A New Genus, Ectemnoides, for Seven Species of Australian Gondwanan Simuliidae (Diptera) With Description of a Novel Form of Larval Attachment

Authors: Moulton, John K., Currie, Douglas C., and Craig, Douglas A.

Source: Insect Systematics and Diversity, 2(4) : 1-54

Published By: Entomological Society of America

URL: https://doi.org/10.1093/isd/ixy009

Insect Systematics and Diversity, (2018) 2 (4): 4; 1–54
doi: 10.1093/isd/ixy009
Research

Taxonomy

A New Genus, *Ectemnoides*, for Seven Species of Australian Gondwanan Simuliidae (Diptera) With Description of a Novel Form of Larval Attachment

John K. Moulton,[1] Douglas C. Currie,[2] and Douglas A. Craig[3,4]

[1]Department of Entomology and Plant Pathology, The University of Tennessee, 370 Plant Biotechnology Building, Knoxville, TN 37996-4560, [2]Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada, [3]Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada, and [4]Corresponding author, e-mail: d.craig@ualberta.ca

Subject Editor: Brian Wiegmann

Received 13 March 2018; Editorial decision 25 June 2018

Abstract

A segregate of Australian simuliids of Gondwanan provenance with unusual attributes is assigned to a new genus—*Ectemnoides*. Only one species was originally known, that from females of the eastern Australian (Victoria) *Paracnephia umbratorum* (Tonnoir) and its presumed larvae, which we fully confirm here. Three previously unknown related species, *Ectemnoides acanthocranius* n. sp., *Ect. faecofilus* n. sp. and *Ect. uvulatus* n. sp. from Western Australia are described. These four species have numbers of unusual synapomorphies. Of note is the habit of larvae of *Ect. umbratorum* and *Ect. faecofilus* to attach to the ends of constructed threads apparently composed of larval fecal pellets and other material, enclosed within a salivary silk matrix. The four species all have short spine-like setae on the larval head capsule and their body physiognomy is unusual, with head large in relation to a tubular body, with that being semitransparent when alive. Three other Western Australia simuliids, *Ect. absitus* n. sp., *Ect. princeae* n. sp. and *Ect.* sp. A., possess more typical attributes. Known larvae of the first two of these simuliids lack the marked head setae; however, in common with *Ect. acanthocranius* of the previous segregate, larvae of the three taxa lack the anal sclerite and have markedly low numbers of hooks comprising the posterior circlet. Details are given for distribution and, where known, bionomics. Trichomycetes are recorded for the second time from simuliids in Western Australia, from *Ect.* sp. A. Brief character analysis is provided, as are comments regarding historical biogeography.

Key words: Australia, Gondwana, Simuliidae, *Paracnephia*, *Ectemnoides*

Larvae of Simuliidae live in a wide array of flow conditions—ranging from almost stationary to full force of water in cascades (e.g., Crosskey 1990, Craig 2003, Adler et al. 2004, Craig et al. 2006). To deal with this variety of habitats, larvae show morphological adaptations as well as behavioral attributes. Those in full force of the current often clump together to produce 'skimming flow' (Nowell and Jumars 1984). This reduces the drag and such larvae often exhibit an expanded posterior abdomen. Others in thin films of water (madicolous flow) often do not twist the body, typical of most other simuliid larvae, and tend to have an amphora-shaped posterior abdomen (e.g., Craig 2003, Craig et al. 2006). Larvae of North American *Ectemnia* Enderlein are unusual and, although mostly inhabit deep fast flow, build a stalk and attach near the top of it (Moulton and Adler 1997, Stuart and Hunter 1998). The larvae have unusual hypostoma, a grooved ventral abdomen and lack the anal sclerite.

Flow forces involved with body stance and filter-feeding of simuliid larvae are moderately well understood (e.g., Chance and Craig 1986, Lacoursière and Craig 1993, Merritt et al. 1996, Hart and Finelli 1999). This, however, only for larvae that attach to solid substrates and twist the body to present the filter-feeding labral fans into the oncoming current. The labral fans of simuliid larvae, as well as the body, create drag (Chance and Craig 1986, Eymann 1988), so a larva needs a firm substrate upon which to attach. This is done by attaching the circlet of hooks on the posterior proleg of the body to a pad of salivary silk (Barr 1984). A substrate of sandy material is rarely appropriate. Simuliidae larvae do occur in habitats with sandy substrates, but typically use trailing vegetation or woody snags and even larger macroinvertebrates as attachment sites (Crosskey 1965, Lewis et al. 1969). Here, we report on examples of Australian simuliid larvae that attach to the end of a thread extended off the tip of trailing vegetation. Such larvae are tubular, the head is of equal or larger diameter and the body does not twist (Fig. 44).

This paper is a continuation of a series (e.g., Craig et al. 2017, 2018a,b) dealing with Australian Gondwanan Simuliidae that have previously been taxonomically difficult to assign to genus. With this work, the number of fully characterized Australian simuliid genera

stands at six—namely, *Austrosimulium* Tonnoir, *Bunyipellum* Craig, Currie, Moulton, *Ectemnoides* n. gen., *Nothogreniera* Craig, Currie, Moulton, *Paraustrosimulium* Craig, Moulton, Currie, and *Simulium* Latreille. In future publications, the remainder of Australian '*Paracnephia*' Rubtsov will be assigned to two new genera.

Only one species dealt with in this paper had originally been formally recognized. Tonnoir (1925) described *Simulium umbratorum* based on female adults from Mt. Dandenong, Victoria (immediately east of Melbourne). The species was distinctive from all then known Australian Simuliidae, possessing an almost straight vein CuA and with the pretarsal claw tooth directed distinctly laterally. As for many Australian simuliids at the time, immature stages were unknown.

Edwards (1931) discussed similarities between the Australian *S. aurantiacum* Tonnoir and similar South American forms, and placed them all in his subgenus *Cnephia*. Smart (1945) included certain Australian simuliids in *Cnephia* (as a genus) and Mackerras and Mackerras (1949) accepted that, assigning *S. umbratorum* to *Cnephia*, placing the species in their *terebrans*-group. They noted, however, problems with fitting Australian simuliids into *Cnephia* as defined by Smart (1945). Later, they (Mackerras and Mackerras 1950) transferred *umbratorum* to the *aurantiacum* group and in 1952 they described larvae of unusual gestalt, putatively of *umbratorum*.

As the history suggests, taxonomic placement of *umbratorum* has been moot. Crosskey (1987, 1989) considered the species to be of undetermined genus along with the other Australian '*Cnephia*' and at that time to be Prosimuliini. Confirmation that the unusual larvae proposed for *umbratorum* was still not forthcoming. However, Zwick (1997) obtained and described larval material similar to that described by Mackerras and Mackerras (1950), and collected a few pupae, one of which contained a pharate male adult and managed a preparation of the genitalia. Portions of that material were examined for this work. Although male *umbratorum* had not previously been described, wing and leg characteristics from the pharate male, plus a poorly developed female pupa, confirmed association of those immatures with known females of *umbratorum*. Zwick (1997) also discussed taxonomic placement, noting that *umbratorum* neither fitted *Cnephia* (as redefined by Crosskey 1969), nor *Gigantodax* Enderlein.

