follows closely that of the other Gondwanan simuliid taxa. This, as discussed by Craig *et al.* (2017, 2018a, 2018b) and Moulton *et al.* (2018) likely involved inundation of the Nullarbor Plain area by the Eromanga Sea during the Eocene and Miocene, and subsequent desertification.

***pilfreyi*-group.** Genital fork with rod-like anterior arm and membranous lateral region (Figs. 5, 35).

Constituents. *Protaustrosimulium pilfreyi* (Davies & Györkös 1988) and *Protaustrosimulium amphorum* n. sp.

***Protaustrosimulium pilfreyi* (Davies & Györkös 1988). New combination**
(Figs. 1–21)

Cnephia pilfreyi Davies & Györkös 1988: 107.

pilfreyi. Crosskey, 1989: 222. Unplaced species of Prosimuliini.

Paracnephia pilfreyi. Crosskey & Howard, 1997:18. New combination. Bugledich, 1999: 328.

"*Cnephia*" *pilfreyi*. Moulton, 2000: 98. Moulton, 2003: 47.

Paracnephia pilfreyi. Adler & Crosskey, 2008: 26. Transferred to Simuliini.

Redescription (based in part on original description by Davies & Györkös 1988: 106).

Adult female. *Body:* total length 2.5–2.7 mm. *Head* (Fig. 1): medium orange brown with silvery concolourous adpressed hair; width 0.80 mm; depth 0.70 mm; 0.75× width of thorax; frons sub-parallel, broadening markedly dorsally; frons:head ratio 1.0:6.1, frontal angle 70°. *Eye:* interocular distance ca. 0.13 mm. *Antenna:* evenly medium orange brown, tapering distally, total length ca. 5.6 mm; scape, pedicel and basal flagellomere 1.5× longer than broad, apical flagellomere IX, twice as long as others. *Mouthparts:* maxillary palpus, pale brown, apical palpomere V elongated; proportional lengths of III–V palpomeres 1.0:1.0:1.5; sensory organ moderately elongated, 0.33× length of palpomere III, opening large, round, 0.6× vesicle width; mandible with ca. 55 poorly developed inner teeth, smaller proximally, 18 outer teeth; lacinia with 16 and ca. 24 teeth on inner and outer edge respectively; cibarium details not known. *Thorax:* length not known; scutum medium even brown with three darker vittae; scutellum light brown medially, scutellar depression with long brown hairs; postnotum medium brown, bare; anepisternal (plural) membrane without hairs; katepisternum longer than deep, sulcus distinct. *Wing:* length 2.6 mm, width 1.3 mm; a:b ratio 1:3; disposition of apices of R₁ and R_s before joining C not recorded; short spinules mixed with setae on distal vein C, but not R, basal section of R haired, R_s simple, S_c haired ventrally, vein CuA slightly curved, A₁ ending near wing margin; basal (bm) cell present. *Haltere:* very pale brown, becoming whitish distally in some specimens. *Legs:* Fore leg and mid leg: coxa and trochanter medium brown (except anterior trochanter surface); femur and tibia light brown darkened slightly at ends and along anterior tibial margin, tarsus

medium brown; fore basitarsus narrow, cylindrical, width:length ratio 1:9. Hind leg (Fig. 2): and trochanter medium brown, rest of leg light brown except basal tip and distal end of femur, basal and distal quarter, anterior edge of tibia, basal and distal quarter of basitarsus, distal half of second tarsal segment and rest of tarsus dark brown, with fine adpressed concolourous hair except long medium-brown erect hairs on anterior tibial edge; hind basitarsus wider than fore basitarsus, but sides subparallel, width:length ratio 1.0:5.2; calcipala (Fig. 3): 1/2 width of basitarsus apex and as wide as long; pedisulcus as wrinkled cuticle; tarsomere II 4× longer than apical width; claw finely tapered with minute basal tooth on inner surface, heel not markedly expressed (Fig. 4). Small intersegmental sclerites between basitarsus and next two tarsal segments, well expressed. *Abdomen*: basal scale (tergite I) pale brown except medium brown edge, covered with fine concolourous hair but with long posterodorsal erect hairs. Dorsum of segment II with large, medium-brown tergite (0.75× abdominal width), segments III & IV with tergites half abdominal width (tergite III medium brown); segments IV–VIII uniformly pale brown; hairs shorter, lighter and finer on tergites II–IV than for rest of dorsum; ventral surface without sternites. *Genitalia* (Fig. 5): hypogynial valves bluntly triangular with medial edges slightly convergent distally; genital fork anterior arm with anterior third slightly expanded; posterolateral arms plus plate subequal in length to anterior arm. Spermatheca elliptical (length:width ratio 1.4:1.0), darkly pigmented and smooth; presence of internal spines (acanthae) unknown; spermathecal duct with pigment extended for short distance. Cercus (Fig. 6) as wide as long, smoothly rounded, anal lobe small with minute central depression.

Male (based on original description). *Body*: colour not given. *Head*: width 0.85 mm. *Eyes*: upper ommatidia diameter 0.034 mm, *ca.* 16 across and 20 down. *Clypeus*: medium brown; vestiture of long concolourous hairs. *Antenna*: total length not given; pedicel swollen, 1.3× wider than first flagellomere. *Mouthparts*: maxillary palpus, palpomere V 1.4× longer than palpomere IV, sensory vesicle small, spherical, occupying 0.2× length of palpomere III, opening 0.33× vesicle width. *Thorax*: width 0.7 mm, medium brown with three dark brown vittae; scutellum light brown, anepisternal membrane without hairs, katepisternum browner, sulcus distinct. *Wing*: length 2.3 mm, width 1.3 mm; short spinules mixed with hairs on vein C, but not R₁ with; basal section of R haired, R_s simple, S_c with ventral hair; CuA and A₁ curved; basal cell absent. *Haltere*: stem mainly translucent to yellowish white opaque, knob yellowish white. *Legs*: pale brown except medium brown at both ends of femur and tibia, and at basal end also on anterior margin of hind basitarsus. Fore basitarsus narrow, cylindrical, width:length ratio 1:8; hind basitarsus somewhat flattened, width:length ratio 1:5; calcipala pronounced. *Abdomen*: basal scale medium greyish brown with margin and long bordering hairs pale yellowish; distal edges of tergites II–V medium greyish brown, narrowing on posterior segments with tergite VI only half width of tergum; sides of abdomen medium to dark brown becoming paler on sterna. *Genitalia*: Lost, but observation prior to that indicated the gonocoxa and gonostylus were subequal in length; gonocoxa a truncate cone slightly narrower distally; gonostylus curved medially with 4 or 5 short spines distally on inner margin.

Pupa. (based on original description) *Body*: length *ca.* 4.0 mm. *Head*: facial and epicranial setae present, the latter closely applied beside antennal sheath. *Thorax*: no details given for cuticle; scutum with three dorsocentral setae. *Gill*: six filaments (original description, Fig. 7), eight (Grampians, Fig. 19), translucent, thin-walled, inflated; original with three main trunks, anterior one extended horizontally beyond head, with distal upturn, posterior one usually extended horizontally to abdominal segment VII, ventral pair of filaments on short base, two other filaments arising individually near base; Grampians (based on pharate specimen) with short basal trunk, giving rise to single thick filament, three short petioles giving rise each to two filaments, with single filament arising directly from base, no distinct annulations, surface with normal array of trabeculae. *Abdomen*: armature, tergites I, II, with posterior row of simple hairs, tergite V with one posterior hair, tergites III, IV with posterior row of 4 abruptly tapered hooks, tergites I–IV also with single hair laterally, tergites VI–VIII with fine spine-combs, tergites IX with four grapnel hooks, terminal spines straight, conical, pointing anterodorsally, plus two dorsal hairs; sternites IV–VI with one small medial spine and two lateral finer hairs on sternite V, sternites VI & VII with median membranous area; pleurites absent.

Cocoon (specimens damaged). Apparently shoe-shaped, not completely covering pupa, finely woven without anterior rim, connected ventrally at collar (Fig. 8).

Larva (based on original description and new material). *Body* (Fig. 9): total length 5.6–7.0 mm, colour pale without segmental markings. *Head* (Fig. 10): overall colour moderate brown, darker medially, head spot pattern lightly positive; length 0.75 mm, maximum width 0.53 mm; distance between antennal bases 0.48 mm; head widest at stemmata, lateral margins convex, more so posteriorly; cervical sclerites weakly sclerotized, but distinct and not

connected to postocciptus. *Antenna* (Fig. 11): extended well beyond labral fan stem; total length 0.65 mm, including elongated apical sensillum, basal and medial articles concolourous medium brown; medial article markedly shorter than basal article, distal article markedly elongated, clear, proportional lengths of basal, medial, and apical articles 1.0:0.25:2.5. *Labral fan*: stem broad, not markedly pigmented, light brown in early last instar larvae, *ca.* 50 (original description) and 70 (Grampians material) fine pale rays, length 0.9 mm, mid-ray width 0.007 mm; microtrichial pattern of one longer with five shorter between. *Maxilla* (Fig. 12): not markedly pigmented; palpus elongated and curved, 2.8× as long as basal width; hair tuft at base of palp poorly developed. *Mandible* (Figs. 13, 14): not markedly pigmented; brushes finely expressed; outer teeth *ca.* half length of larger apical tooth; subapical teeth poorly expressed; *ca.* 10 fine spinous teeth, two sensilla with marked bases, serration barely evident; blade region long and slightly concave. *Postgenal cleft* (Fig. 15): essentially absent, minute, slot-shaped; posteroventral muscles spots obvious; ratio of hypostoma: genal bridge: postgenal cleft 1.0:6.0:3.0. *Hypostoma* (Fig. 16): dome-like; tooth 0 (median) and 4 (lateral), subequal in length, teeth 1–3 small and largely obscured by edge of hypostoma, teeth 5 & 6 small, tooth 7 occasionally present; lateral serrations absent; hypostoma sloped smoothly laterally to edge of genae; 6–8 markedly fine hypostomal setae on each side. *Thorax* (Fig. 17): pale; the immature pharate pupal gill shows poorly, filaments indistinct. *Prothoracic proleg*: not markedly developed, lateral sclerite narrowed (Figs. 17, 18). *Abdomen*: markedly pale anteriorly, light orange posteriorly, narrow anteriorly with segmental expansions; markedly expanded laterally at segment VI, smoothly tapered posteriorly, amphora-shaped laterally. *Ventral tubercles*: well expressed. *Rectal papillae*: three simple lobes, well developed. *Anal sclerite* (Figs. 20, 21): anterior and posteroventral arms subequal in length, former with basal flange, median region not markedly developed, interarm struts absent; accessory sclerites well developed, extended slightly as semicircular sclerite (Grampians), apparently not so in typical material, clear basal cuticular sclerite underlying circlet of hooks visible, fully sclerotized semicircular sclerite absent. *Posterior circlet*: numbers of hooks *ca.* 85 rows of hooks, 14 per row (total *ca.* 1,200).

Etymology. Named by Davies & Györkös (1988: 111) for Ron Pilfrey, who collected the original material.

Types. *Holotype.* Davies & Györkös (1988: 107) designated a reared female in ethanol as the holotype, with exuviae and parts mounted on slides. However, as noted previously, this material was never deposited in the Australian National Insect Collection (ANIC). Of the material recovered by Craig (2011) and now deposited in ANIC, just three legs and the head minus the labellum remain; all now in glycerine in a pinned microvial. Label data: [HOLO/ TYPE] [*Paracnephia/pilfreyi*] [AUSTRALIA, ACT/ Tidbinbilla Rd/ S35.4200° E148.9400°/ 15-ix-1964/ Coll. R. Pilfrey].

Paratypes. Little was recovered of the paratype adults, pupae and larvae originally designated by Davies & Györkös (1988: 107). The following material is stored in glycerine in pinned microvials, as follows: a pupal gill histoblast, a larval mandible plus hypostoma, a single complete immature larva, and a single mature last instar larva. Other material is mounted on slides: two male pupal exuviae, two female pupal exuviae, and a single last instar larval anal sclerite. Label data: as above, but with [Paratype]; all in ANIC.

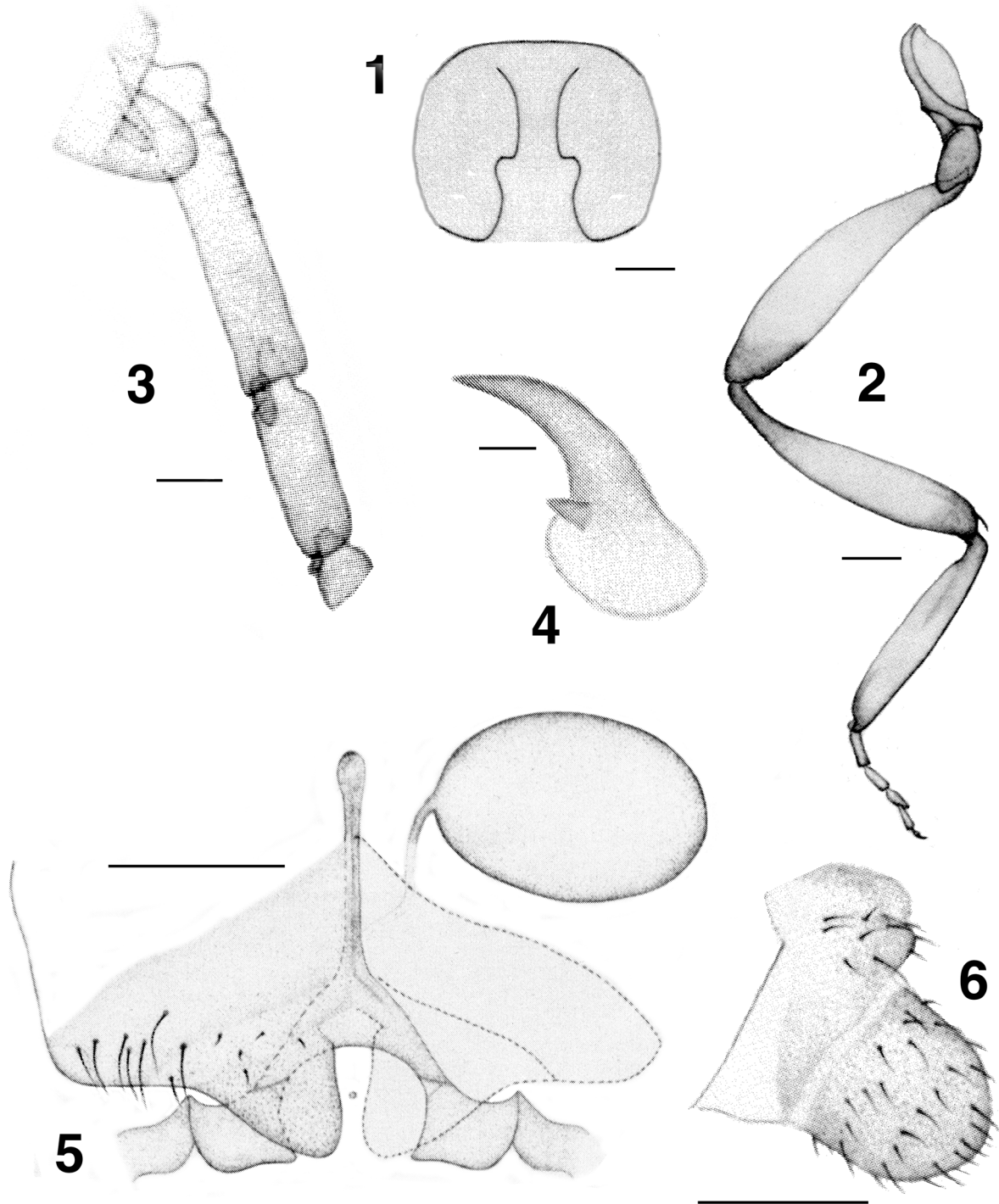
Additional material. Early last instar larvae of *Prot. pilfreyi*. [AUSTRALIA VIC./ Grampians National Park/ Small tributary of Glenelg/ River, ex. Glenelg River. Rd./ 26 September 1996/ Coll. J.K. Moulton], (*ca.* S37.2500° E142.4200°, elev. 226m.). (ETOH: UASM# 370857), (Slide: UASM# 370929) and personal collection of JKM.

The whereabouts of immature larvae collected by R. Pilfrey from an intermittent stream draining into Paddys River, ACT (Davies & Györkös, 1988: 107) is unknown.