Crosskey and Howard (1997) on the basis of similarity of larval labral fans of the Australian '*Cnephia*' *strenua* Mackerras and Mackerras to those of the South African *Paracnephia thornei* (De Meillon), transferred *umbratorum* along with the other Australian '*Cnephia*' to the latter genus—at the time still in Prosimuliini and unnecessarily amended the species name to *umbratora* to agree with gender of the genus name. Later, *Paracnephia* was transferred to Simuliini (Adler and Crosskey 2008).

The objectives of this paper are to 1) reassign *umbratorum* and related undescribed species within Australian Gondwana Simuliidae to a new genus, 2) confirm and expand on the larval behavior of some of the species that attached to a thread, and 3) offer comments about historical biogeography and relationship of *Ectemnoides* to other austral simuliid genera.

Materials and Methods

Apart from older pinned specimens of *Ectemnoides umbratorum* (Tonnoir) in the Australian National Insect Collection (ANIC), CSIRO, Canberra, we examined material of this species collected by P. and H. Zwick from the early 1970s and by the present authors variously in 2012, 2014, and 2016. Western Australian material of the other simuliids studied here were collected by J.K.M. in 1996, and by D.C.C. and J.K.M. in 2014, and D.C.C. in 2016. Dissection techniques and photography were as for Craig et al. (2012), and unless indicated, all images are by D.A.C. Terms for most structures follow those of Craig et al. (2012) and are based on Adler et al. (2004); with some exceptions, such as use of claw 'tooth', not thumb. For designation of wing veins (e.g., Fig. 9) we follow Cumming and Wood (2017) and de Moor (2017). We report on the a:b ratio, where a = base of Sc to rm, b = rm to wing tip.

A term applied to the anterolateral arms of the male ventral plate is 'basal arm' (Adler et al. 2004). These arms attach to their respective paramere (e.g., Fig. 55, 102), via what we term a 'paramere connector'. The marked development of that structure here is only seen elsewhere in Australian simuliids in *Bunyipellum gladiator* (Moulton and Adler) (Craig et al. 2018a). Similar expression, however, occurs in other simuliids such as *Prosimulium*, *Greniera*, and *Tlalocomyia* (e.g., Adler et al. 2004).

The pupal gills of *Ect. acanthocranius*, *Ect. faecofilus*, *Ect. umbratorum*, and *Ect. uvulatus* have a unique elongated delicate tubular structure arising from the basal fenestral region. We refer to this as the 'fenestral diverticulum' (e.g., Figs. 24 and 25). The probable homolog is discussed later.

For hypostomal teeth, we use the numbering system employed in Craig et al. (2018a) where the median tooth is deemed '0' and those lateral on either side are numbered in sequence '1, 2, 3, etc.'. Thence the 'lateral or corner tooth' is '4' and the so-called 'paralateral teeth' are designated '5–8' (Fig. 38).

Distributions (Fig. 229) are based on literature localities (e.g., Horne and Pettigrove 1989), databases (e.g., Environmental Protection Agency, Victoria, Australia), label data on collection material (e.g., ANIC) and localities given by various authors herein. Where possible, coordinates are given for localities in degree decimal format (e.g., S32.8708° E116.4524°), with significant decimals indicating accuracy; at best 30 m. If localities for species are widespread, figure captions mention the locality for the material illustrated.

Codons for Institutions Known to Hold *Ectemnoides* Material

ANIC—Australian National Insect Collection, CSIRO, Canberra, ACT, Australia.
EPA—Environmental Protection Agency, Victoria, Australia.
J.K.M.—Private collection of J.K.M., University of Tennessee, Knoxville, TN, USA.
ROM—Royal Ontario Museum, Toronto, Ontario, Canada.
UASM—Strickland Museum, Biological Sciences, University of Alberta. Edmonton, Canada.

Nomenclature

This paper and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:94E9B153-7F16-4FE0-9210-46F174C8060A.

Ectemnoides n. gen.

Type species: *S. umbratorum* Tonnoir, 1925.

(LSID: urn:lsid:zoobank.org:act:6C775ED8-9EEB-49AC-99ED-CE5D9598C757)

Adults: small to medium sized (total body length 1.9–2.9 mm); overall dark colored to blackish. Antenna with nine flagellomeres. *Female*: frons broad; mandible with teeth on both edges of mandible; terminal palpomere V not elongated; wing not pigmented, apices

of R_1 and Rs closely appressed before joining C (*umbratorum*) or not (all others), CuA not sinuous (*umbratorum*), slightly sinuous (*faecofilus*), or moderately sinuous (*acanthocranius*), costa with or without spinous setae on distal half, radius not branched with minor exceptions, M_1 thickened, not doubled, a:b ratios 1.0:2.7–2.8; legs dark brown to blackish, hind basitarsus with calcipala small (*acanthocranius*) or moderately developed with dorsobasal notch (*umbratorum*), tarsomere II with pedisulcus absent to barely expressed; claw tooth if present small; female genital fork with long anterior arm; spermatheca, where known, with either clear area at duct junction or pigment extended down duct; male ventral plate, where known, with small median keel, hirsute; male parameral connector poorly expressed (*umbratorum*, *faecofilus*) to markedly so (*acanthocranius*); parameres present, possibly absent in *umbratorum*, parameral spines possibly absent (*umbratorum*), but present as elongated single or double spines (*faecofilus*, *acanthocranius*), absent (*princeae, absitus*); gonostyli broadly curved distally with one terminal spine (*umbratorum*), or two (*faecofilus, acanthocranius, princeae, absitus*); dorsal plate absent. *Pupa*: thoracic cuticle with or without low clear granules; frontal plate with setae doubled or absent (*acanthocranius*), cuticle with minute granules, pale yellow (*umbratorum*), light brown (*faecofilus, absitus*) or with dense granules and darker pigmentation (*acanthocranius*, *princeae*), facial setae present and with curled tips; gill with two or three long main trunks with 18–20 fine filaments either arising predominantly basally, or three trunks and more typical filaments, or filaments arising directly from base; with or without fenestral diverticulum; pupal abdominal chaetotaxy and armature not markedly expressed; pleurites present, but poorly expressed; grapnel hooks poorly expressed as such, rather as stiff curved setae; dorso-terminal spines small, sharp, not sinuous. *Cocoon*: coarsely woven and unstructured. *Larva*: body either markedly elongated and narrowed, or more typical and smoothly expanded posteriorly (*absitus*); head pattern markedly expressed (*acanthocranius*) or not; head either expanded dorsoventrally anteriorly, or more typical; labral fan either slightly enlarged in size with narrow stalk, or more typical; cephalic apotome either sub-parallel-sided (e.g., *faecofilus, umbratorum, uvulatus*) or expanded posteriorly (e.g., *absitus, princeae*), cephalic cuticle with (e.g., *acanthocranius*) or without (e.g., *princeae*) short spine-like setae; antenna markedly short, colorless, apical antennomere subequal to medial antennomere (*faecofilus, umbratorum*), or longer with apical antennomere subequal to two basal antennomeres (*acanthocranius*), brown, or apical antennomere subequal to medial antennomere (*absitus*), dark brown; mandible with spinous teeth saw-like, serrations and sensillum hair-like (*faecofilus, umbratorum*), well posterior of blade-like region, or with sensillum more cone-like (*acanthocranius*), or all sharply cone-shaped on raised region more typically placed (*absitus, princeae*); hypostomal lateral teeth of unusual configuration with teeth 4–8 forming major lateral structure (*faecofilus, umbratorum*), or flanked by hypostomal cone (*acanthocranius*), or teeth 4–6 slightly protrusive with smaller hypostomal cone (in part, e.g., *acanthocranius, princeae*), one main hypostomal seta per side; suboesophageal ganglion slightly pigmented; anterior proleg elongated, paddles absent; if abdomen elongated, posterior circlet of hooks directed ventrally (*acanthocranius, faecofilus, umbratorum*), if not elongated, body smoothly expanded posteriorly and circlet of hooks directed posteriorly; abdominal cuticle with (*faecofilus, umbratorum*) or without (*absitus, acanthocranius, princeae*) hexagonal patterning; posteroventral tubercles absent; anal sclerite if present with anterodorsal arms absent and only central region and posteroventral arms present (*faecofilus, umbratorum*), or sclerite absent; markedly low numbers of hooks in circlet. Larvae attached, or not, to trailing thread.