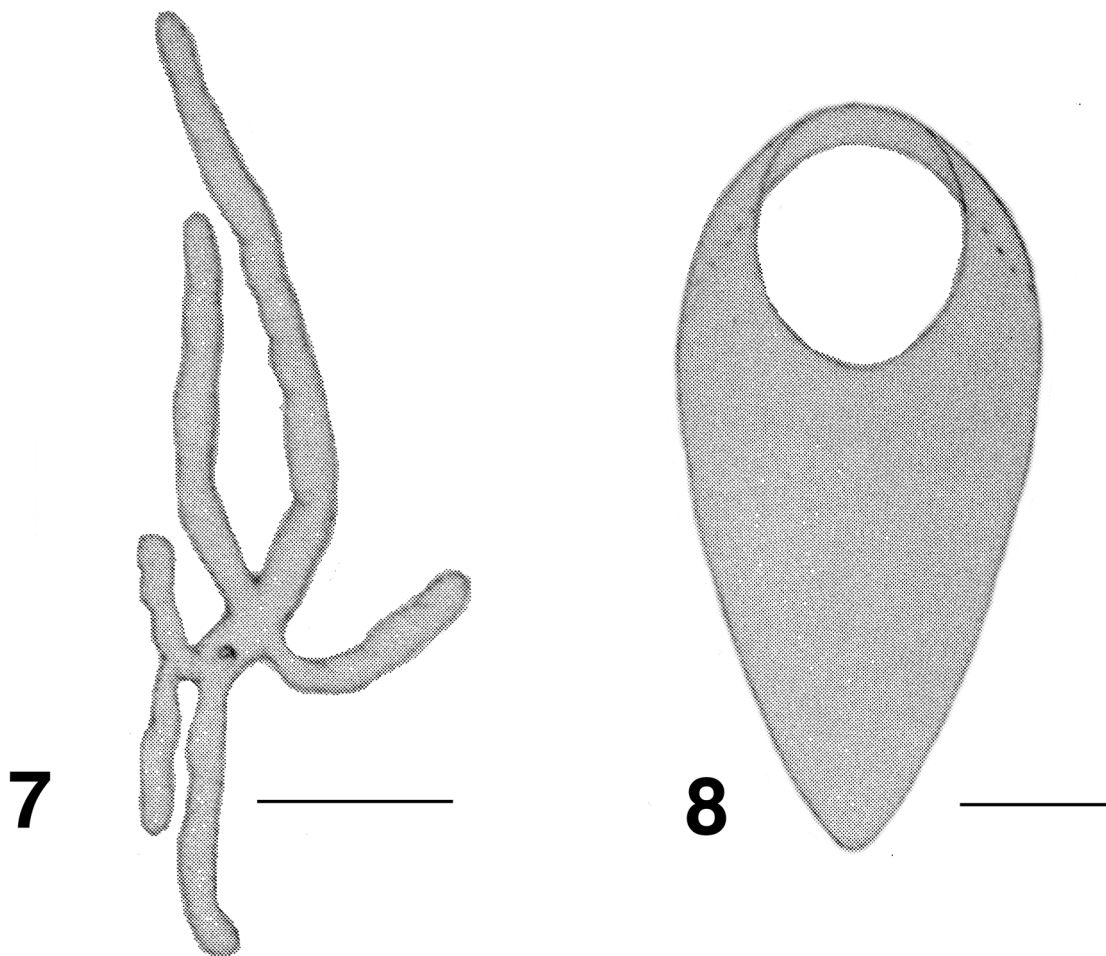
Distribution (Fig. 99). *Australian Capital Territory.* Davies & Györkös (1988: 107) listed four localities in the Tidbinbilla Road region, south of Canberra; namely a trickle above Tidbinbilla Road draining into Paddys River (*ca.* S35.4200° E148.9400°, elev. 670m., 15-ix-1964); Gibraltar Creek (S35.4500° E148.9785°, elev. 667m., 10-ix-1964); Oakey Creek (S35.4145° E148.9456°, elev. 650m., 1-x-1966) and a temporary stream draining into Paddys River (28-vii-1964, 21-ix-1966, 5-x-1966). *Victoria.* Grampians National Park, Glenelg River Road, small tributary of Glenelg River, 26 September 1996. Coll. J.K. Moulton (*ca.* S37.2500° E142.4200°, elev. 226m.).

Bionomics. Little is known about the biology of *Protaustrosimulium pilfreyi*. Attempts were made in 2011 and 2014 to recollect material from Gibraltar Creek (Fig. 97) and the creek at Oakey Farm (Fig. 96); however, no specimens of *Prot. pilfreyi* were recovered—even though the season corresponded with Pilfrey's original collections in 1964 and 1966. Oakey Creek yielded *Austrosimulium (Novaustrosimulium) furiosum* (Skuse), *A. (A.) crassipes* (Tonnoir), and *Simulium (Nevermannia) ornatipes* (Skuse), while Gibraltar Creek yielded *A. (N.) victoriae* (Roubaud) and "*Paracnephia*" *orientalis* (Mackerras & Mackerras). This latter creek is larger and less

ephemeral than the originally described localities (e.g., "trickles crossing Paddy's Road") and the Oakey Farm creek (cf. Figs. 96 & 97). Davies & Györkös (1988) noted that D.G. Bedo attempted to find more *pilfreyi* material in 1985 and 1986, but he too was unsuccessful. Dates given in Davies & Györkös (*loc. cit.*: 107) indicate that *Prot. pilfreyi* is a late Austral winter/early spring species, as are many of the Gondwanan Australian species. This agrees well with the seasonality of the *Prot. pilfreyi* population from Grampians National Park.



FIGURES 1–6. *Protostomus pilfreyi*. Female adult. (Modified from Davies & Györkös 1988: 106). (1) Frontal view of head. Scale bar = 1.0 mm. (2) Hind leg. Scale bar = 0.2 mm. (3) Calcipala & tarsomere II. Scale bar = 0.05 mm. (4) Claw & basal tooth. Scale bar = 0.05 mm. (5) Genitalia (spermatheca, genital fork, hypognial valves). Scale bar = 0.1 mm. (6) Cercus & anal lobe; lateral view. Scale bar = 0.1 mm.

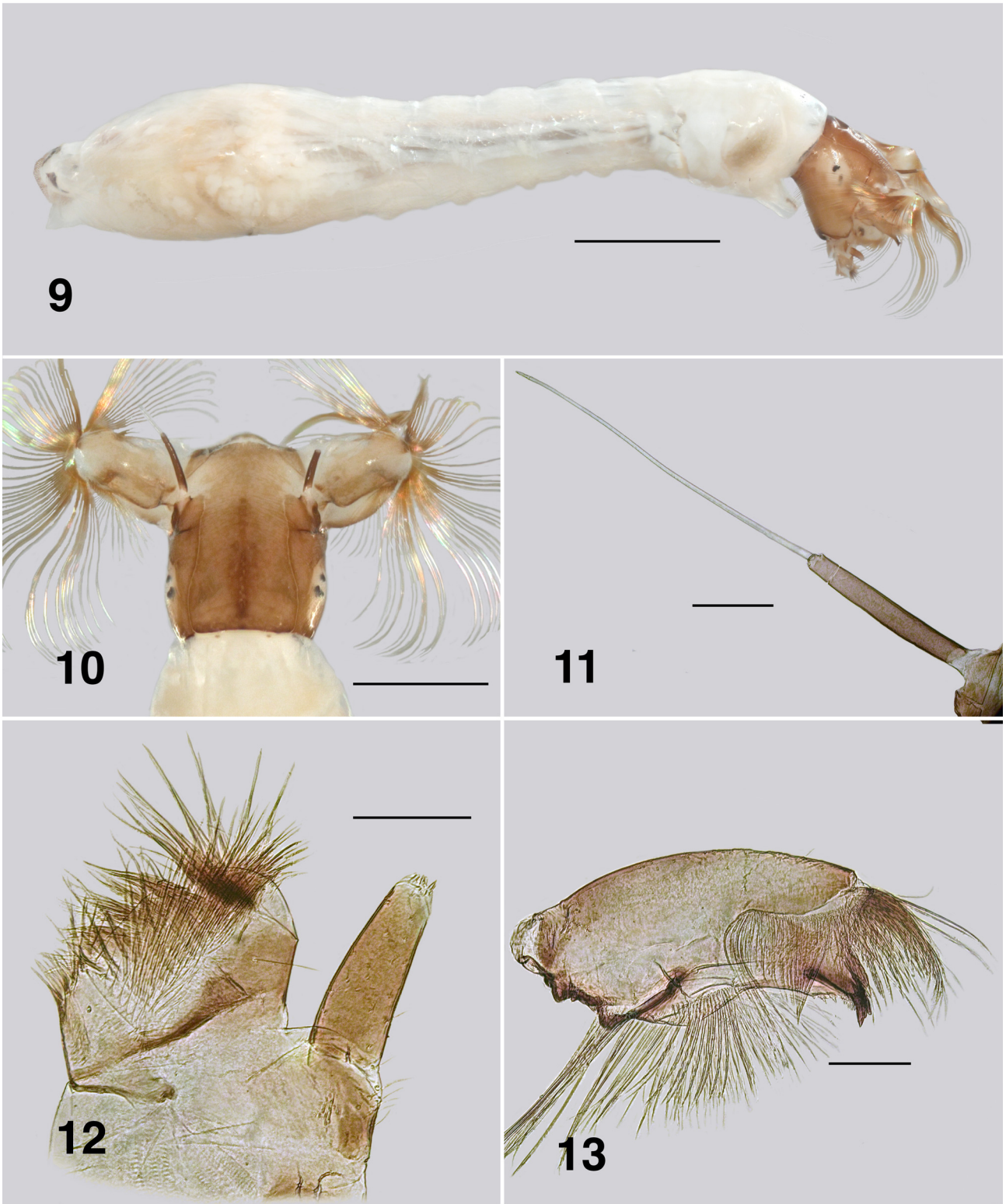


FIGURES 7, 8. *Protostrobus pilfreyi*. Pupa. (Modified from Davies & Györkös 1988: 107). (7) Frontal view of gill. Scale bar = 0.1 mm. (8) Dorsal view of cocoon. Scale bar = 0.1 mm.

Tidbinbilla Road is now a fully paved thoroughfare and any water crossing the road flows through a culvert. Agricultural impacts on the surrounding land appear considerable. Similarly, climate change for the Australian Capital Territory (ACT) has seen maximum temperatures increasing since the 1950's, with a concomitant decrease in spring rains. Indeed, the Oakey Farm creek when visited in early October, 2014, was dry. There were serious droughts in the early 2000's and major fires in the Tidbinbilla region during January, 2003. In short, it is possible that *Prot. pilfreyi* no longer exists in the Tidbinbilla area. The only other known locality for this species is Grampians National Park, Victoria; however, exact coordinates are unknown. Given the general warming trend in the region, perhaps collection efforts should be made earlier in the year.

Remarks. The latitude and longitude (35° 26'S 142° 56'E) given for the type locality of *Prot. pilfreyi*, by Davies & Györkös (1988: 107) is incorrect; the degrees longitude should be 148° and such corrected coordinates (35° 26'S 148° 56'E) place this near the Tidbinbilla Nature Reserve (a National Park since 1962). The spelling "Oakley Ck" for one locality is incorrect and should be "Oakey". The property on which the original collections were made still existed at the time of writing and is named "Oakey Farm".

While there is good concordance between the Australian Capital Territory (Davies & Györkös, 1988) and the Grampians larval material described here, differences in pupal gill filament, labral fan ray numbers and accessory sclerites of the larvae are suggestive of a species complex. Indeed, the Grampians larvae are more similar to those of the Western Australian species *Prot. amphorum* than they are to typical larvae. More material of *Prot. pilfreyi* is clearly needed.



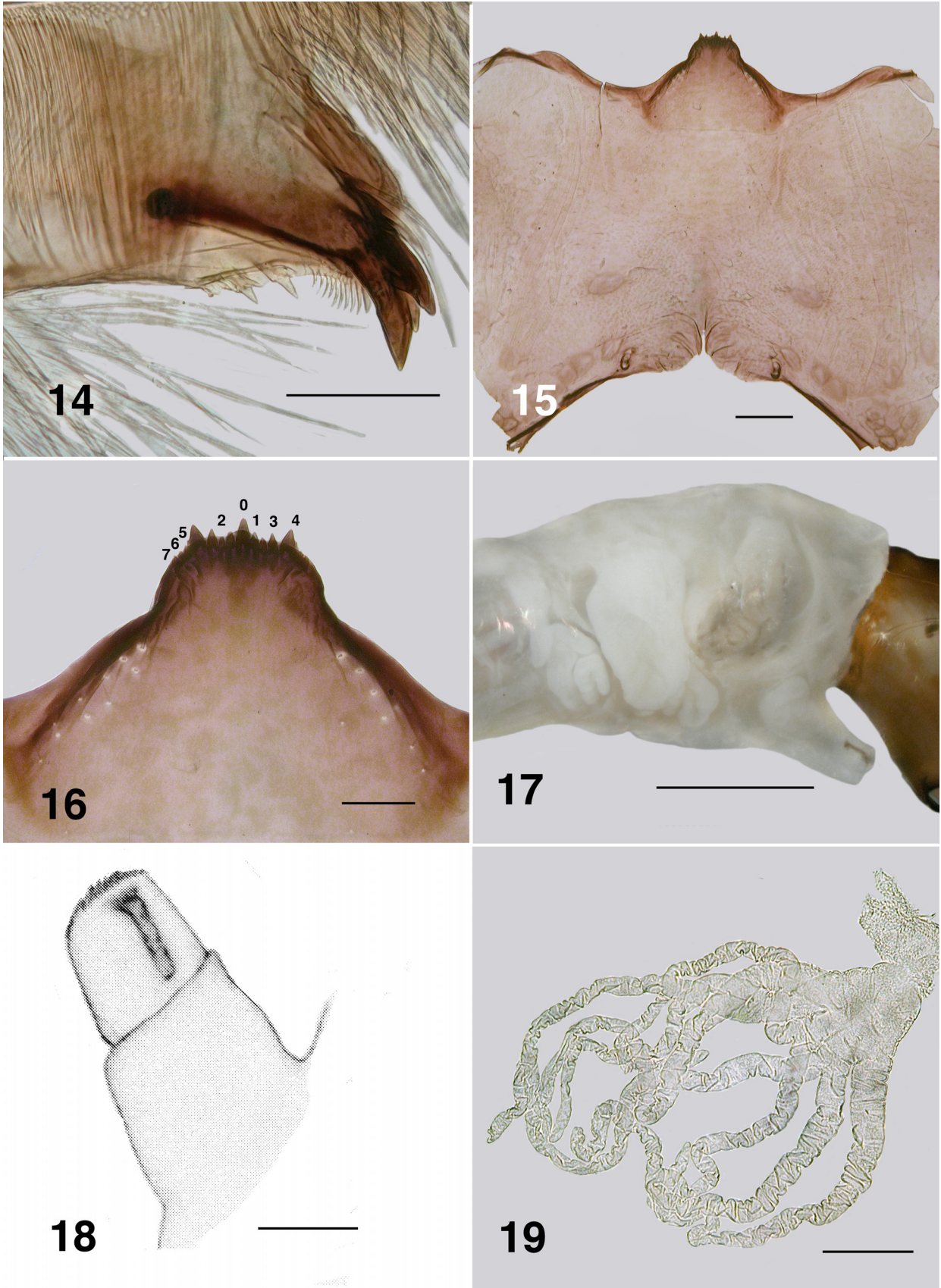
FIGURES 9–13. *Prot austrosimulium pilfreyi*. Last instar larva (Grampians). (9) Habitus. Scale bar = 1.0 mm. (10) Dorsal view of head. Scale bar = 0.5 mm. (11) Antenna. Scale bar = 0.1 mm. (12) Maxilla. Scale bar = 0.1 mm. (13) Mandible. Scale bar = 0.1 mm.

***Protaustrosimulium amphorum* Currie, Craig & Moulton. n. sp.**

(Figs. 22–66)

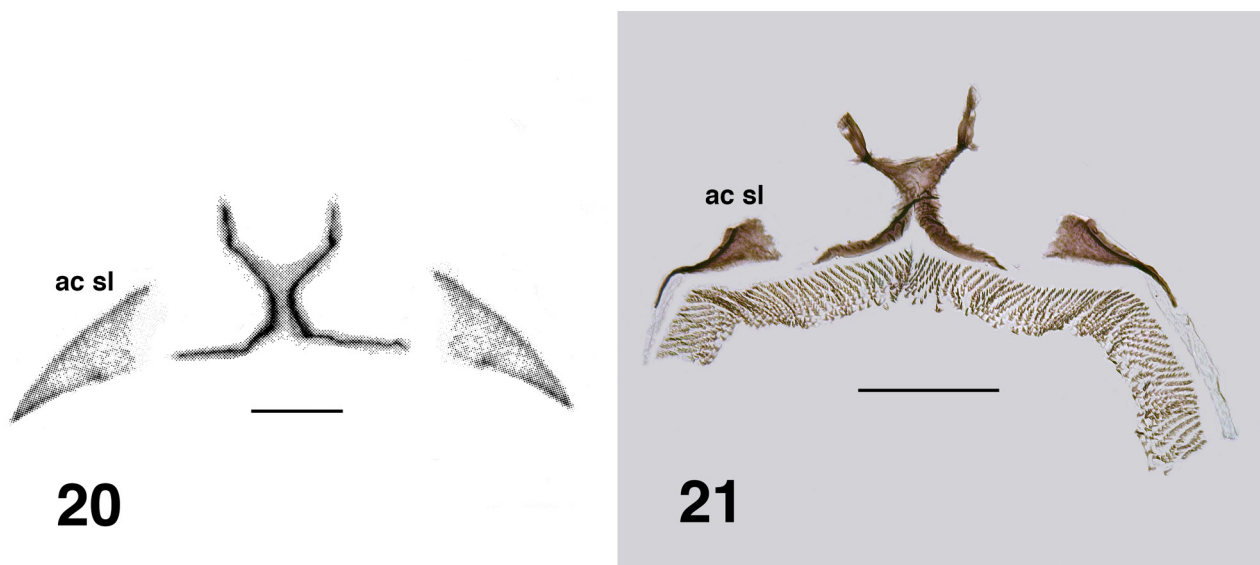
Description. *Female* (based on four reared specimens). *Body* (Fig. 22): overall blackish brown; total length 2.3–2.5 mm. *Head* (Fig. 24): overall markedly dark in colour; width 0.79–0.81 mm; depth 0.50–0.54 mm; postoccipt not markedly hirsute with long pale hairs, frons divergent, not markedly narrow, dark brown–black; frons:head ratio 1.0:7.0. *Eye*: interocular distance ca. 0.1 mm; eye evenly dark red, ommatidia diameter 0.01 mm; ca. 26 rows across and 36 down at mid–eye. *Clypeus*: width 0.19 mm; shiny black, vestiture of sparse small hairs. *Antenna* (Fig. 25): extended well beyond head margins; total length 0.56 mm; evenly blackish brown; pedicel narrowed basally slightly broader apically than flagellomere I, others angulate, proximal flagellomeres wider than long, little tapered to apex. *Mouthparts*: ca. 0.4× length of head depth; maxillary palp (Fig. 26), total length 0.6 mm, evenly dark brown, palpomere II narrowed and slightly elongated, palpomere III with denser vestiture, palpomere IV smaller, V (apical) palpomere subequal to III; proportional lengths III–V palpomeres 1.0:0.7:1.1; sensory organ 0.33× length of palpomere III, opening moderate, 0.3× vesicle width; mandible (Fig. 27) narrowed and finely pointed with ca. 50 poorly developed inner teeth, ca. 15 slightly larger outer teeth; lacinia with ca. 20 teeth on inner and outer edges; cibarium (Fig. 28) with broad sclerotized cornuae, slightly sculpted apically, median gap lacking armature, shallowly V-shaped. *Thorax*: length 1.3 mm; width 0.4 mm; evenly blackish brown; pronotal lobe well developed with fine hair longer than those on scutum (even fine small hairs); scutellar depression with long black hairs; scutellum concolourous to scutum, vestiture of long black hairs; postnotum black; antepronotal lobe with dense patch of black hairs; proepisternum and forecoxa, essentially bare; pleuron and anepisternal (pleural) membrane dark yellowish brown, without hairs; katepisternal sulcus distinct and deep. *Wing* (Figs. 29, 30): very slightly dusky on apex and anal lobe, length 2.6–2.8 mm; width 1.3–1.4 mm; anterior veins dark; basal (bm) cell minute; a:b ratio 1.0:2.8; distal 2/3 of costa with mixture of spines and hairs, R_s not divided; M_1 appearing double; CuA slightly sinuous; CuP markedly sinuous apically, not reaching wing margin. *Haltere*: stem grey, knob dark brown. *Legs* (Fig. 31): all evenly blackish brown; hind basitarsus lacking ventral row of stout spines; calcipala moderately well expressed, slightly tapered, pedisulcus present as single wrinkle; tarsomere II short, 2.0× longer than distal width; claws (Fig. 32), smoothly tapered, heel massively expressed, basal tooth moderately expressed, 0.25× length of claw, arising laterally on heel. *Abdomen* (Fig. 33): abdomen dark brown/black, anterior segments slightly lighter; vestiture not markedly expressed, more so posteriorly; tergites markedly sclerotized, well discernable from remainder of dorsum, tergite II protruded centrally, wing-like laterally, III U-shaped, IV rectangular, V slightly larger and rounded VII, others broader. *Genitalia*: blackish brown; sternite VIII with distinct pigmented median region, dense vestiture of microtrichia, sparse hairs posterolaterally; spermatheca ovoid (Fig. 34), smooth, darkly pigmented, internal fine spines (acanthae) sparse, clear area at spermathecal duct junction absent, pigment extended substantially down duct; genital fork (Fig. 35) unusual, anterior arm substantial, slightly expanded apically, membranous lateral areas, lateral arms markedly short and broad, lateral apodeme extended anteriorly as edge of membranous region, lateral arm apodeme expressed as ridge, posterolateral expansions markedly developed, all well pigmented; hypogynial valves (Fig. 36), median edges of valves slightly convex, not touching, markedly sclerotized, broadly rounded apically; cercus in lateral view distinct, rounded cone-shaped, anal lobes rounded, small, both darkly pigmented (Fig. 37).

Male (based on four reared and two pharate specimens). *Body*: overall colour blackish brown including head and thorax (Fig. 38); total length 2.4–2.6 mm. *Head* (Fig. 39): width 0.82 mm; depth 0.5 mm. *Eyes*: upper ommatidia blackish orange, not markedly enlarged, diameter 0.03 mm, ca. 15 across and 18 down; lower ommatidia black to blackish orange, diameter 0.014 mm, ca. 28 across, 33 down. *Clypeus*: black; width 0.16 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 40): total length 0.55–0.57 mm; evenly blackish brown; scape short, pedicel spherical, flagellomere I longer than wide, remaining flagellomeres angulate and barely tapered apically, distal few flagellomeres occasionally aberrant. *Mouthparts*: insubstantial; length 0.3× head depth; maxillary palpus (Fig. 41) 0.65 mm long, palpomere II slightly elongated, palpomeres III & IV subequal in length, III slightly swollen basally, palpomere V fine and elongated, proportional lengths of palpomeres III–V 1.0:0.9:1.5, sensory vesicle small, spherical, occupying 0.3× length of palpomere III, opening 0.33× vesicle width; lacinia finely expressed, with apical hairs; mandible with serrated apex. *Thorax*: length 1.0 mm; width 0.8 mm; lateral cervical sclerites well expressed; scutum not markedly domed, head angled anteriorly; postpronotal lobe concolourous with scutum, antepronotal lobe with patch of sparse fine dark hairs, proepisternum bare; scutum essentially black, vestiture of evenly sparse fine hairs, longer in scutellar depression; scutellum concolourous with scutum with long black hairs laterally, postpronotal lobe concolourous with scutum; pleurae dark orange, anepisternal membrane without hairs, katepisternum browner, sulcus distinct and deep. *Wing*: length 2.0–2.3 mm, width 0.9–2.0 mm; as for female. *Haltere*: stem dark, knob dark orange. *Legs*: overall blackish yellow, hind leg



FIGURES 14–19. *Prot austrosimulium pilfreyi*. Last instar larva (Grampians; except Fig. 18). (14) Mandible apex. Scale bar = 0.05 mm. (15) Postgenal cleft. Scale bar = 0.1 mm. (16) Hypostoma. Scale bar = 0.05 mm. (17) Thorax showing pupal gill histoblast. Scale bar = 0.5 mm. (18) Anterior proleg (modified from Davies & Györkös 1988: 109). Scale bar = 0.1 mm. (19) Pharate pupal gill. Scale bar = 0.2 mm.

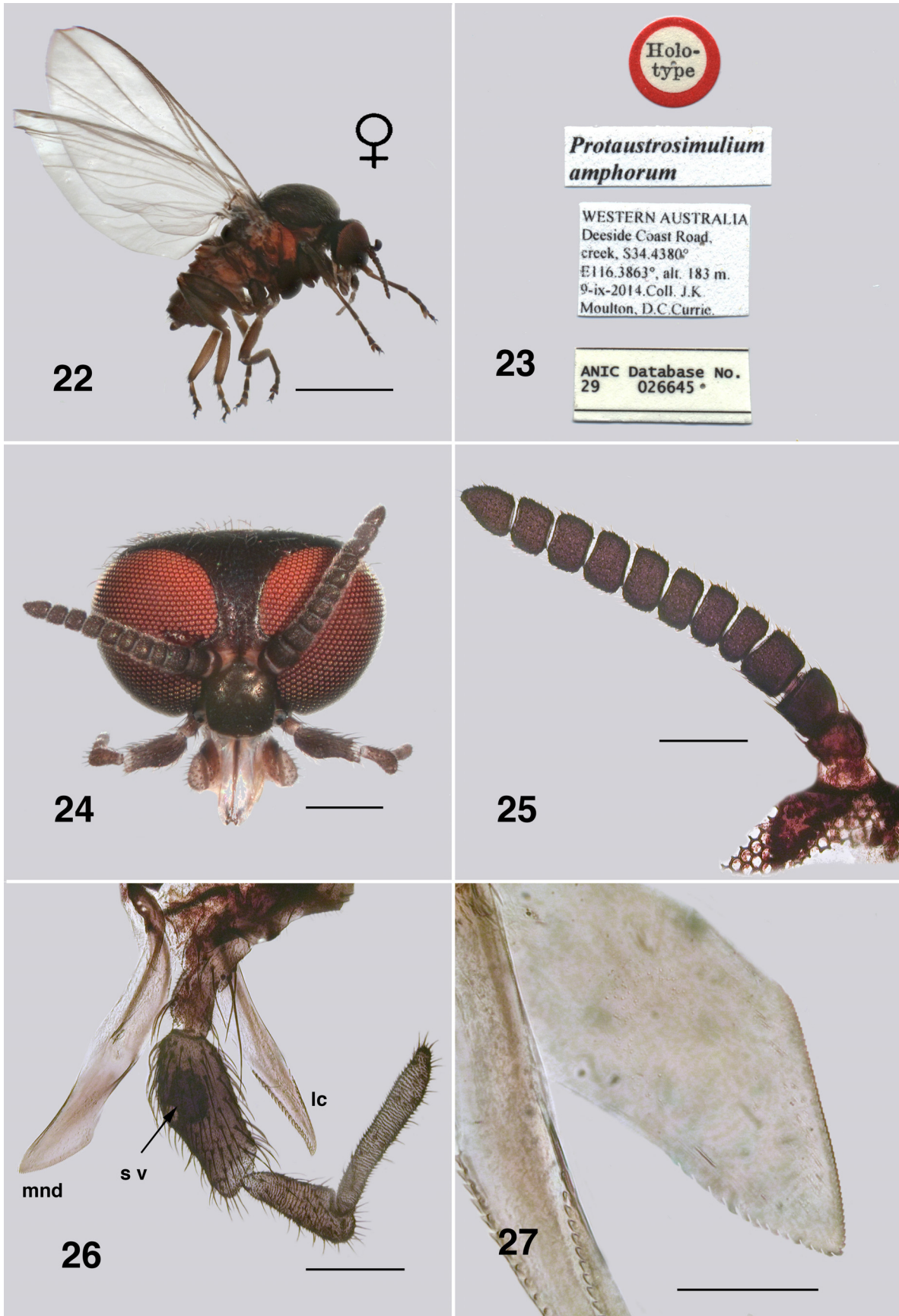
with tibia and hind basitarsus expanded medially (Fig. 42), ventral row of stout spines absent, calcipala small, 0.5× width of basitarsus apex, pedisulcus absent (Fig. 43); tarsomere II 2.0× length of apical width; tarsal claw with truncated basal tooth and grappling pad of *ca.* 20 teeth (Fig. 44). *Abdomen* (Fig. 45): overall black, vestiture of markedly long hairs, more so anteriorly; basal scale (tergite I) black, hairs markedly black and long, extended to posterior of segment III; tergite II 2.2× wider than long, rectangular, remainder increasingly broad further posteriorly, more rounded; sternite I present, II absent, III and those more posterior rounded and hirsute; small pleurae present, concertinaed. *Genitalia*: smaller and heavily pigmented (Fig. 46); gonocoxa 1.6× longer than basal width, vestiture of sparse long black hairs; gonostylus in lateral view not tapered, approximately 2.0× longer than basal thickness, strengthened along inner edge, three substantial short, blunt, apical spines (Fig. 47); ventral plate markedly sclerotized and strengthened around edges, 1.6× wider than long, keeled, posteromedial apex slightly convex, shallowly concave anteromedially, vestiture of evenly distributed hairs, longer on keel (Fig. 48), anterobasal arms markedly expressed and narrowed; parameral connections absent, parameres as triangular plates, strengthened anteromedially, tapered posteriorly and crenulated, four long parameral spines per side, one shorter, arrayed together medially; median sclerite well expressed and bifurcate apically; aedeagal membrane with dense microtrichia.



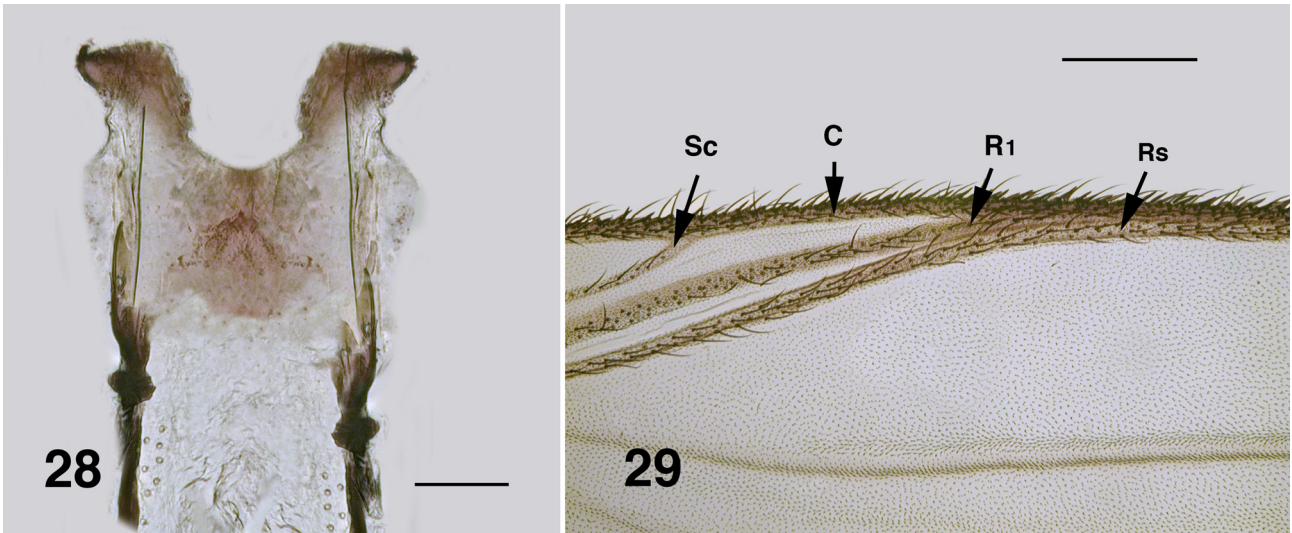
FIGURES 20, 21. *Protaustrosimulium pilfreyi*. Last instar larva. (20) Anal sclerite & accessory sclerites (ac sl) (modified from Davies & Györkös 1988: 109). Scale bar = 0.1 mm. (21) Anal sclerite, accessory sclerites (ac sl) & circlet of hooks (Grampians). Scale bar = 0.2 mm.

Pupa. Body: length 2.5–3.2 mm, (Fig. 49), markedly pale yellow to colourless, cuticle smooth. *Head*: frons of female angulate, ratio of basal width to vertex width 1.0:1.5 and basal width to length 1.0:1.6 (Fig. 51); that of male, ovoid and elongate, ratios 1.0:1.5 and 1.0:1.7 respectively (Fig. 52); cuticle faintly patterned; only facial setae present, frontal setae absent, epicranial setae present, closely applied beside antennal sheath. *Thorax* (Fig. 54): notum not markedly domed, with minute flattened tubercles, dorsal setae trichoid, short and curved. *Gill* (Figs. 50, 65): three short trunks arising directly from base, one flexed dorsally, the others ventrally and laterally, tubular, filaments finger-like, thin-walled, colourless, branching irregularly for total of 10; maximum length *ca.* 1.5 mm; form various, tubular along full length, or narrowed abruptly apically, or with apex ballooned (Fig. 50); surface featureless apart from normal trabeculae. *Abdomen* (Fig. 53): overall cuticle markedly thin, unpigmented and with poorly expressed armature; minute low clear tubercles; tergites II–IV extended ventrally to incorporate pleural region, tergite III only tenuously so, tergites I & II with fine hairs, tergites III & IV with small posterior hooks, tergites V & VI essentially bare, tergites VI–IX with fine minute spine combs; pleurites absent, pleural regions V–VII each with small hook; sternite VI & VII with hooks; segment IX with minute terminal spines, other setae exacerbadated but not grapnel hook-like (Fig. 55).