Etymology

In reference to behavior of a component of the genus where larvae construct and attach to a thread, reminescent of larvae of the North American genus *Ectemnia*. The gender is masculine (International Code of Zoological Nomenclature, Article 30.1.4.4).

Included Taxa

The following described material is assigned to *Ectemnoides* n. gen. with one new combination established.

Ect. umbratorum (Tonnoir 1925). Type species. New combination
Ect. faecofilus n. sp.
Ect. acanthocranius n. sp.
Ect. uvulatus n. sp.
Ect. princeae n. sp.
Ect. absitus n. sp.
Ectemnoides sp. A.

Distribution (Fig. 229)

Southeastern Australia (Victoria): *Ect. umbratorum*.
Western Australia: *Ect. absitus*; *Ect. acanthocranius*; *Ect. faecofilus*; *Ect. princeae*; *Ectemnoides* sp. A, *Ect. uvulatus*.

Key to *Ectemnoides* Species

Larvae (larvae of *Ect.* sp. A, known only from partial exuviae)

1. Head capsule (slide mounted) with short spine-like setae (Fig. 32) 2
- Head capsule (slide mounted) lacking short spine-like setae (Fig. 170) 3

2. Abdominal cuticle with hexagonal pattern (Fig. 41), anal sclerite present (Fig. 42) 4
- Abdominal cuticle lacking hexagonal pattern, anal sclerite absent (Fig. 121) ..... *Ect. acanthocranius*; *Ect.* sp. A
3. Body elongated, anterior proleg markedly elongated, circlet of hooks not markedly small (Fig. 169) ..... *Ect. princeae*
- Body not markedly elongated, anterior proleg not markedly elongated, circlet of hooks markedly small (Fig. 210) .... *Ect. absitus*
4. Postgenal cleft U-shaped, extended 0.5× distance to hypostomal groove (Fig. 37). Hypostoma with lateral teeth (4–8) fused basally into single structure (Figs. 38 and 73) 5
- Postgenal cleft small, angulate, extended 0.3× to hypostomal groove (Fig. 116). Hypostoma teeth all subequal, lateral structure formed by hypostoma, not teeth (Fig. 117) .... *Ect. acanthocranius*
5. Postgenal cleft lacking medial projection (Fig. 37), larvae attached to threads (Fig. 44) ..... *Ect. umbratorum* (Victoria); *Ect. faecofilus* (Western Australia)
- Postgenal cleft with medial projection (Fig. 133), larvae not on threads ..... *Ect. uvulatus*

Pupae (only partially known for *Ect. uvulatus*)

1. Gill, two main trunks with fine filaments (Figs. 24 and 25), basal fenestral diverticulum present (poorly expressed in *Ect. acanthocranius*)..... *Ect. uvulatus* 2
- Gill, not as above (Figs. 163, 206, and 224) 3
2. Frontal plate of female, narrow, ovoid, frontal setae doubled (Fig. 60) ..... *Ect. umbratorum*; *Ect. faecofilus*.
- Frontal plate of female, broader, angulate, frontal setae absent (Fig. 103) ..... *Ect. acanthocranius*

3. Gill, three main trunks with fine filaments (Fig. 163) .... *Ect. princeae*
- Gill, three trunks with thicker filaments, or lacking trunks (Figs. 206 and 224) ..... *Ect. absitus*; *Ect.* sp. A.

Adults (Adults of *Ect.* sp. A, and *Ect. uvulatus* are unknown)
1. Western Australia 2
- Eastern Australia ..... *Ect. umbratorum*
2. Wing lacking substantial spinous setae on costa (Fig. 86) 3
- Wing with substantial spinous setae on costa (Fig. 50) .... *Ect. faecofilus*
3. Calcipala small, but distinct (Fig. 87) ..... *Ect. acanthocranius*
- Calcipala essentially absent (Fig. 146) .... *Ect. princeae*; *Ect. absitus*

Ect. umbratorum (Tonnoir), n. comb (Figs. 1–44)

S. umbratorum Tonnoir 1925: 238 (Original description, female only).

Cnephia umbratorum, Mackerras and Mackerras 1949: 385 (New combination. Assigned to *terebrans* species-group).

C. umbratorum, Mackerras and Mackerras 1950: 167 (Transferred to *aurantiacum* species-group).

C. umbratorum, Mackerras and Mackerras 1955: 104 (Description of possible larvae).

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

C. umbratorum, Zwick 1997: 49 (Description of new material, discussion of taxonomic placement).

'*Cnephia*' *terebrans*, Moulton and Adler 1997: 1907. Not *terebrans*.

P. umbratora, Crosskey and Howard 1997: 18, 117 (Unnecessary emendation. Prosimuliini, unplaced to subgenus, new combination).

P. umbratorum, Bugledich 1999: 329 (Compilation of data).

'*Cnephia*' *umbratorum* Tonnoir, Moulton 2000: 98. 2003: 47 (Molecular analysis).