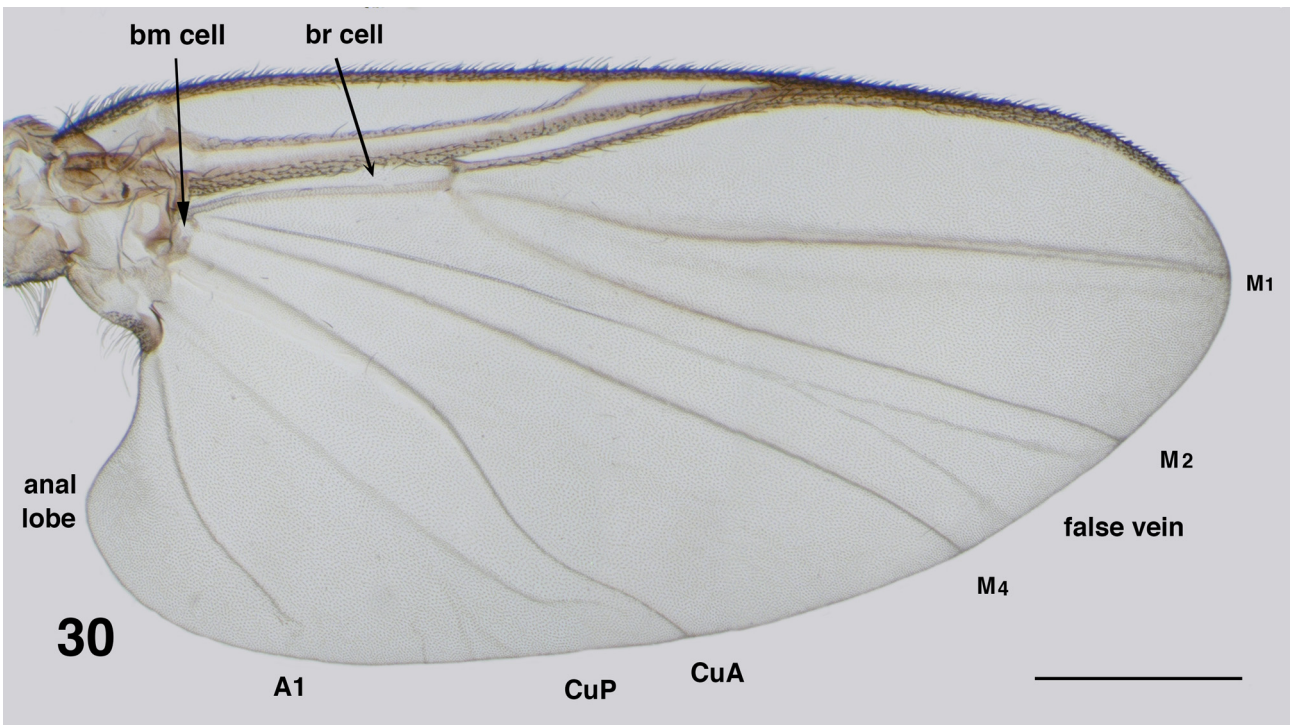
Cocoon (Fig. 49). Slipper-shaped, constructed of fine loosely- or irregularly-woven silk covering abdomen and most of thorax; extraneous material from substrate incorporated into cocoon.



FIGURES 22–27. *Protostrosimulium amphorum*. Female adult. (22) Holotype, habitus. Scale bar = 1.0 mm. (23) Holotype labels. (24) Frontal view of head. Scale bar = 0.2 mm. (25) Antenna. Scale bar = 0.1 mm. (26) Maxillary palp showing sensory vesicle (s v), mandible (mnd) & lacinia (lc). Scale bar = 0.1 mm. (27) Mandible apex. Scale bar = 0.05 mm.



FIGURES 28, 29. *Protastrosimulium amphorum*. Female adult. (28) Cibarium. Scale bar = 0.1 mm. (29) Wing veins. Scale bar = 0.5 mm.



FIGURES 30. *Protastrosimulium amphorum*. Female adult. Wing. Scale bar = 0.5 mm.

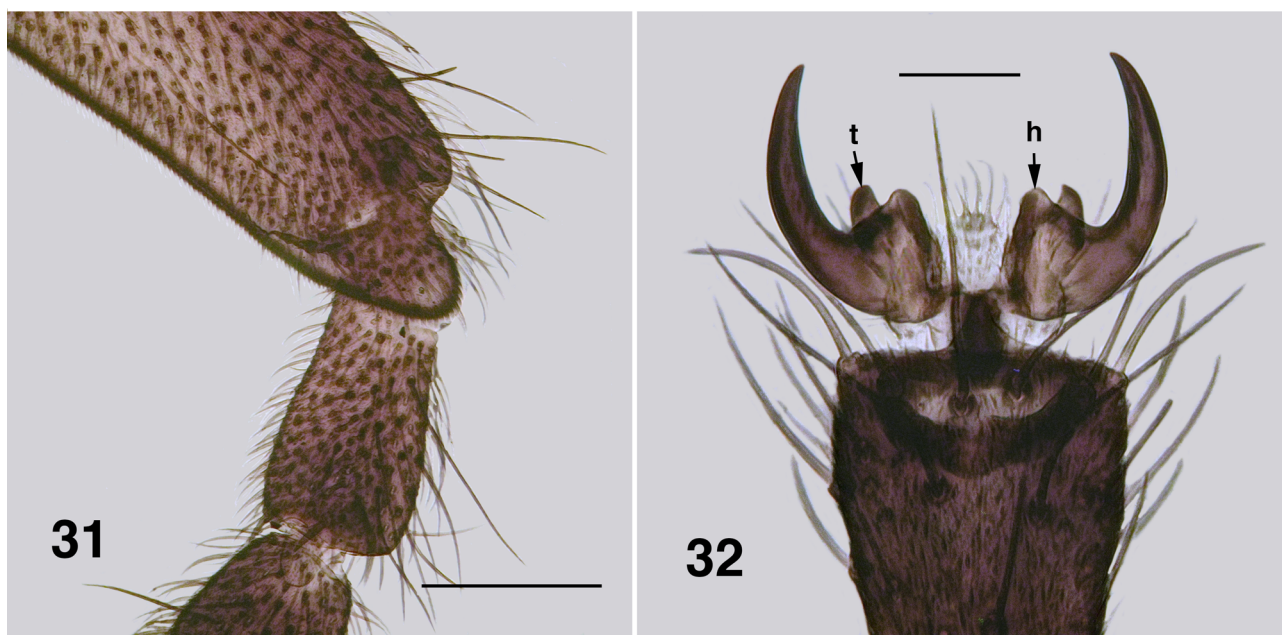
Larva. Body (Fig. 56): length 5.9–6.2 mm, Colour mottled orange; expanded markedly at segment V, smoothly tapered to posterior, amphora-shaped in dorsal view. *Head* (Fig. 57): length 0.74–0.76 mm, maximum width 0.52–0.56 mm; distance between antennal bases 0.34–0.36 mm; overall medium brown, pigment surround antennal base extended posteriorly and medially to ecdysial line and along that; head spot pattern markedly developed and positive; anteromedial and posteromedial head spots forming distinct line, flanked by first and second anterolateral spots, posterolateral spots not as markedly expressed; head widest just posterior to the stemmata, narrowed smoothly anteriorly, convex posteriorly; ecdysial line slightly sinuous anterior of stemmata; cervical sclerites finely fused to posterior of apotome and laterally to postociput. *Antenna* (Fig. 58): extended well beyond labral fan stem; total length 0.56–0.58 mm, proximal article clear basally otherwise dark brown, medial article brown, distal article colourless, medial article markedly shorter than proximal article, distal article elongated and thin, proportional

lengths of basal, medial and distal articles 1.0:0.3:2.2; sensory organs on medial article small, apical one elongated. *Labral fan*: stem subequal in length and breadth, lightly pigmented, *ca.* 57 markedly fine rays, length *ca.* 0.6 mm, mid-ray width 0.006 mm; microtrichial pattern with sparse long ones (0.007 mm), smaller microtrichia apparently absent. *Mandible* (Figs. 59, 60): not markedly pigmented; brushes not markedly developed; outer and subapical teeth small and grouped closely with well-developed apical tooth; *ca.* 11 fine spinous teeth; serrations and sensilla markedly defined, serrations as two cones (variable between sides), sensillum as single spike; blade region straight and smooth. *Maxilla* (Fig. 61): not markedly pigmented; palpus broad, 2.0× as long as basal width; not markedly separated from lobe, brush at base poorly expressed. *Postgenal cleft* (Fig. 62): present merely as small notch; region well sclerotised; posterior tentorial pits distinct, small and oval; postgenal bridge evenly light mottled brown; posteroventral muscles spots large, oval, not obvious; ratio of hypostoma: genal bridge: postgenal cleft 1.0:2.0:0.2. *Hypostoma* (Fig. 63): protruded anteriorly, teeth darkly pigmented; tooth 0 (median) slightly prominent, flanked by smaller tooth 1 (sublateral), the next (2) markedly smaller, the next (3) slightly larger, tooth 4 (lateral) subequal in length to tooth 0; teeth 5, 6, markedly small (paralaterals), others apparently absent; anterior ventral edge of hypostoma obscuring teeth 1 to 3; lateral serrations essentially absent; hypostoma sloped smoothly laterally; 4 or 5 fine hypostomal setae on each side; suboesophageal ganglion not pigmented. *Thorax* (Fig. 64): dark orange anteriorly; pharate pupal gill with filament bases visible, curled clockwise (with head to the right). *Prothoracic proleg*: small, lateral sclerites elongated, as in *Prot. pilfreyi* (e.g. Fig. 18). *Abdomen*: segments I–IV distinct with pale intersegmental regions, mottled orange; expanded laterally at segment V producing an amphora-shaped posterior, evenly mottled. *Ventral tubercles*: distinct, but not marked. *Anal sclerite* (Fig. 66): distinct, X-shaped, finely expressed, interarm struts absent; dorsolateral accessory sclerites expanded, connected to finely expressed complete semicircular sclerite, variously connected at ventral midline. *Rectal papillae*: three simple lobes, well developed. *Posterior cirrlet*: unremarkable, numbers of hooks, *ca.* 100 rows, 11 or 12 hooks per row (total *ca.* 1,150).

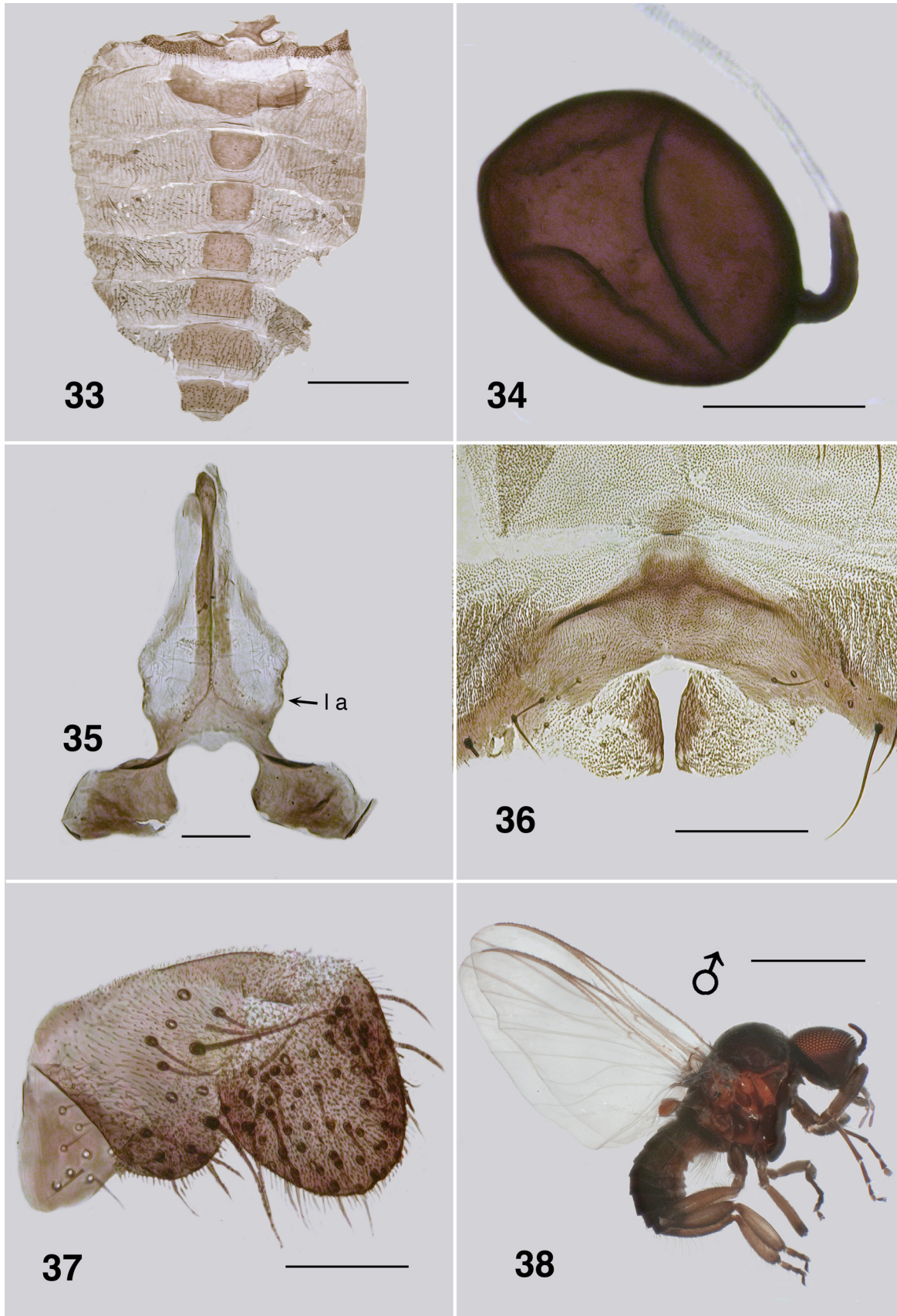
Etymology. In reference to the distinct amphora shape of the larval posterior abdomen.

Types. *Holotype* (Figs. 22, 23): pinned female, dried via Peldri™. Label data:- [Holo/type] [*Protaustrosimulium*/ *amphorum*] [WESTERN AUSTRALIA/ Deeside Coast Road/ creek, S34.4380° female symbol/ E116.3863°, alt. 183 m./ 9-ix-2014./ Coll. J.K./ Moulton, D.C.Currie.] [ANIC database No./ 29 026645].

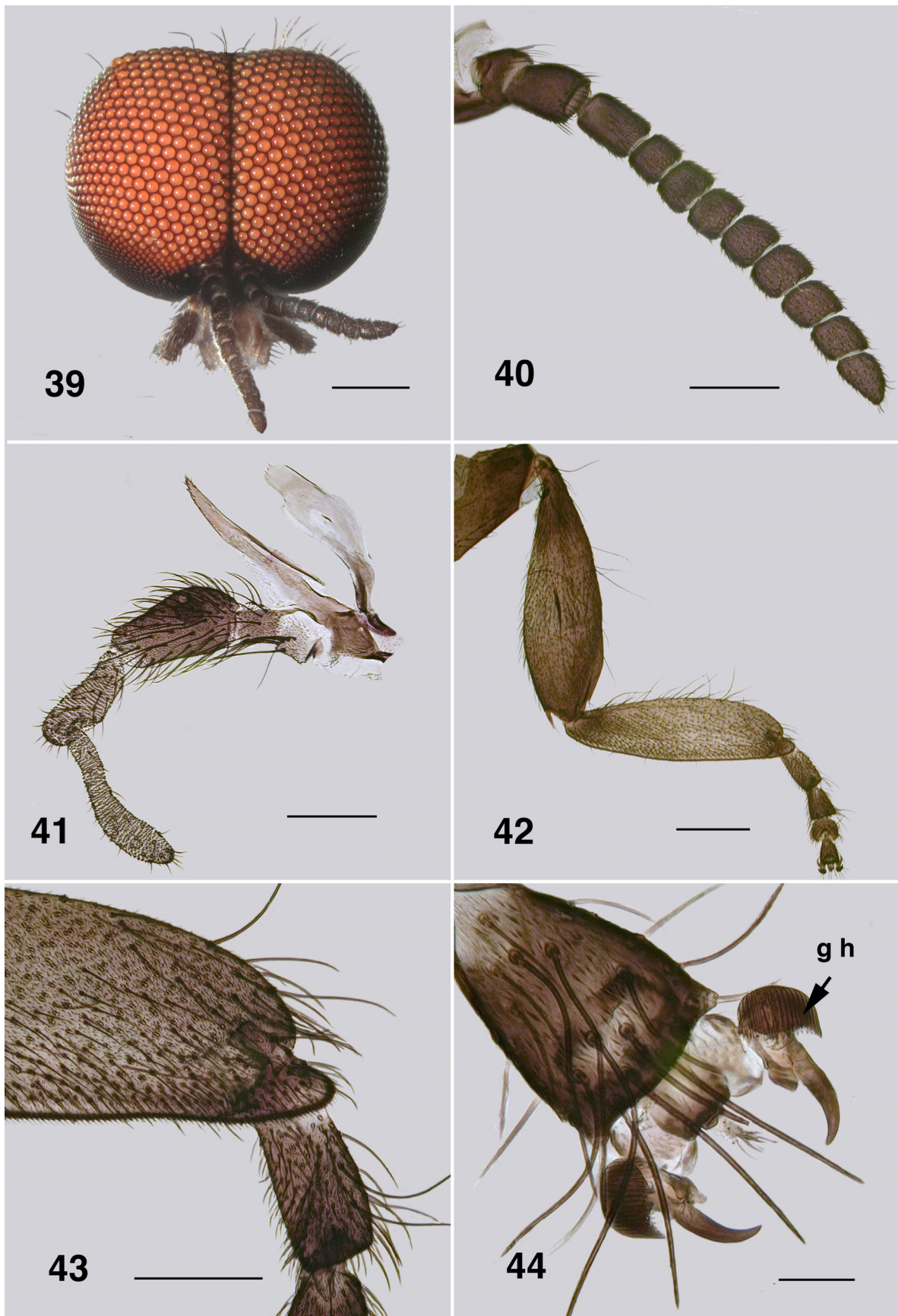
Paratypes: Pinned:- one female, two males. Label data as for Holotype, but with [PARATYPE]. Female with [ANIC database No./ 29 026646], males with [ANIC database No./ 29 026647] and [ANIC database No./ 29 026648]. Alcohol material. Two reared females and one male with pupal exuviae; two pupae, one with cocoon; four last instar larvae [ANIC database No./ 29 026649]. Seven last instar larvae, numerous early pupae and cocoons, reared male and female, pharate pupae, numerous pupal exuviae [UASM#/ 370906].



FIGURES 31, 32. *Protaustrosimulium amphorum*. Female adult. (31) Calcipala & tarsomere II Scale bar = 0.1 mm. (32) Claw showing heel (h) and basal tooth (t). Scale bar = 0.02 mm.



FIGURES 33–38. *Protastrosimulium amphorum*. Female adult. (33) Abdominal tergites. Scale bar = 0.5 mm. (34) Spermatheca. Scale bar = 0.05 mm. (35) Genital fork. (lateral apodeme – la). Scale bar = 0.05 mm. (36) Hypogynial valves. Scale bar = 0.1 mm. (37) Cercus & anal lobe. Scale bar = 0.05 mm. **Fig. 38.** *Protastrosimulium amphorum*. Male adult. (38) Habitus. Scale bar = 1.0 mm.

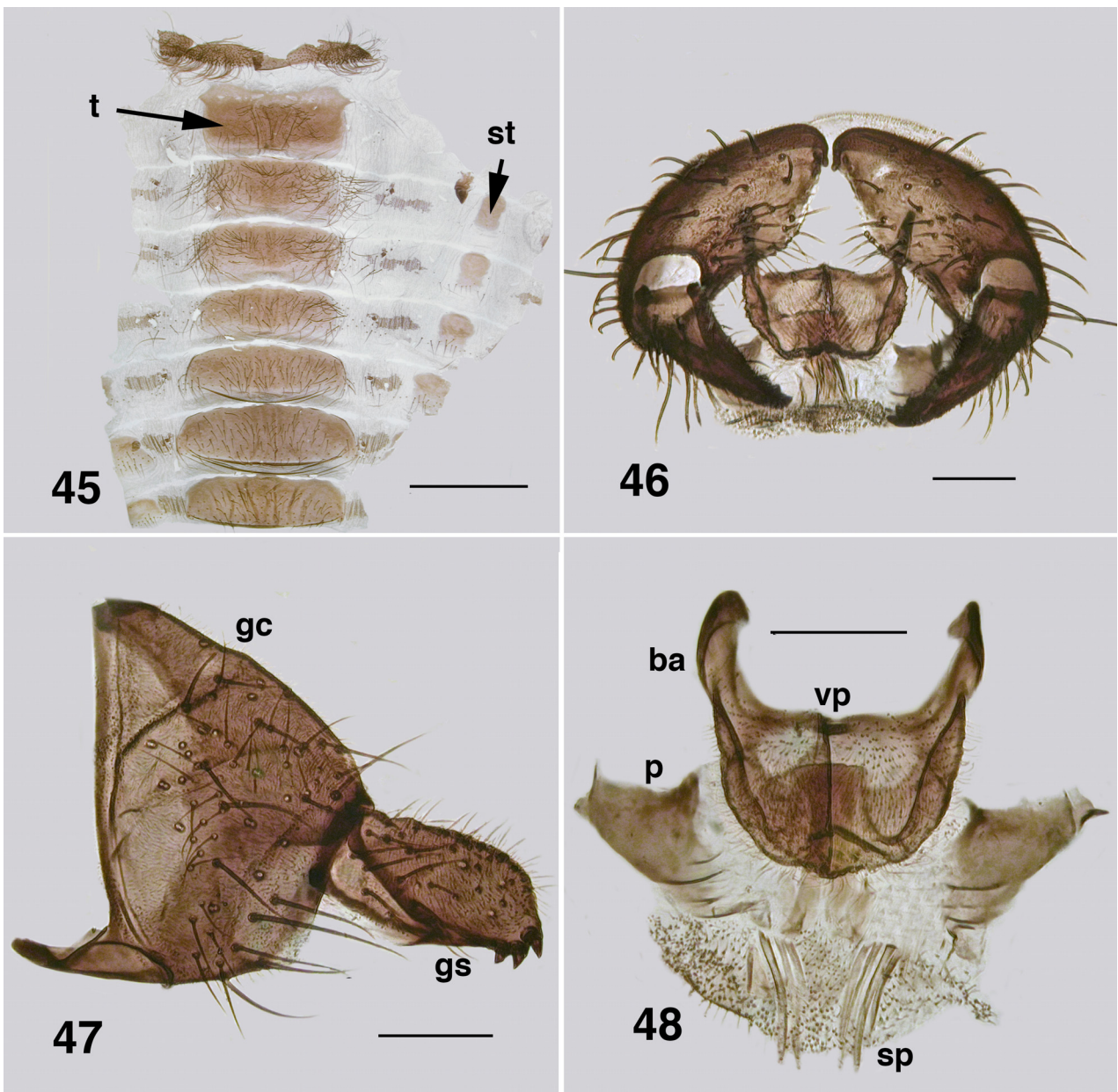


FIGURES 39–44. *Protastrosimulium amphorum*. Male adult. (39) Frontal view of head. Scale bar = 0.2 mm. (40) Antenna. Scale bar = 0.1 mm. (41) Maxillary palp, mandible & lacinia. Scale bar = 0.1 mm. (42) Hind leg. Scale bar = 0.2 mm. (43) Calcipala & tarsomere II. Scale bar = 0.1 mm. (44) Claw & grappling hooks (g h). Scale bar = 0.02 mm.

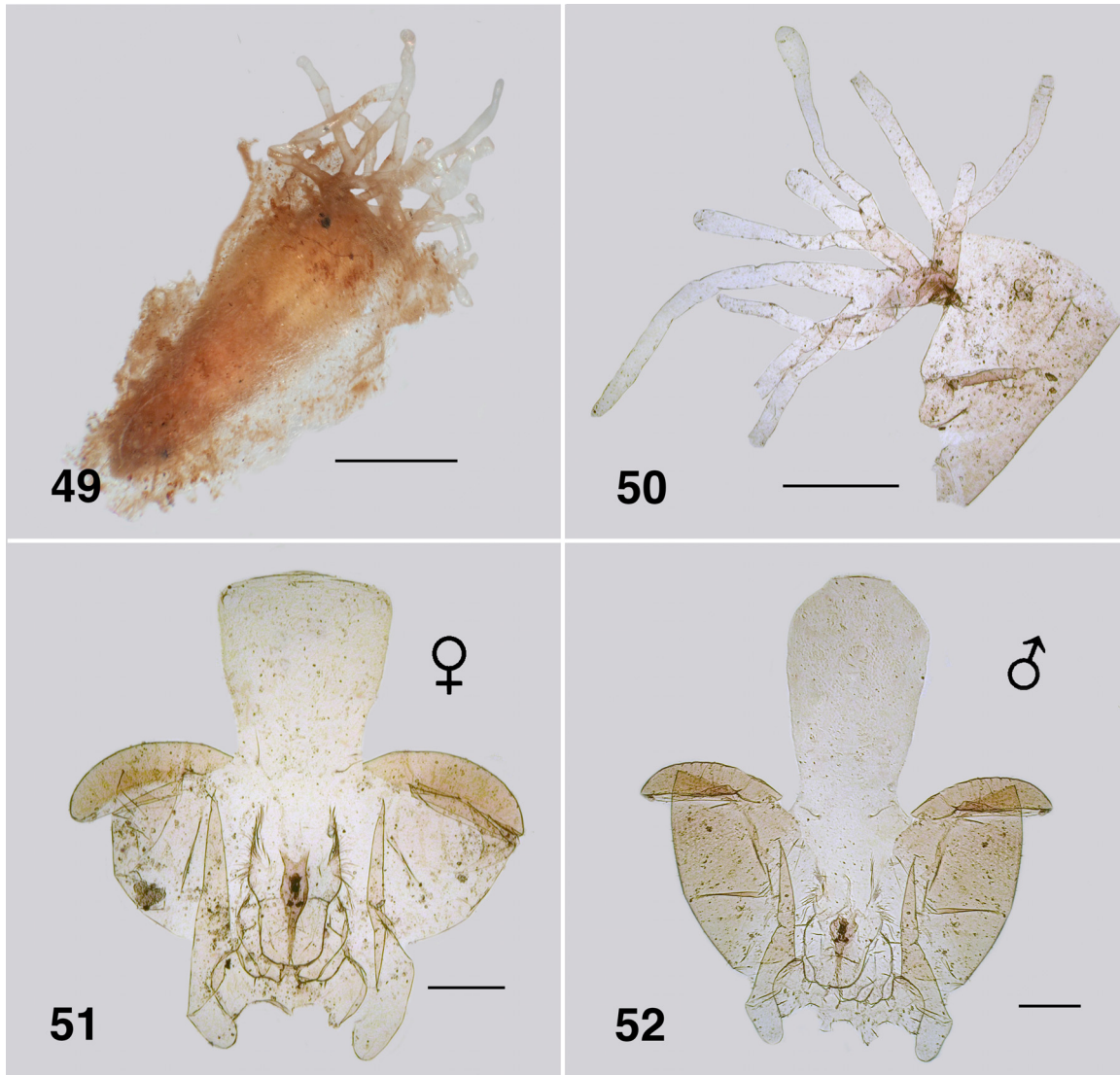
Additional material. Slide mounts (UASM# 370921-0928).

Distribution (Fig. 99). *Western Australia*: Churchman Brook, Canning Dam Rd., S32.1869° E116.1164°, elev. 282m., 8-ix-1996, Coll. J.K. Moulton. Deeside Coast Road, creek, S34.4380° E116.3863°, elev. 183m., 2 & 9-ix-2014. Colls. J.K. Moulton, D.C. Currie.

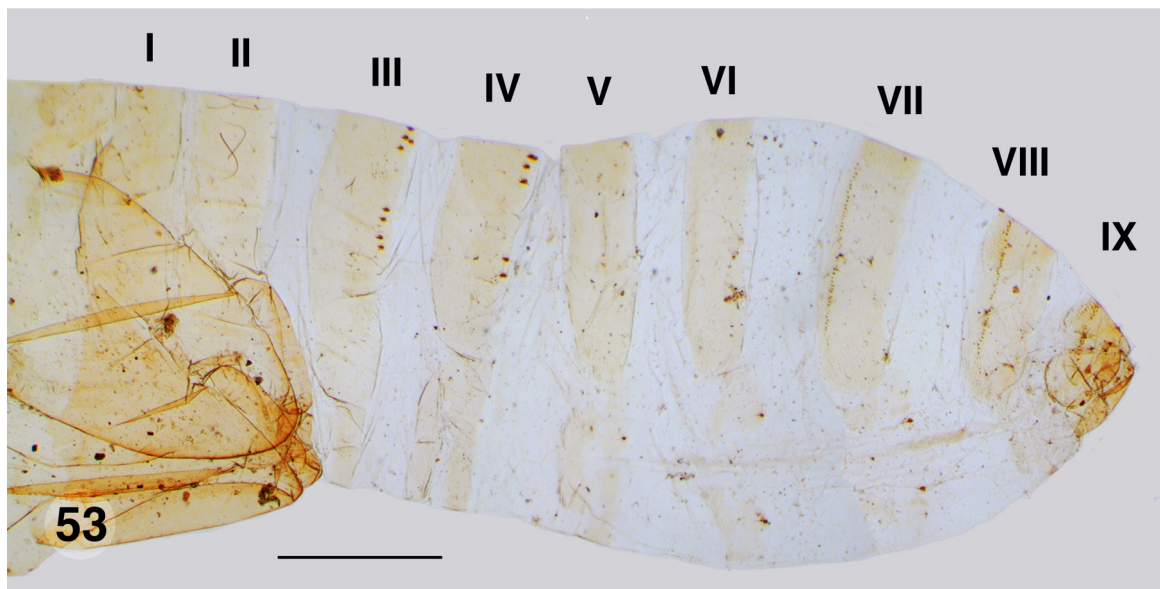
Bionomics. Little is known about the biology of this species. The dates of collection, with larvae taken on the 2nd September and pupae on the 9th, indicate that this is an Austral-spring species specialized for intermittent streams, similar to other Gondwanan simuliids of Western Australia. The type locality is a small slow-flowing muddy stream (Fig. 98) typical of the Warren bioregion (aka Kauri Forest bioregion). Apart from the amphora-shaped abdomen of the larva there is little unusual about the immature stage. Shape might indicate a preference for thin films of water, as noted for the Tahitian *Simulium (Inseliellum) cataractarum* Craig, where similar-shaped larvae inhabit madicolous flow (Craig, 2003). The feebly developed cocoon (Fig. 49) and markedly reduced pupal armature (Fig. 53) also point to slow-flowing streams being the preferred habitat. The number of hooks (*ca.*, 1,150) comprising the cirlet of the posterior proleg, however, indicates moderate flow, albeit less than 1.0 m/s (Palmer & Craig, 2000).



FIGURES 45–48. *Prot austrosimulium amphorum*. Male adult. (45) Abdominal tergites (t) and sternites (st). Scale bar = 0.5 mm. (46) Ventral view genitalia (cleared). Scale bar = 0.05 mm. (47) Gonocoxa (gc) & gonostylus (gs). Scale bar = 0.05 mm. (48) Basal arms (ba), ventral plate (vp), parameres (p) & spines (sp). Scale bar = 0.05 mm.



FIGURES 49–52. *Protastrostimulium amphorum*. Pupa. (49) Cocoon & pupa. Scale bar = 1.0 mm. (50) Gill. Scale bar = 0.5 mm. (51) Female head capsule. Scale bar = 0.2 mm. (52) Male head capsule. Scale bar = 0.2 mm.



FIGURES 53. *Protastrostimulium amphorum*. Pupa. Abdomen. Scale bar = 0.5 mm.



FIGURES 54, 55. *Prot austrosimulium amphorum*. Pupa. (54) Thoracic cuticle. Scale bar = 0.2 mm. (55) Abdominal segment IX. Arrows indicate terminal spines. Scale bar = 0.1 mm.

The female has moderately small abdominal tergites and that, along with the sharply-pointed mandible, toothed on both sides, plus a moderate-sized sensory vesicle on the maxillary palp suggests that this species is capable of blood feeding. Nothing is known about host preferences, although the small size of the basal tooth perhaps suggests a predilection for mammals.

Remarks. Simuliids associated with *Prot austrosimulium amphorum* in the Deeside Coastal Road stream were *Nothogreniera occidentalis* (Mackerras & Mackerras) (Craig *et al.*, 2018b) and *Ectemnoides faecofilus* Moulton, Craig & Currie.

terebrans-group. Genital fork with laterally flattened anterior arm, lobe-like junction at lateral arms (Figs. 81, 95).

Constituents. *Prot austrosimulium terebrans* (Tonnoir) and *Prot austrosimulium opscurum* n. sp.

***Prot austrosimulium terebrans* (Tonnoir). New combination**

(Figs. 67–83)

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

Simulium (*Cnephia*) *terebrans*. Edwards, 1931: 131.

Cnephia terebrans. Smart, 1945:499.

(*Cnephia* of authors) *terebrans*. Crosskey, 1987: 443. Unplaced species of Prosimuliini.

Paracnephia terebrans. Crosskey & Howard, 1997: 18. Bugledich 1999: 329.

Paracnephia terebrans. Adler & Crosskey, 2008: 26. Transferred to Simuliini.