P. umbratora, Crosskey and Howard 2004: 10 (Prosimuliini, unplaced to subgenus).

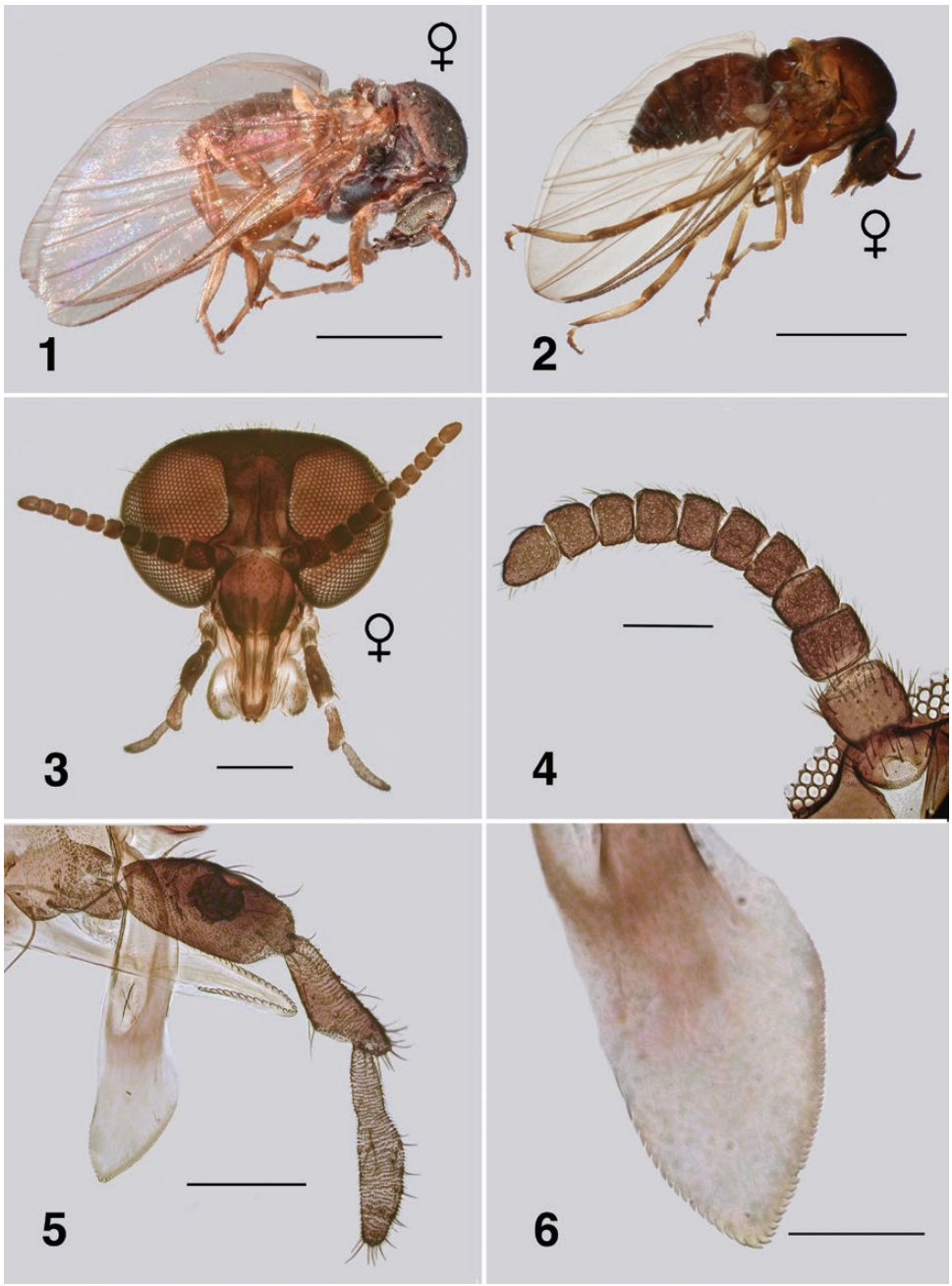
P. umbratora, Adler and Crosskey 2008: 26 (Transferred to Simuliini, unplaced to subgenus)

P. umbratora, Adler and Crosskey 2018: 30 (Unplaced to subgenus).

Ect. umbratorum (Tonnoir 1925) (New combination).

Adult Female (based on one paratype, plus four other specimens from ANIC, plus material from Zwick, Moulton, and Craig). *Body* (Figs. 1 and 2): head and thorax overall dark brown, with abdomen dark brown anteriorly, vestiture yellow; total length 1.9–2.7 mm. *Head* (Fig. 3): overall evenly dark brown; frons broad; upper ommatidia sometimes lighter; width 0.57–0.68 mm; depth 0.51–0.61 mm; postocciput dark brown, vestiture sparse; frons dark brown, essentially bare; frons:head ratio 1.0:4.6. *Eyes*: interocular distance 0.15–0.16 mm; ommatidia diameter 0.018 mm; ca. 37 rows across and down at mid-eye. *Clypeus*: width 0.24–0.26 mm; dark brown, vestiture of sparse fine hairs apically, lateral edges slightly angulate. *Antenna* (Fig. 4): evenly dark brown; extended well beyond head margins; total length 0.61–0.81 mm; nine flagellomeres, scape small, pedicel angulate, slightly larger than flagellomere I, flagellomeres II–X subequal in size and shape, flagellomere IX bluntly cone-shaped. *Mouthparts*: substantial, ca. 0.5× length of head depth; maxillary palp (Fig. 5), total length 0.55 mm, palpomeres I & II small, palpomere III ovoid, darker brown than remainder, not extended distally beyond articulation with palpomere IV, sensory organ spherical, 0.3× length of palpomere III, palpomere IV with apex extended laterally, palpomere V (distal) not markedly elongate; proportional lengths of III–V palpomeres 1.0:0.8:1.0; mandible (Fig. 6) with ca. 15 outer and 34 inner even teeth; lacinia with 14 inner and 21 outer teeth; cibarium (Fig. 7) central depression broadly U-shaped, cornuae not marked developed, lacking sculpture. *Thorax*: noticeably domed; length 1.1–1.2 mm; width 0.8–0.9 mm; pronotal lobe well developed, with longer hairs than on scutum, that overall with even sparse fine pale hairs, vittae visible in some lighting; scutellar depression with long coarse black hairs laterally; scutellum slightly paler than scutum, vestiture also of with long coarse black hairs laterally; postnotum slightly lighter than with scutellum; anteprotonal lobe (propleuron) with long fine yellowish hairs, proepisternum bare; fore coxa bare; anepisternal evenly dark brown, membrane without hairs (Fig. 10); katepisternum dark brown, sulcus distinct. *Wing* (Fig. 9): slightly dusky apically as on anal lobe; length 2.7–3.0 mm; width 1.2–1.5 mm; a:b ratio 1.0:2.7; small basal cell present; veins yellowish, Rs not branched, but slightly thickened distally, closely applied to R_1, costa with spiniform setae, not markedly developed, interspersed with hair-like setae (Fig. 8), M_1 thickened, not obviously double, CuA only slightly sinuous. *Haltere*: stem light orange, knob pale. *Legs* (Fig. 2): bicolorous, medium brown and yellow, darker on posterior femora and tibiae; hind basitarsus with row of markedly stout spines; calcipala about as long as wide with dorsobasal notch (Fig. 11); pedisulcus poorly developed (Tonnoir 1925: did not illustrate it. Mackerras and Mackerras 1949: show it as given here); tarsomere II 2.8× longer than distal width; claw (Fig. 12), with main talon elegantly curved, slightly serrated on inner edge, basal tooth ca. 0.3× as long as claw, distinctly peg-like, well separated from claw and slightly off-set from line of claw, various, smaller on some claws, even on same leg, heel minute. *Abdomen* (Fig. 13): basal scale grayish brown, vestiture not markedly elongated; segment II yellow, III darker, remainder dark grayish brown, tergites not markedly pigmented or sclerotized, vestiture of sparse small hairs, vestiture on pleurae moderately developed and yellow, increasingly so posteriorly. *Genitalia*: sternite VIII evenly pigmented medially, vestiture of rows of microtrichia, large strong hairs posterolaterally; hypogynial valves (Fig. 14), broad, lightly pigmented, vestiture of microtrichia with scattered setae, median edges of valves straight to slightly divergent, not markedly strengthened on median edge, slightly flanged apically; genital fork (Fig. 15) with stem narrowed, pigmented, substantial, knee bend at junction with lateral arms broadly expanded and angulate, lateral arms with distinct cone-shaped apodeme posterolaterally, lateral plates angulate; spermatheca ovoid, externally smooth, internal fine spines (acanthae) present, but hard to observe, no clear area at spermathecal duct junction, pigmentation continued for short distance along duct (Fig. 16); cerci in lateral view bluntly rounded, occasionally with apical depression; anal lobes low, broadly rounded (Fig. 17).