Redescription. *Adult female* (based on five pinned specimens from ANIC and one from McKenzie Falls). *Body* (Fig. 67): markedly evenly blackish brown with dark brown abdomen; total length *ca.* 3.5 mm. *Head* (Figs. 68, 69): frons moderately narrowed, tapered only slightly towards antennae; width *ca.* 0.13 mm; depth *ca.* 0.56 mm; postoccipt black, vestiture of markedly sparse, long black hairs; frons, dark brown-black, vestiture of markedly sparse hairs; frons:head ratio 1.0:6.5. *Eyes*: interocular distance *ca.* 0.13 mm; ommatidia diameter 0.014–0.016 mm; *ca.* 33 rows across and down at mid-eye. *Clypeus*: width 0.23–0.25 mm; moderate vestiture of fine silvery hairs. *Antenna* (Fig. 70): dark brown; total length 0.70–0.72 mm; scape small, pedicel and flagellomere I similar in size, rectangular, next five flagellomeres broader than long, apical flagellomere cone-shaped; antenna overall not

tapered. *Mouthparts*: substantive, 0.5–0.7× length of head depth (longest in McKenzie Falls specimen); cibarium (Fig. 73) median depression flat, cornuae short, broadly flared and substantially sclerotized; mandible (Fig. 71, 72) with ca. 18 outer and 57 inner teeth, many finely expressed; lacinia with ca. 19 and 26 teeth; maxillary palp (Fig. 71), dark brown, total length ca. 0.70 mm, basal two palpomeres small, palpomere III darker brown than remainder, only slightly extended beyond articulation; palpomere IV markedly extended apicolaterally beyond articulation with palpomere V; proportional lengths of palpomeres III–V 1.0:0.7:1.0; sensory organ spherical, 0.3× length of palpomere III, opening 0.5× vesicle width. *Thorax*: length 1.6 mm; width 0.95–1.20 mm; evenly black; pronotal lobe slightly lighter in colour with fine hair longer than on scutum, scutum black with overall even sparse fine small golden hairs; scutellar depression similar; scutellum concolourous with scutum, vestiture of long hairs, black laterally, pale medially; postnotum concolourous with scutellum, pollinose in some lighting; anteprenotal lobe (propleuron), proepisternum and forecoxa with long fine hairs; pleuron and anepisternal membrane dark brown, without hairs, pollinose in some lighting; katapisternal sulcus shallow. *Wing* (Figs. 74, 75): length 2.3–3.5 mm; a:b ratio 1.0:2.7, width 1.5–1.7 mm; anterior veins dark brown, small basal cell present; costa with spines, R_s not branched, M₂ markedly double, CuA sinuous, but not markedly so. *Haltere*: knob dark brown, stem testaceous. *Legs*: (Fig. 76): evenly dark brown; hind basitarsus lacking ventral row of stout spines; calcipala ca. half width of basitarsus, as long as wide; intersegmental plate ventrally between basitarsus and basal tarsomere distinct; pedisulcus deeply incised near base, area lacking pigmentation; tarsomere II not markedly elongated, 2.3× longer than apical width; claws small (Fig. 77), serrated, basal tooth small and distinctly lateral to broad heel, (as illustrated by Tonnoir, 1925: his Fig. 3H. In Mackerras & Mackerras, 1949: their Fig. 10, the tooth is shown as double). *Abdomen* (Fig. 78): basal scale dark brown, vestiture of long yellow hairs; remaining segments dark brown, tergites dark orange brown; tergite II markedly broadly bowl-shaped, tergites III–VI rectangular, wider than long and similar sized; vestiture of markedly sparse small hairs increased in length and density posteriorly; remainder of tergites enlarged laterally and rounded; pleurites poorly developed, cuticle markedly pleated; sternites apparently absent; tergites broader in McKenzie Falls specimen. *Genitalia*: sternite VIII evenly pigmented across full width, vestiture of rows of microtrichia, large strong hairs posterolaterally; hypogynial valves (Figs. 79, 80), lightly pigmented, vestiture of triads of microtrichia, median edges of valves variable, either slightly concave or convex, but markedly strengthened, moderately rounded apicolaterally; genital fork (Fig. 81) anterior arm flattened laterally as a bar (distorted in Figure), two rounded lobes at junction with remainder, lateral arms broad, apodeme small and close to posterolateral expansions, rounded laterally, rectangular medially; spermatheca spherical, dark brown, externally smooth, sparse acanthae, clear area at junction with duct absent, pigment extended for short distance along spermathecal duct (Fig. 82); cerci in lateral view slightly extended, rounded apically, anal lobe not markedly expressed (Fig. 83).

Male: unknown.

Pupa: unknown.

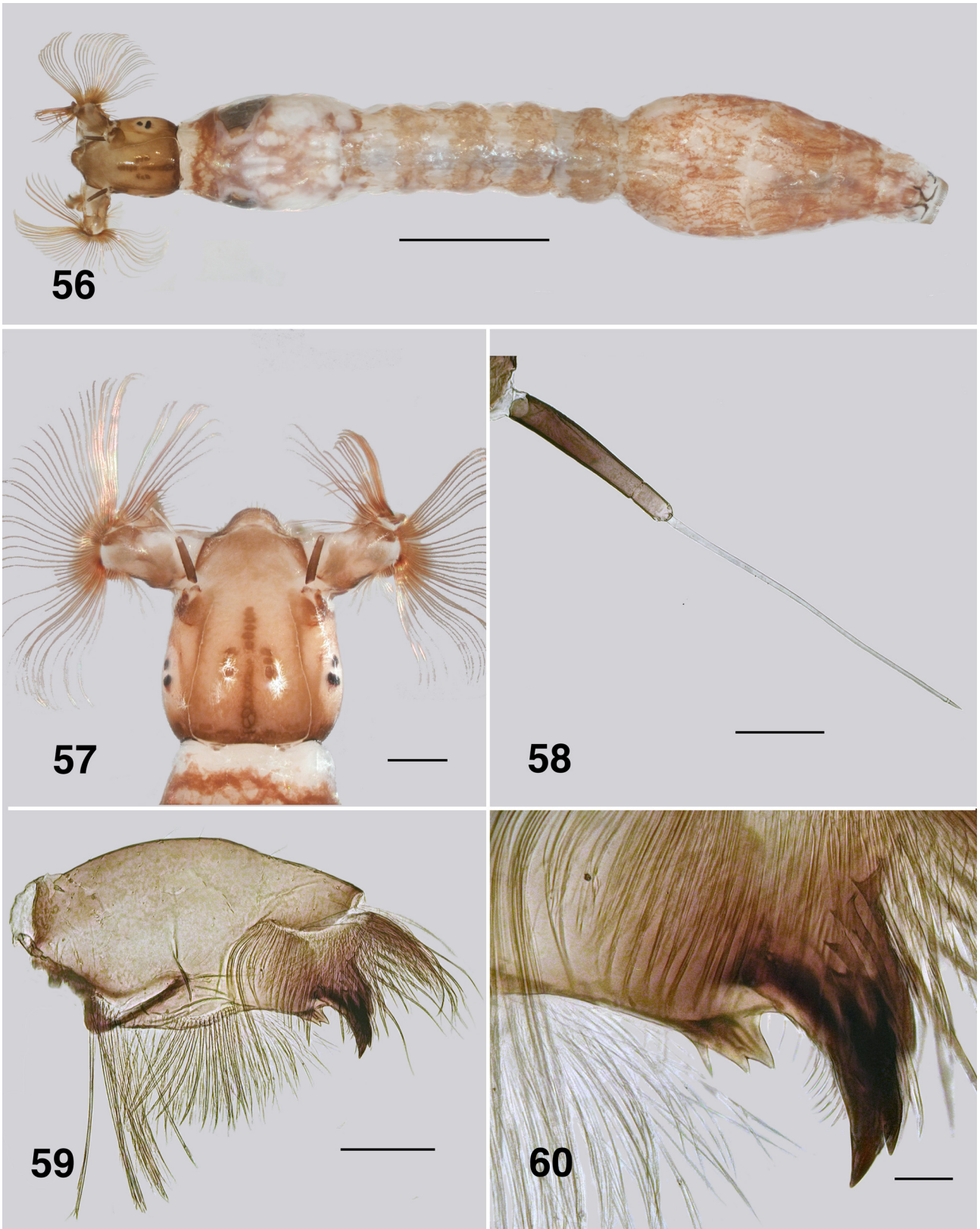
Larva: unknown.

Types. *Holotype*. Pinned female. Label data: [Victoria, Sassafras/ 22-x-1922. Coll. Tonnoir/ Caught while biting]. (ca. S37.8600° E145.3500°). ANIC.

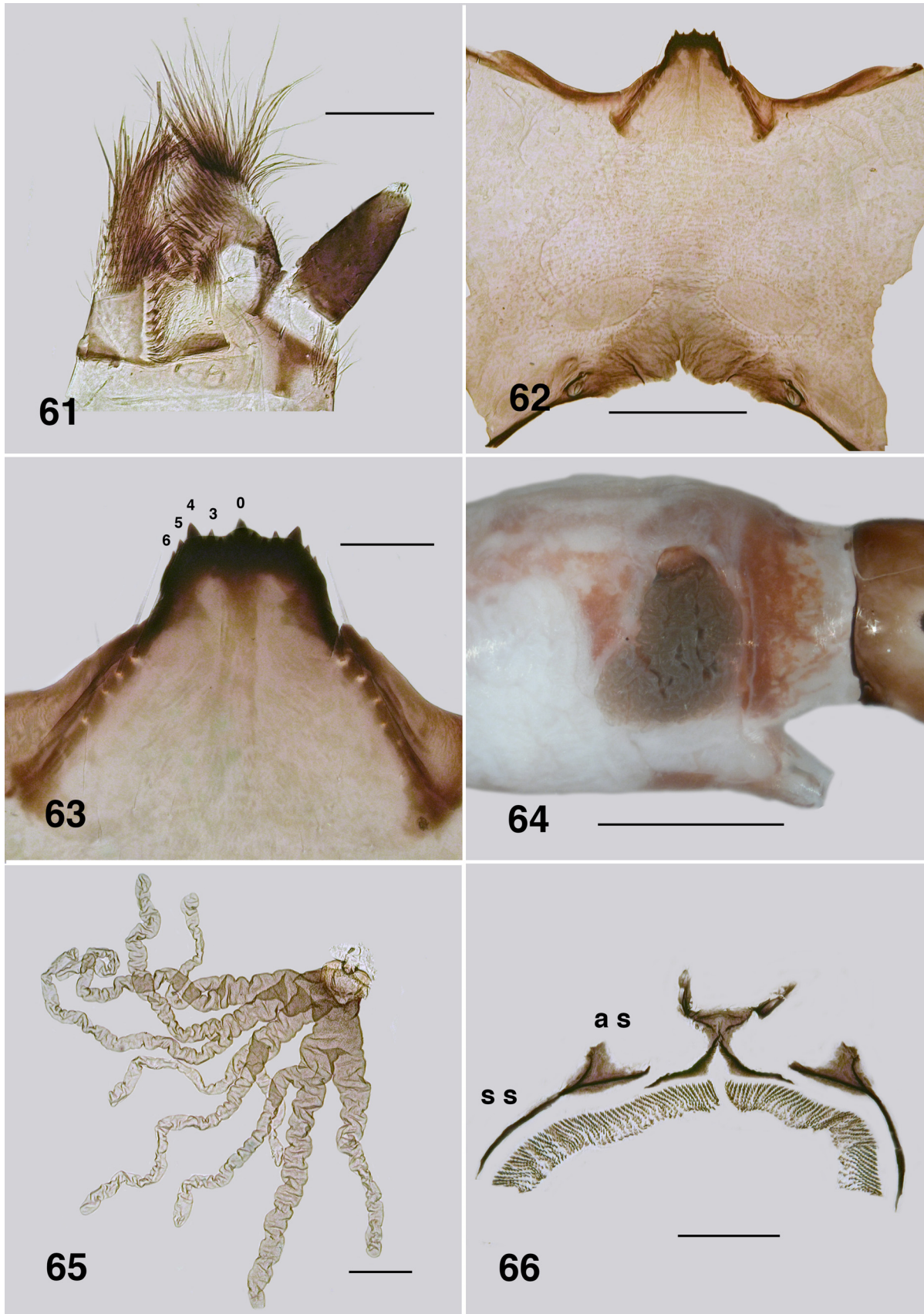
Additional material. Tonnoir (1925: 238) mentioned four females of this species from Canoblas, NSW, 11-x-1916, at the time deposited in the collection of the Board of Health, Sydney; however, he did not refer to them as paratypes. Although Bugledich (1999: 329) refers to them as such, she neither examined these specimens nor explained why she deemed them paratypes. Because Tonnoir (1925) did not explicitly designate these four females as paratypes, and given that they are not from the type locality, and of different date from the type, we consider them merely as ‘additional material’. One of these specimens was examined by us and is now mounted on a slide. We also examined three adult females from Middle Creek, one of which is also now slide mounted. One other specimen—from McKenzie Falls, Grampians—is slide mounted. All of this material is deposited in ANIC.

Etymology. Not given by Tonnoir (1925), but probably from Latin “*tenebris*” [= dark], in reference to the dark colour of the holotype female.

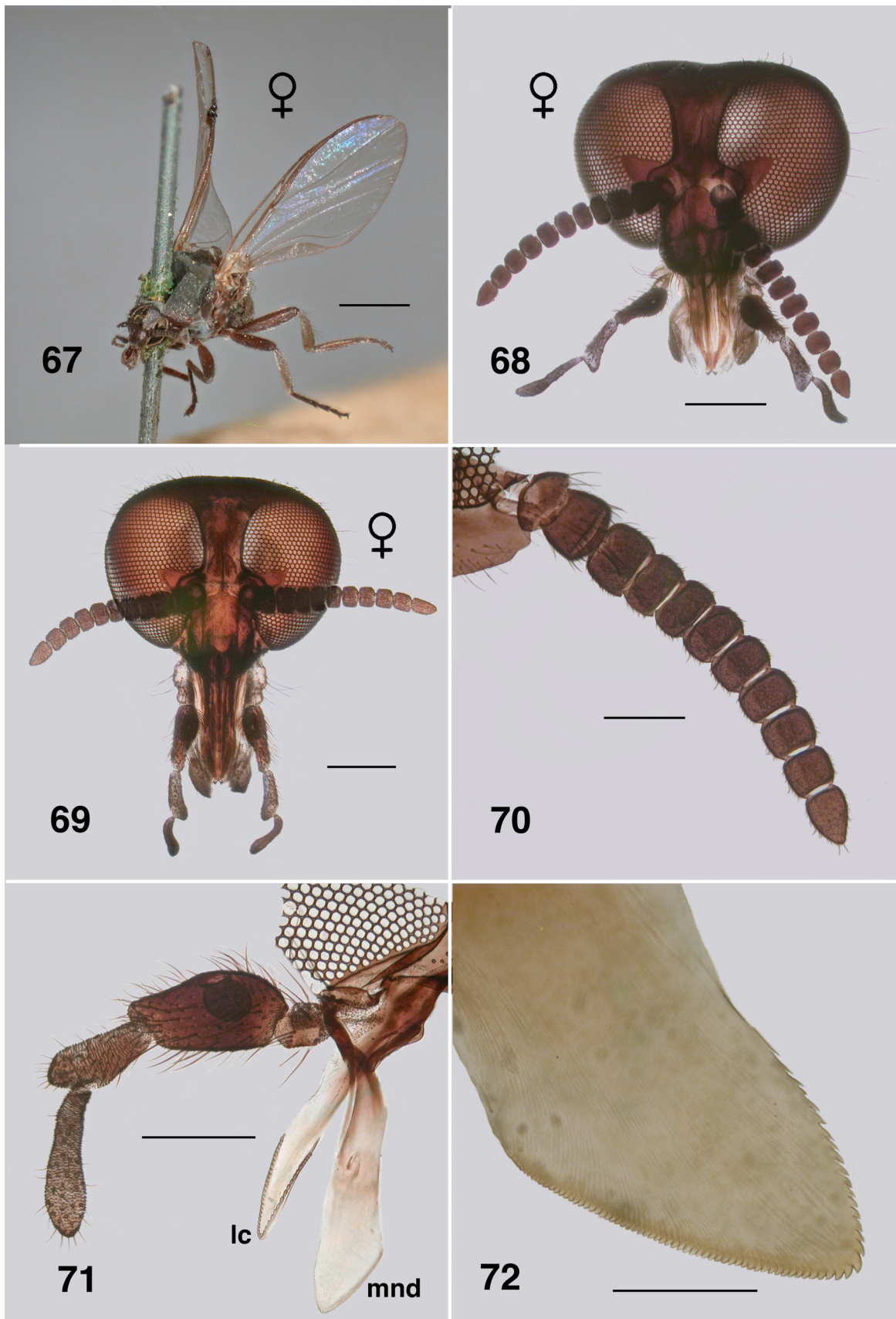
Distribution (Fig. 99). *New South Wales*: Mt. Canoblas, 11-x-1916, Coll. Tonnoir; Molong Creek, Mt. Canoblas, nr. Orange, 8-x-1950. det. Mackerras (S33.3192° E149.0239°, elev. 914m.). Colo Vale, 28-ii-1956, Coll. A.K. Grower (S34.3667° E150.4352°, elev. 690m.). Way Way, 3-x-1925, Coll. Mackerras (S30.7600° E152.9700°, elev. 26m.). *Australian Capital Territory*: Black Mountain, 8-ix-1953. Coll. A. Dyce (S35.2738° E149.1135°, elev. 580m.). *Victoria*: Sassafras, 22-x-1922. Coll. Tonnoir (S37.8628° E145.3536°, elev. 470m.). Middle Creek, Beaufort, 29-x-1952, Coll. Neboiss (S37.4032° E143.2415°, elev. 350m.). McKenzie Falls, Grampians, 26-ix-1953. Coll. Neboiss; 12-ix-2014, Coll. J.K. Moulton (S37.1109° E142.4088°, elev. 368m.).



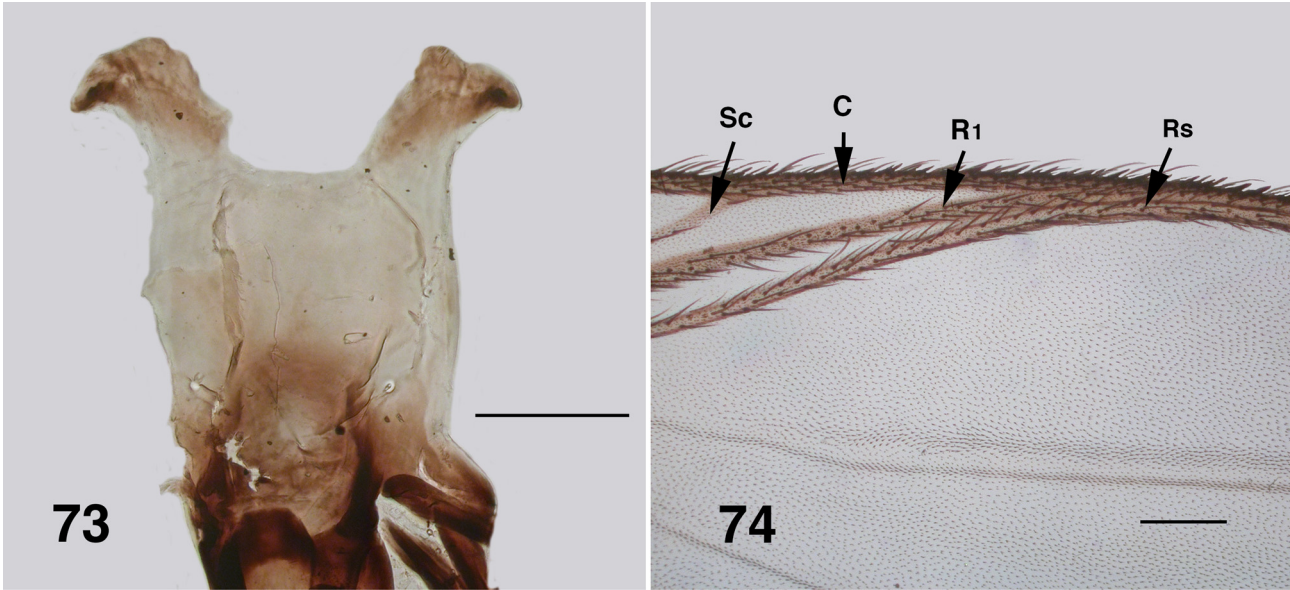
FIGURES 56–60. *Protaustrosimulium amphorum*. Last instar larva. (56) Habitus, dorsal view. Scale bar = 1.0 mm. (57) Dorsal view of head. Scale bar = 0.2 mm. (58) Antenna. Scale bar = 0.1 mm. (59) Mandible. Scale bar = 0.1 mm. (60) Mandible apex. Scale bar = 0.02 mm.



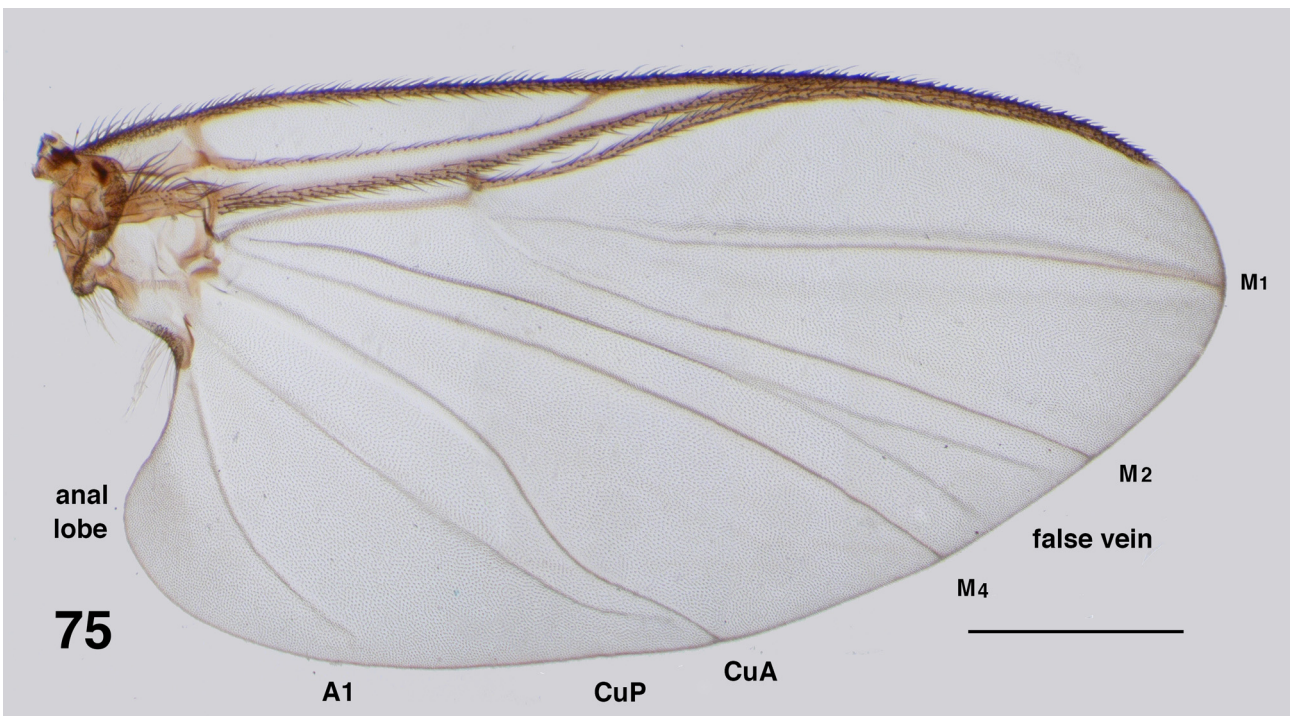
FIGURES 61–66. *Protostrosimulium amphorum*. Last instar larva. (61) Maxilla. Scale bar = 0.1 mm. (62) Postgenal cleft. Scale bar = 0.2 mm. (63) Hypostoma. Scale bar = 0.05 mm. (64) Thorax showing pupal gill histoblast. Scale bar = 0.5 mm. (65) Pharate pupal gill. Scale bar = 0.2 mm. (66) Anal sclerite, accessory sclerites (a s), semicircular sclerite (s s) & circlet of hooks. Scale bar = 0.2 mm.



FIGURES 67–72. *Protastrosimulium terebrans*. Female adult. (67) Habitus. (Canobolas, 1916). Scale bar = 1.0 mm. (68) Frontal view of head (cleared). (Middle Creek). Scale bar = 0.2 mm. (69) Frontal view of head (cleared). (McKenzie Falls). Scale bar = 0.2 mm. (70) Antenna. (Middle Creek). Scale bar = 0.1 mm. (71) Maxillary palp, mandible (mnd) & lacinia (lc) (Canobolas, 1916). Scale bar = 0.2 mm. (72) Mandible apex (Canobolas, 1916). Scale bar = 0.05 mm.



FIGURES 73, 74. *Protastrosimulium terebrans*. Female adult. (73) Cibarium (Canobolas, 1916). Scale bar = 0.1 mm. (74) Wing veins (Middle Creek). Scale bar = 0.1 mm.



FIGURES 75. *Protastrosimulium terebrans*. Female wing (Middle Creek). Scale bar = 0.5 mm.

Bionomics. Little is known about the biology of this species, although Tonnoir's label data indicate that females bite. Males, pupae or larvae are unknown, despite extensive searching by Mackerras & Mackerras (1952: 105) and our own collecting efforts. With the exception of the Colo Vale locality, dates of collection indicate an Austral spring species. Colo Vale is at a higher elevation than other sites, so perhaps later emergence at that site is related to cooler temperatures.

Remarks. An attempt by DAC in 2014 to collect new material from Middle Creek, Victoria, was unsuccessful. As with many collection sites referred to in the early literature, human activities have rendered such streams unsuitable for simuliids (e.g., Moulton *et al.*, 2018: 10).



FIGURES 76–77. *Protostrosimulium terebrans*. Female. (76) Calcipala & tarsomere II (Middle Creek). Scale bar = 0.05 mm. (77) Claw showing basal tooth (Canobolas, 1916). Scale bar = 0.02 mm.

The mouthparts of known females are substantial, in particular the single specimen from McKenzie Falls (Fig. 69). Such mouthparts suggest that females are blood-feeders, although the large size of their abdominal tergites is more typical of non-bloodsucking species.

The genital fork of *Protostrosimulium terebrans* is unique among Australian simuliids and differs in a number of respects from those of *Prot. pilfreyi* and *Prot. amphorum*. The stem is strongly curved ventrally and laterally flattened—thence contorted when slide mounted (e.g., Fig. 81). There are unusual lobes at the junction of the anterior and lateral arms, and no evidence of membranous areas lateral to the anterior arm.

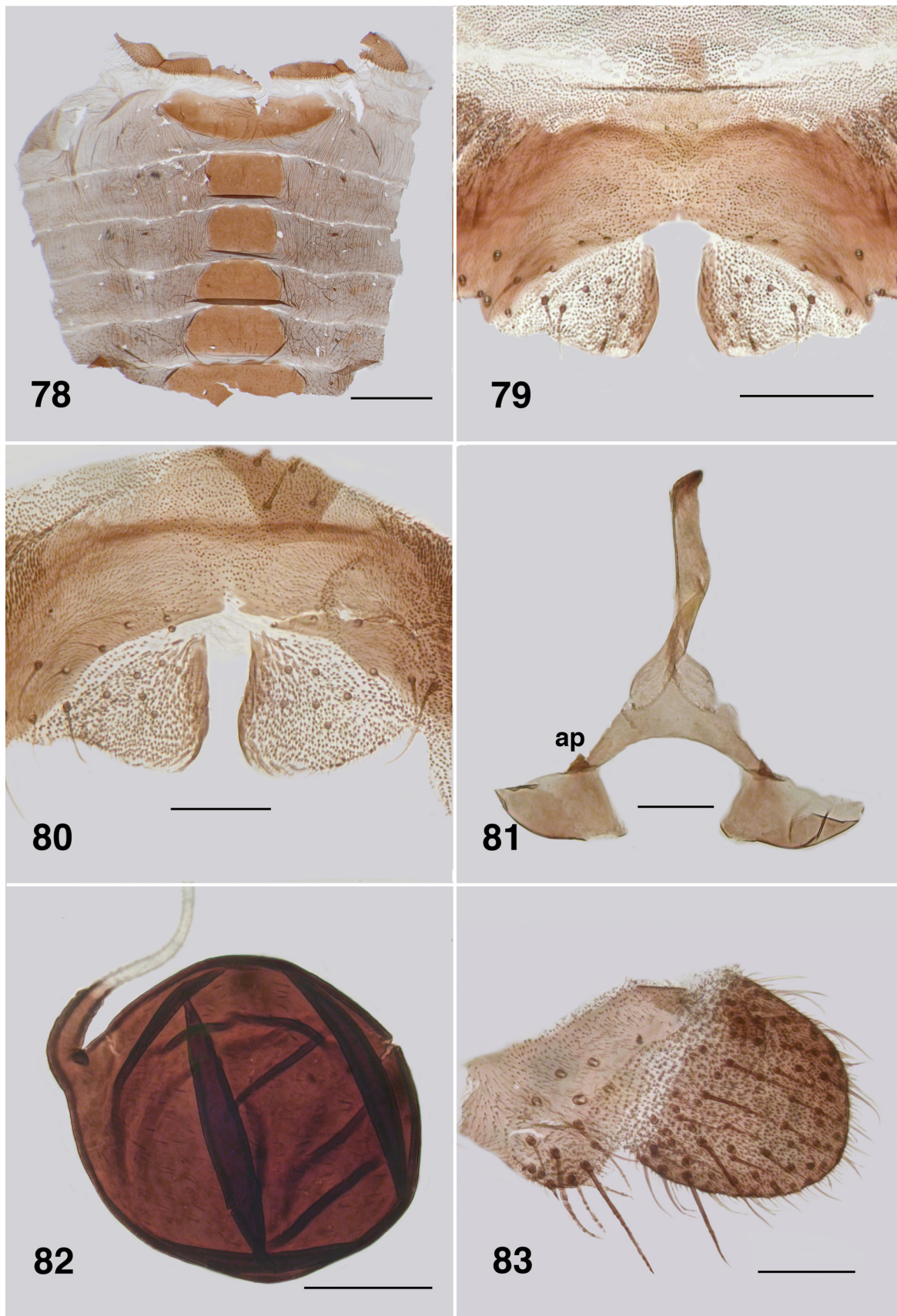
***Protostrosimulium opscurum* Currie, Craig, Moulton. n. sp.**
(Figs. 84–95)

Cnephia sp. A Mackerras and Mackerras 1949: 385 (not *Cnephia* A Rothfels 1979: 522 or *Cnephia* sp. A Pruess *et al.*, 2000: 287).

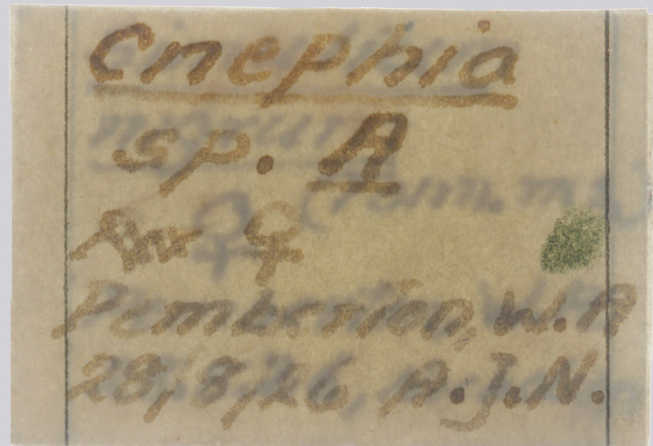
Simulium nigrum Mackerras and Mackerras, 1949: 385. Preoccupied

Paracnephia 'A' Mackerras & Mackerras 1949. Crosskey & Howard, 1997.

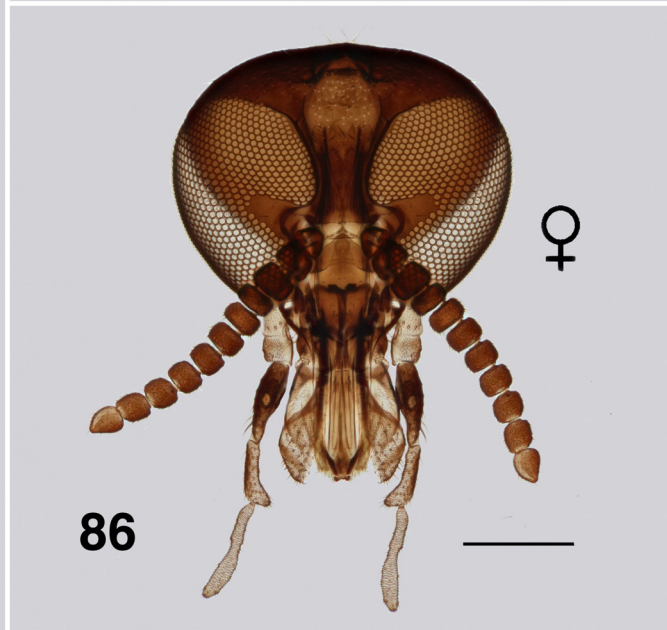
Description. *Female* (based on a single slide-mounted specimen (Fig. 84) and literature description by Mackerras & Mackerras, 1949: 385–6). *Body*: Blackish, with dark brown legs. *Head* (Fig. 86): frons:head width ratio 1:6.3. *Eyes*: interocular distance 0.13 mm; ommatidia diameter *ca.* 0.009 mm; *ca.* 36 rows down and across at mid-eye. *Clypeus*: not markedly enlarged, width 0.16 mm; black, vestiture of sparse fine black hairs. *Antenna* (Fig. 87): extended well beyond head margins; total length 0.6 mm; nine flagellomeres, scape small, pedicel broad distally, flagellomere I broad and rounded, second flattened, remainder subequal in size to each other, except distal flagellomere cone-shaped; antenna overall not markedly tapered. *Mouthparts*: substantial, *ca.* 0.4× length of head depth, black; cibarium apparently with substantially sclerotized cornuae and broadly rounded medial depression; mandible markedly finely tapered, *ca.* 50 markedly small inner and 7 outer teeth (Figs. 88, 89); lacinia with 21 and 16 substantial teeth on inner and outer edge respectively; maxillary palp (Fig. 88), elongated, total length 0.62 mm, basal two palpomeres small, palpomere III darker brown than remainder, narrowed basally, expanded at sensory vesicle, narrowed distally, subequal in size to apical palpomere V; palpomere IV extended slightly at distal junction; proportional lengths of palpomeres III–V 1.0:0.7:1.2; sensory organ narrow and elongated, 0.4× length of palpomere III, opening distinct, 0.7× vesicle width and elongated. *Thorax*: anteprenotal lobe (propleuron) hairs absent or reduced to a few fine hairs at the lower margin. *Wing* (Figs. 90, 91): length 2.8 mm; width 1.3 mm; basal



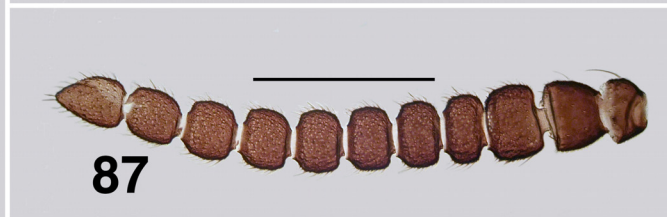
FIGURES 78–83. *Prot austrosimulium terebrans*. Female adult. (78) Abdominal tergites (Canobolas, 1916). Scale bar = 0.5 mm. (79) Hypopygial valves (Canobolas, 1916). Scale bar = 0.1 mm. (80) Hypopygial valves (Middle Creek). Scale bar = 0.05 mm. (81) Genital fork (Canobolas, 1916), apodeme (ap). Scale bar = 0.05 mm. (82) Spermatheca (Canobolas, 1916). Scale bar = 0.05 mm. (83) Cercus & anal lobe (Middle Creek). Scale bar = 0.05 mm.