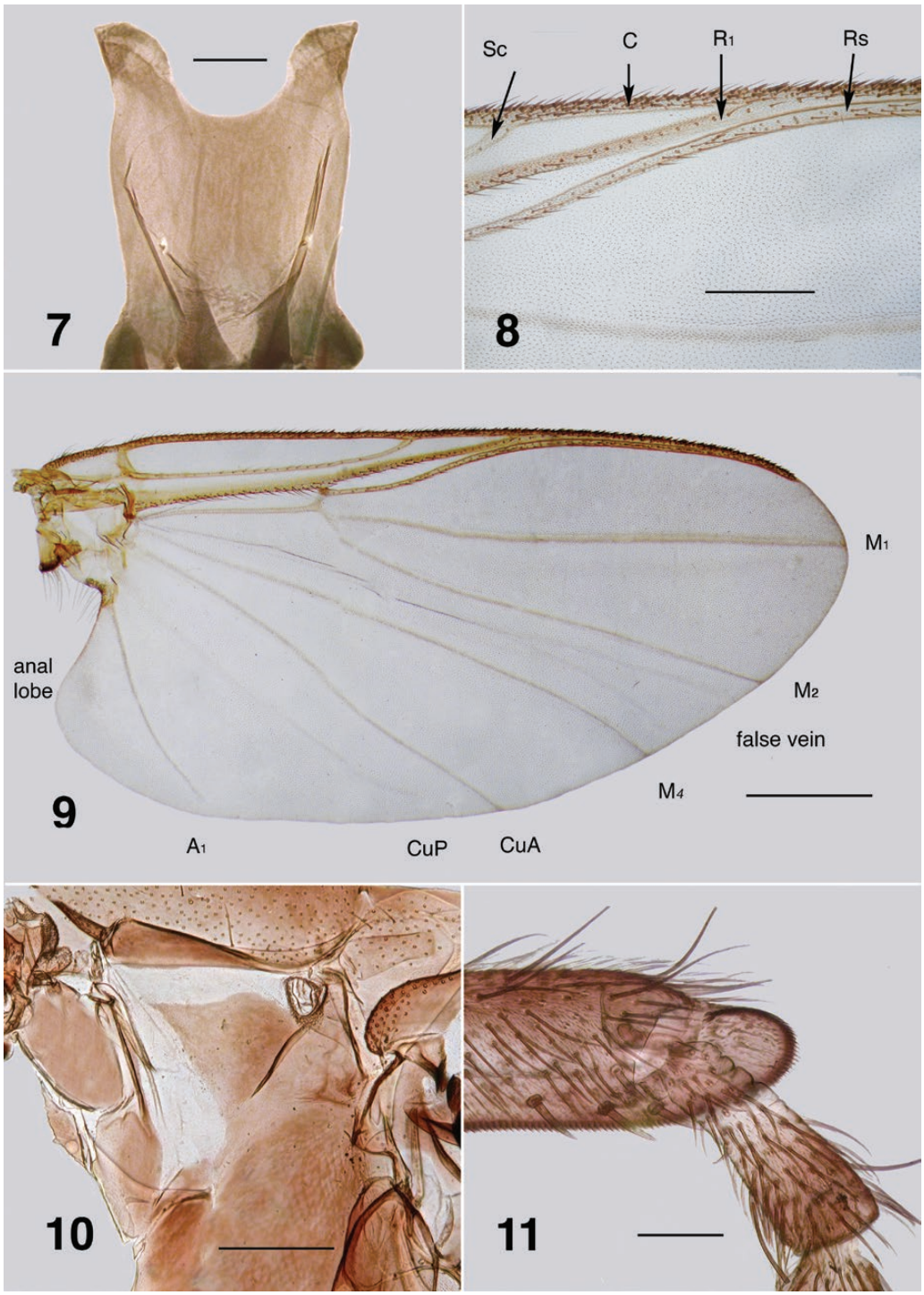
Adult male (based on a single damaged pharate specimen from Zwick material). Head (Fig. 18). Wing. (not illustrated), length ca. 3.4 mm, width ca. 1.8 mm. *Antenna* (Fig. 19): length 0.5 mm; evenly medium brown; flagellomere I longer than wide, flagellomeres II–VIII subequal in size, flagellomere IX slightly elongated, rounded apically *Maxillary palp* (Fig. 20): light brown, length 0.4 mm, palpomeres III & IV subequal in length, palpomere V longer, proportional lengths 1.0:0.9:1.3; mandible and lacinia haired apically. *Genitalia* (Fig. 21): gonocoxa narrow, 2.5× as long as maximum width, vestiture of sparse fine hairs; gonostylus ca. 3.0× longer than basal width, smoothly curved, vestiture of fine sparse hairs, one short apical spine; ventral plate 2.0× wider than length, broadly concave posteriorly,



Figs. 1–6. *Ectemnoides umbratorum* female. (1) Habitus, paratype (Mt. Dandenong). Pinned. Scale bar = 1.0 mm. (2) Habitus (Grampians). Alcohol. Scale bar = 1.0 mm. (3) Frontal view of the head, cleared (Narbethong). Scale bar = 0.2 mm. (4) Antenna (Narbethong). Scale bar = 0.2 mm. (5) Maxillary palp, mandible, and lacinia. Paratype. Scale bar = 0.1 mm. (6) Mandible (Acheron). Scale bar = 0.05 mm.

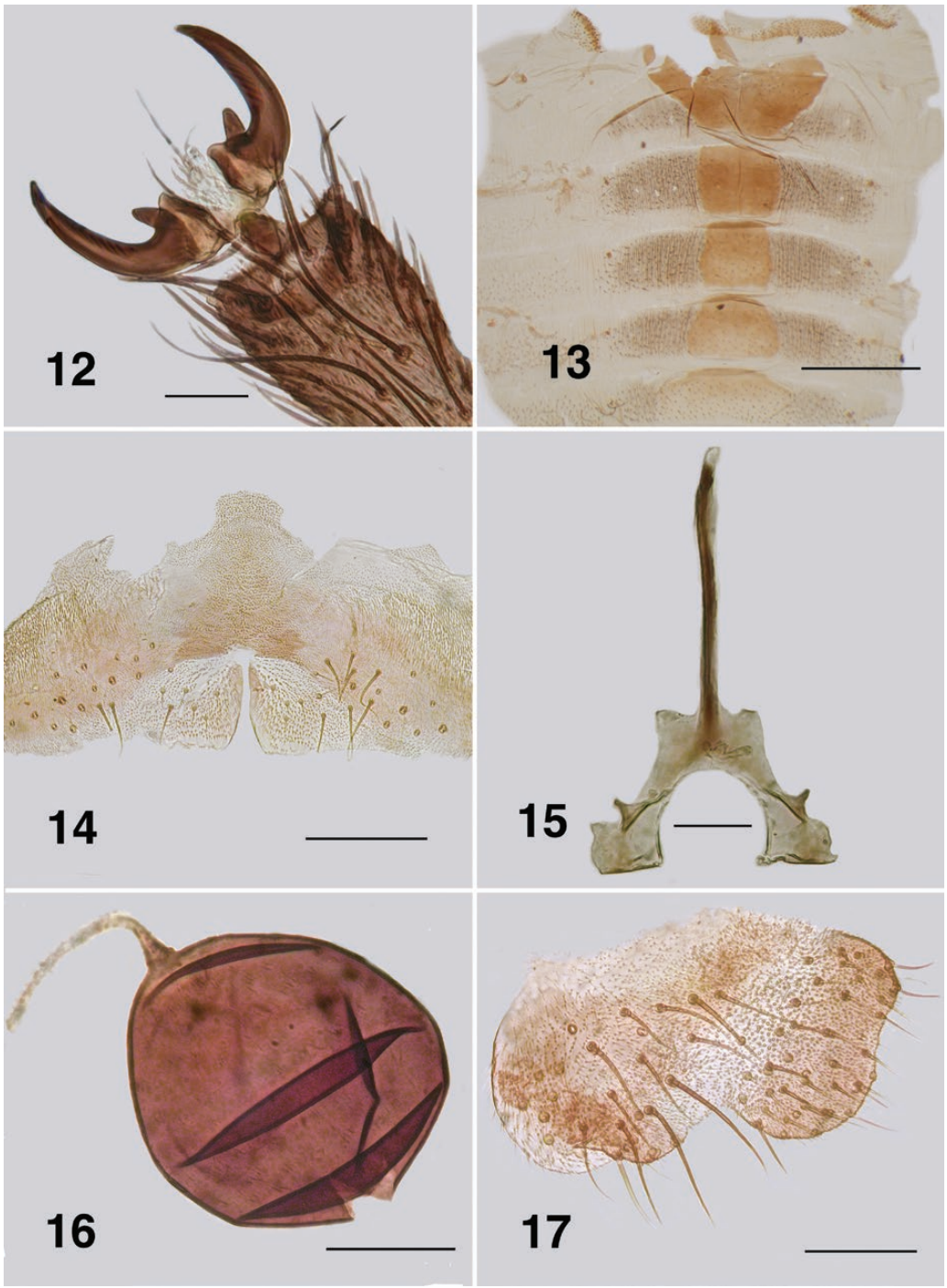
lobed laterally, broadly concave anteromedially; vestiture of coarse hairs; distinct central keel; basal arms narrowed, tapered smoothly; parameral connectors, plates and spines not observed; median sclerite well developed, expanded distally. Cerci well expressed.

Pupa (based on two partial exuviae plus damaged pharate male. Male from Acheron River, female from the Grampians). *Body*: length; male 3.5 mm (Fig. 22) cuticle essentially colorless. *Head*: frontal plate of female bluntly ovoid and ratio of frons width to vertex width 1.0:1.5 (Fig. 26); that of male narrowed with pointed vertex; ratio 1.0:1.8 (Fig. 27), covered with barely visible minute clear tubercles; facial setae elongated and curled, frontal setae doubled, bifurcated. *Thorax*: anterior dorsal shield apparently smooth, but with small clear tubercles, dorsocentral setae long, substantial and curled apically (Figs. 22 and 23). *Gill* (Fig. 24): total length 2.6–2.8 mm; markedly elongated and fine, light brown; single basal trunk with fenestra enlarged and longer than typical—associated is a markedly thin-walled tubular structure, termed the 'fenestral diverticulum' (Fig. 25); gill base bifurcating into two moderately long secondary trunks, further divided into 17 or 18 long thin filaments, with occasional shorter filament. Surface proximally pseudoannulated (i.e., annulations do not continue completely around the filament) to fully annulated, finely distally. *Abdomen* (Figs. 28 and 29): cuticle covered with minute tubercles; armature not markedly developed; tergites I, II, with four finely curved hairs; tergite III with three finer curved hairs and two on the pleural region; tergite IV similar but lacking plural hairs; tergite V with hairs; tergites I–IV lacking other armature; tergite VI with anterior row of spine comb and two