85



86



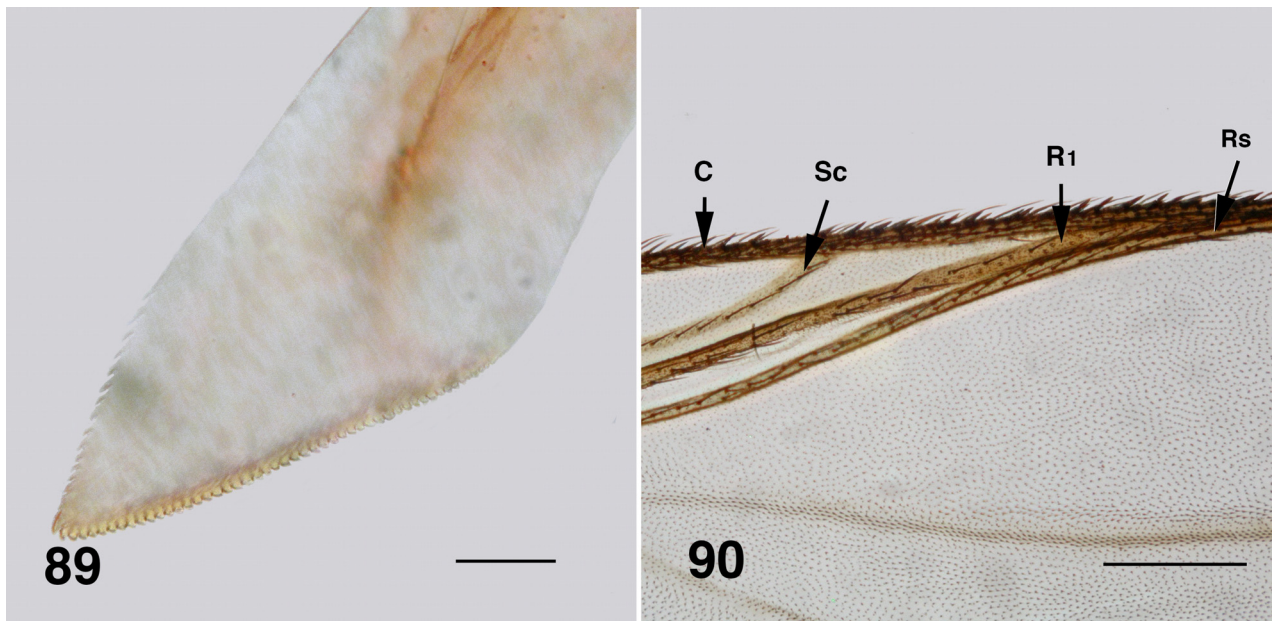
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88

FIGURES 84–88. *Protostrosimulium opscurum*. Female adult. (84) Holotype, slide mount. (85) Overexposed scan of labels showing hidden original labelling. (86) Head. Partially reconstructed. Scale bar = 0.2 mm. (87) Antenna. Scale bar = 0.2 mm. (88) Maxillary palp, mandible, lacinia. Scale bar = 0.05 mm.

(bm) cell poorly developed; costa with well-developed spines, R_s not branched, M_2 appears double for 2/3 length—effect produced by concentration of microtrichia, CuA markedly sinuous, a:b wing ratio 1:3, pigmentation at junction of r-m veins absent. *Haltere*: unknown. *Legs* (Fig. 92): overall dark brown; hind basitarsus lacking ventral row of stout spines; calcipala distinct and slightly elongated; pedisulcus moderately developed, tarsomere II *ca.* 3× as long as apical width; claws large and black (Fig. 93), smoothly curved, basal tooth small, triangular, as is heel. *Abdomen* (Fig. 94): overall black, basal scale dark yellowish brown with vestiture of sparse long pale hairs; tergites markedly broader than long, tergite II markedly broad in dimensions, tergites III–V subequal in dimensions, those more posterior wider; overall vestiture black. *Genitalia*: hypogynial valves not observed; genital fork (partially reconstructed) (Fig. 95) anterior arm markedly narrowed with rounded anterior expansion, lateral membranous areas, possible lateral apodeme at junction with lateral arms, but not clear, lateral arms broad, poorly sclerotized with slight knee-bend, apodeme as raised ridge at junction with posterolateral expansions, those pointed laterally, rounded medially; cerci in ventral view apparently ovoid, anal lobe with median notch; spermatheca not observed.



FIGURES 89, 90. *Prot austrosimulium opscurum*. Female adult. (89) Mandible apex. Scale bar = 0.02 mm. (90) Wing veins. Scale bar = 0.2 mm.

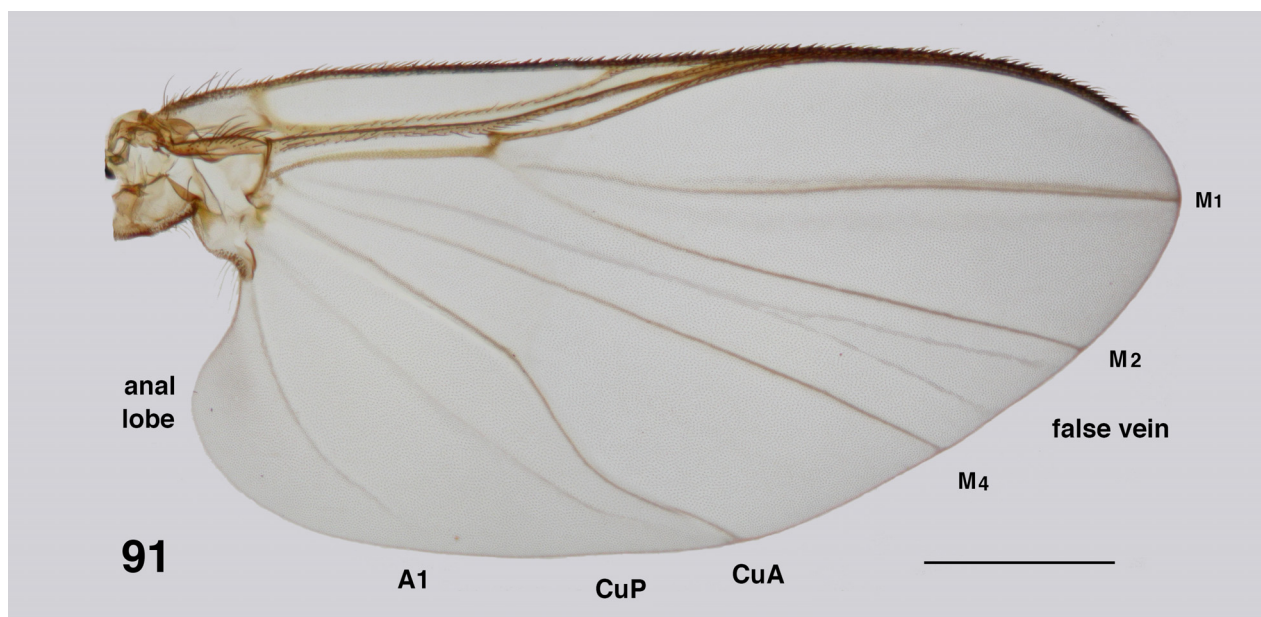
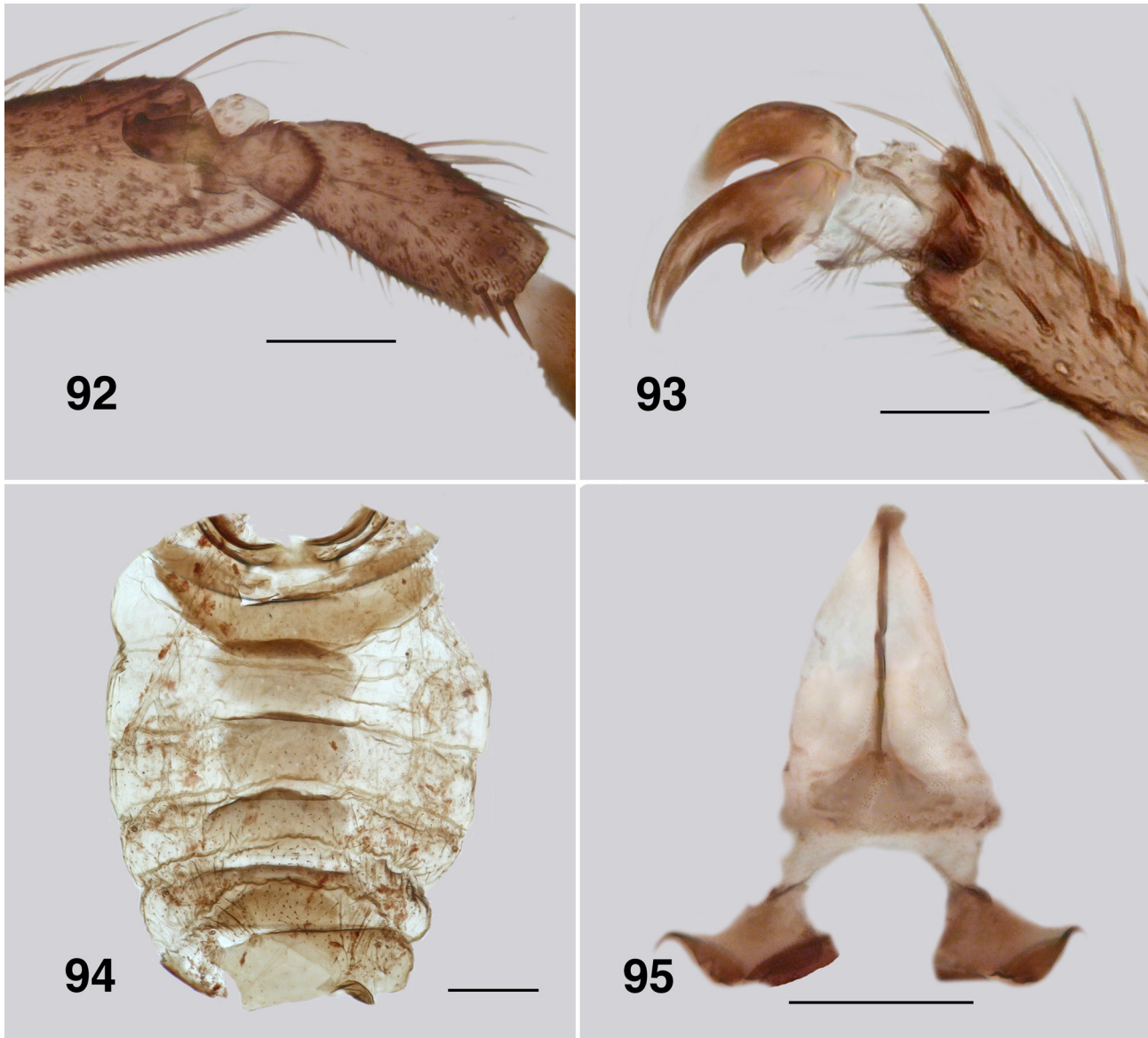


FIGURE 91. *Prot austrosimulium opscurum*. Female wing. Scale bar = 0.5 mm.



FIGURES 92–95. *Prot austrosimulium opscurum*. Female adult. (92) Calcipala & tarsomere II. Scale bar = 0.05 mm. (93) Claw. Scale bar = 0.02 mm. (94) Abdominal tergites. Scale bar = 0.2 mm. (95) Genital fork (partially reconstructed). Scale bar = 0.1 mm

Adult male: Unknown.

Pupa: Unknown.

Larva: Unknown.

Type. The nomenclatural history of this species is rather muddled. Mackerras and Mackerras (1949: 385) referred to a Western Australian species named "*Simulium nigrum*" in an unpublished manuscript by Tonnoir. Tonnoir designated a holotype for that species and evidently deposited it in the School of Public Health and Tropical Medicine, Sydney, although the name was never validated as Tonnoir died (Nicholson 1940: 139) and the manuscript never submitted for publication. Mackerras and Mackerras inadvertently took authorship of the name by listing it as a synonym of an entity they dubbed "*Cnephia* sp. A". Since the name "*Simulium nigrum*" that Tonnoir proposed was preoccupied by *Simulium nigrum* (Meigen 1804) and never published, it consequently has no formal standing. We found a single slide-mounted female of Tonnoir's originally collected material in the ANIC—the specimen here designated as holotype of *Prot austrosimulium opscurum*.

Holotype: Dissected female mounted on glass slide in Canada Balsam. (Figs. 84, 85). Label data:- [S. nigrum. (scratched into glass)] [*Prot austrosimulium opscurum*] [ANIC Database No./ 29 026695] [Australian/ National/ Insect/ Collection (green)] [Holo-/type (red)]. Two labels superimposed—upper [*Cnephia*/sp. A/ undecipherable

mark, {F}, green spot/ Pemberton, W.A/ 28/8/26 A.J.N]. Lower label (Fig. 85) [*Simulium/ nigrum/* (Tonn. ms)/ {F} / (remainder as for superimposed upper label)]. Both in same handwriting. The collector was A.J. Nicholson, (see Waterhouse, 2000). Details of the lower label can be discerned by using strong back lighting, as used here (Fig. 85). The name “*S. nigrum*” was presumably scratched into the glass slide by Tonnoir. Other labels are not by him and were probably applied by either Ian or Margaret Mackerras. The lower label was probably applied before the Mackerras’ settled on the name “*Cnephia* sp. A.”, as inscribed on the upper label.

Etymology. From the Latin ‘*opscurum*’ [= dark], to preserve the sense of Tonnoir’s original unpublished description.

Distribution (Fig. 99). *Western Australia*: Pemberton (ca. S34.4400° E116.0340°, elev. 127m.); Bridgetown (ca. S33.9600° E116.1370°, elev. 168m.).



FIGURES 96–98 Habitats of *Protostrosimulium* immatures. (96) *Prot. pilfreyi*. Oakey Creek, Paddys Road, Australian Capital Territory (S35.3929° E148.9603°), 3-x-2011. (97) *Prot. pilfreyi*. Gibraltar Creek, Tidbinbilla Road, Australian Capital Territory (S35.4499° E148.9785°), 18-ix-2011. (98) *Prot. amphorum*. Deeside Coast Road creek, south Western Australia (S34.4380° E116.3863°), 9-ix-2014. (Image by DCC).

Bionomics. Mackerras & Mackerras (1949: 386) noted that females were collected along with those of what is now referred to as *Nothogreniera occidentalis*, and may also have been biting humans. Nothing else is known about the biology of this species, except that collections were made in August.

Remarks. The specific distinctiveness of *Protaustrosimulium opscurum* has long been recognized. According to Mackerras & Mackerras (1949: 386) "There is no doubt that this species is quite distinct from any other Australian member of the family". In their Table 1: 380, they suggest that *Prot. opscurum* (as *Cnephia* sp. A) is "nr. *terebrans*"—a conclusion supported by the present study. A better understanding of relationships among *Protaustrosimulium* spp. will be gained when the immature stages of *Prot. terebrans* and *Prot. opscurum* are known.

The holotype of *Protaustrosimulium opscurum* from Pemberton, WA, is the only specimen of this species examined by us. The whereabouts of the Bridgetown, WA, material mentioned by Mackerras & Mackerras (*loc. cit.*) is unknown.

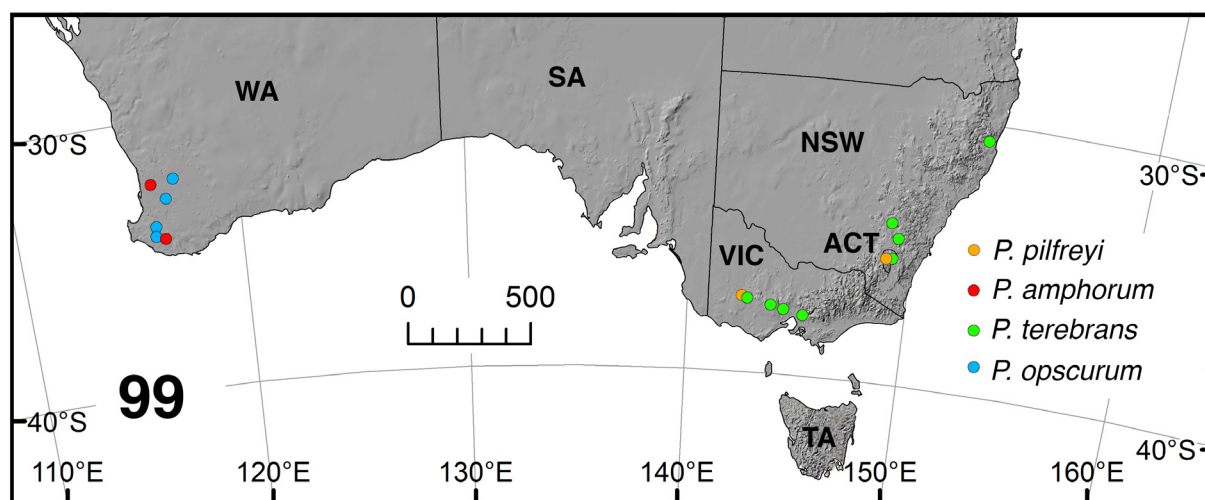


FIGURE 99. Distribution of *Protaustrosimulium*. (99) Map of southern portion of Australia.

Acknowledgements

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