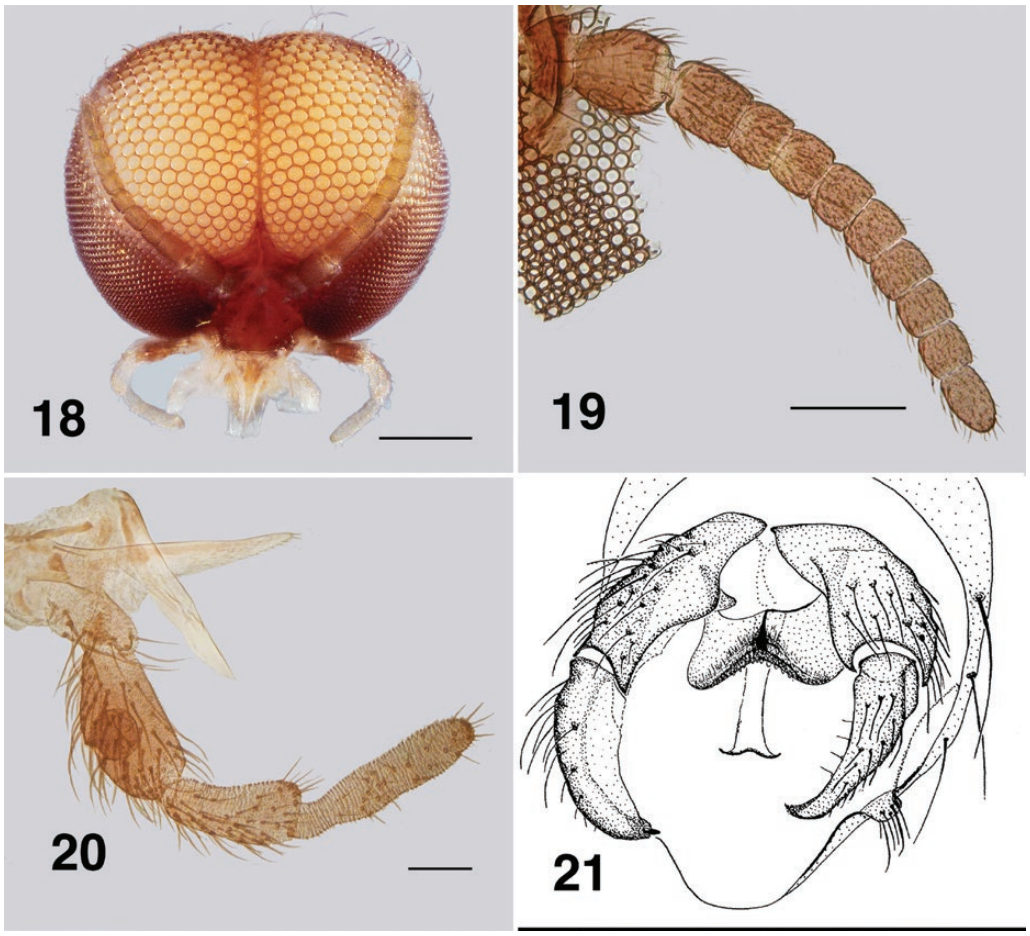
Figs. 7–11. *Ectemnoides umbratorum* female. (7) Cibarium (Acheron). Scale bar = 0.05 mm. (8) Wing veins (Acheron). Sc – subcosta; C – costa; R_1 – radius; Rs – radial sector. Scale bar = 0.1 mm. (9) Wing (Acheron). A_1 – anal; CuA, CuP – cubital; M_1, M_2, M_4 – medial. Scale bar = 0.5 mm. (10) Anepisternal membrane, cleared (Grampians). Scale bar = 0.2 mm. (11) Hind basitarsus and tarsomere II (Narbethong). Scale bar = 0.05 mm.

posterior hairs; tergite VII similar, but with one hair; tergite VIII with finer spine comb and two grapnel hooks; tergite IX with two terminal spines not markedly developed, but substantial and sharply tapered, not markedly curved; tergites II, III, IV extended ventrally onto pleural region, but separate from the respective sternites, segment V lacking pleurite, but with single substantial hair; segments VI, VII similar with two and one hair respectively; sternite II lacking armature; sternite III with four fine hairs; sternite IV with two substantial hairs and three branched hairs; sternite V with two substantial hairs and marked sockets, one single fine hair and one branched hair; sternite VI with single substantial hook and large base, one other moderately substantial spine-like hair and two finer ones; sternite VII with single spine and enlarged base; sternite VIII with two grapnel hooks; sternite IX with two fine posteriorly-directed hairs, two other smaller hairs and two grapnel hooks. *Cocoon* (based on single male pupa; Acheron River). Coarse weave, silk fibers not markedly thick; shapeless bag covering much of the abdomen; sparse material from substrate incorporated.



Figs. 12–17. *Ectemnoides umbratorum* female. (12) Tarsal claws (Narbethong). Scale bar = 0.02 mm. (13) Abdominal tergites ((Narbethong). Scale bar = 0.5 mm. (14) Hypogynial valves, paratype (Mt. Dandenong). Scale bar = 0.1 mm. (15) Genital fork, paratype (Mt. Dandenong). Scale bar = 0.05 mm. (16) Spermatheca, paratype (Mt. Dandenong). Scale bar = 0.05 mm. (17) Cercus and anal lobe, paratype (Mt. Dandenong). Scale bar = 0.05 mm.

Larva (based on last instar larvae from Acheron and Grampians). *Body* (Fig. 30): total length 5.5–6.3 mm; depending on habitat the larvae can range from almost transparent to grayish yellow. *Head* (Fig. 31): evenly markedly pale with sclerotized structures dark; total length 0.8 mm, width 0.6 mm; distance between antennal bases 0.5 mm; antennal phragma markedly expressed posteromedially; anterior margins of head subparallel, posterior of the stemmata slightly convergent; apotome narrow, head spot pattern positive, but barely obvious; ecdysial lines well visible, essentially parallel and straight until extreme posterior of head, then rounded; cervical sclerites, small, separate from darkly pigmented, finely sclerotized postocciput; apotome with short stout secondary setae producing roughened spotted appearance (Fig. 32), posterior third bare, genae also with such setae (Fig. 37); suboesophageal ganglion lightly pigmented (as for *Ect. faecofilus*, e.g., Fig. 68). *Antenna* (Fig. 33): markedly pale and hard to observe; extended to only half length of labral fan stem; total length 0.25 mm; basal antennomere short, medial and apical antennomeres subequal in length; proportional lengths of antennomeres 1.0:1.5:1.3. *Labral fan*: stalk thin and elongated, ca. 50 markedly fine rays, length 0.84 mm, mid-ray



Figs. 18–21. *Ectemnoides umbratorum* pharate male (Acheron). (18) Frontal view of the head. Scale bar = 0.2 mm. (19) Antenna. Scale bar = 0.1 mm. (20) Maxillary palp, lacinia, mandible. Scale bar = 0.05 mm. (21) Genitalia, oblique ventral view. Original by H. Zwick, used with permission.

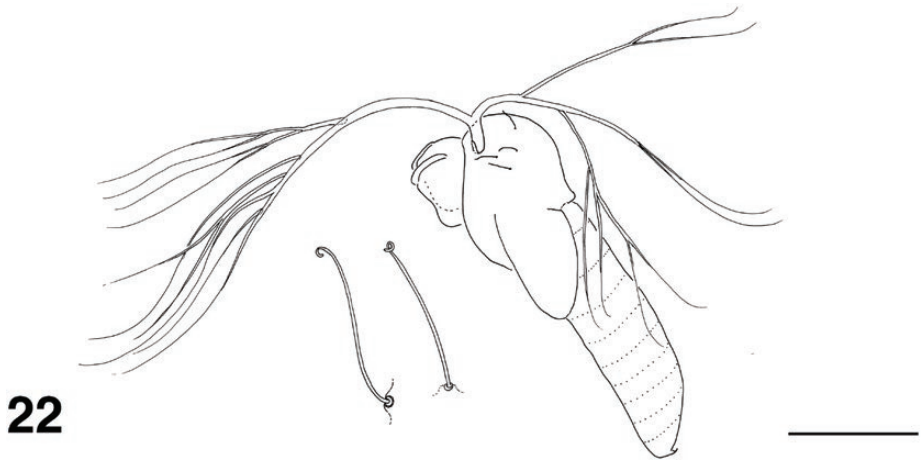
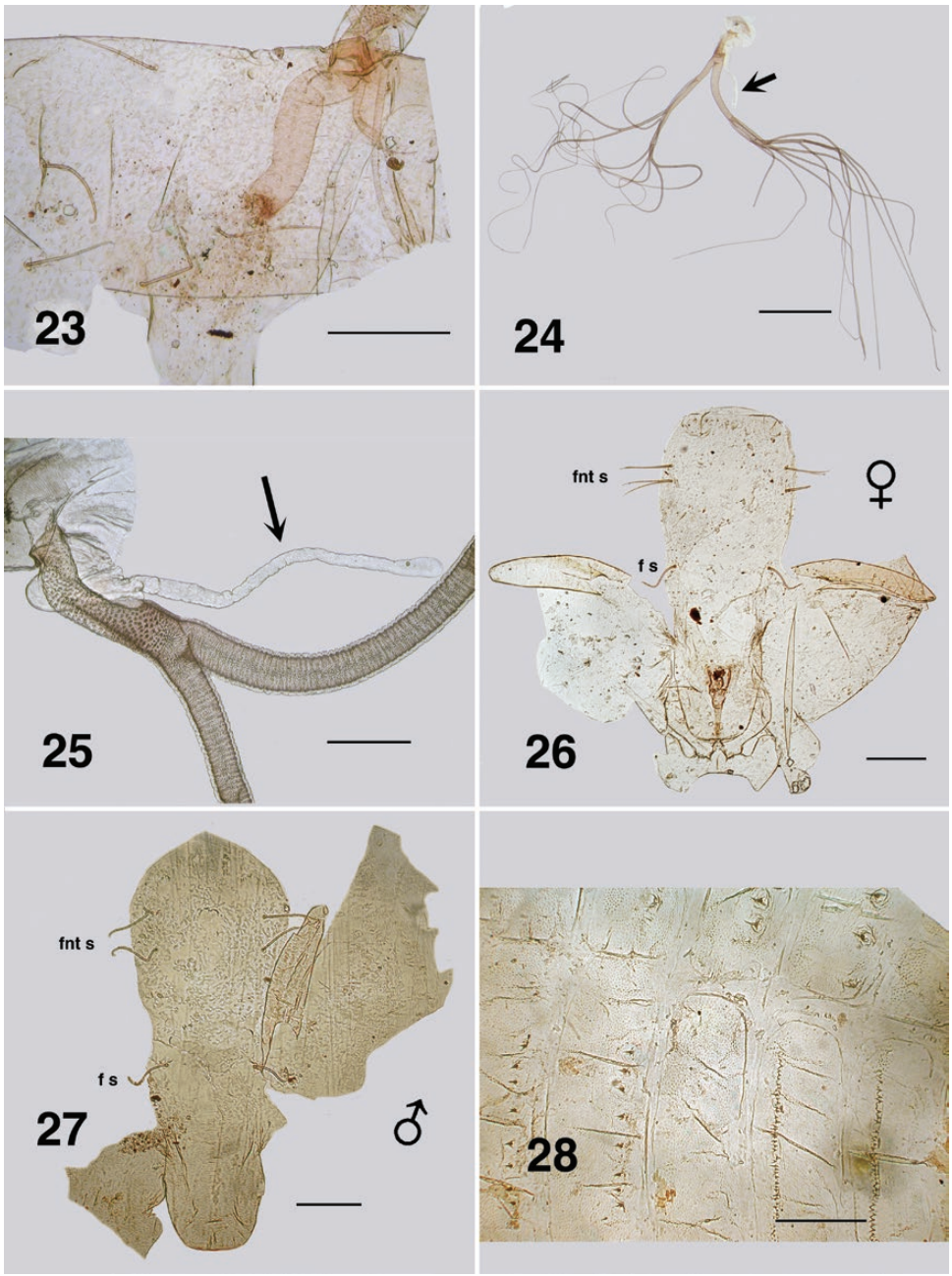


Fig. 22. *Ectemnoides umbratorum* pupal habitus. Insert: dorsocentral thoracic hairs. Original as for Fig. 21. Scale bar = 1.0 mm.

width 0.01 mm; microtrichia 0.008 mm in length, no distinct pattern. *Maxilla* (Fig. 34): maxillary lobe cone-shaped, palp elongated, and curved, 4.0× as long as basal width; tuft of hair at base of palp not markedly expressed. *Mandible* (Figs. 35 and 36): overall lightly pigmented and slightly elongated; brushes reduced; outer apical teeth poorly developed; apical tooth not markedly produced; subapical teeth not obvious; ca. 8 markedly cone-shaped spinous teeth; sensillum and serration present merely as fine spines posterior of slightly convex blade-like region. *Postgenal cleft* (Fig. 37): well developed, deeply U-shaped, sclerotized anterolaterally of poorly expressed posterior tentorial pits, small posteromedial projection; postgenal bridge without stout setae; ratio of hypostoma, postgenal bridge and postgenal cleft 1.0:1.5:0.8; suboesophageal ganglion pigmented light gray. *Hypostoma* (Fig. 38): unusual configuration, darkly pigmented; tooth 0 (median) and teeth 1, 2, 3 (sublateral) small, subequal and depressed below general line of remaining teeth, tooth 4 (lateral) massive and flattened apically; teeth 5–8 (paralaterals) teeth recurved toward tooth 4; lateral serrations



Figs. 23–28. *Ectemnoides umbratorum* pupa. (23) Thoracic cuticle (Acheron). Scale bar = 0.2 mm. (24) Gill, from histoblast (Grampians). Arrow indicates fenestral diverticulum. Scale bar = 0.2 mm. (25) Gill base. Arrow as for Fig. 24. Scale bar = 0.5 mm. (26) Head capsule, female (Grampians). f s – facial setae; fnt s – frontal setae. Scale bar = 0.2 mm. (27) Head capsule, male (Acheron). Incomplete. Abbreviations: as for Fig. 26. Scale bar = 0.2 mm. (28) Abdominal armature (Acheron). Scale bar = 0.2 mm.

poorly expressed; one main hypostomal seta on each side; 2 or 3 other small setae variously arrayed more basally. *Thorax* (Fig. 40): prothorax grayish brown, remainder of thorax lighter; the mature pharate pupal gill with filaments directed ventrally then broadly posteriorly to produce a broad U-shaped structure with opening dorsal; one basal branch showing anteriorly. *Prothoracic proleg* (Fig. 39): markedly elongated, lateral plates distinct and elongated V-shaped. *Abdomen*: evenly mottled medium yellowish gray—various—almost transparent in some populations; cuticle with hexagonal patterning (Fig. 41). *Ventral tubercles*: absent. *Anal sclerite* (Fig. 42): markedly reduced, anterodorsal arms absent, remainder simply two lightly sclerotized posteroventral arms, (as indicated by campaniform sensilla), clear cuticular ring around circlet of hooks present, well expressed adjacent to posteroventral arms, less so elsewhere. *Posterior circlet*: markedly directed ventrally; ca. 60 rows of hooks, 6 or 7 per row (total ca. 390).

Type Material

Holotype

Tonnoir (1925) stated that the holotype was in the Cawthron Institute (Nelson, New Zealand) and that three paratypes were in his possession. Mackerras and Mackerras (1949: 385) recorded that the holotype was in Canberra, as does Bugledich (1999) with that and other types in ANIC. The holotype was not available for our

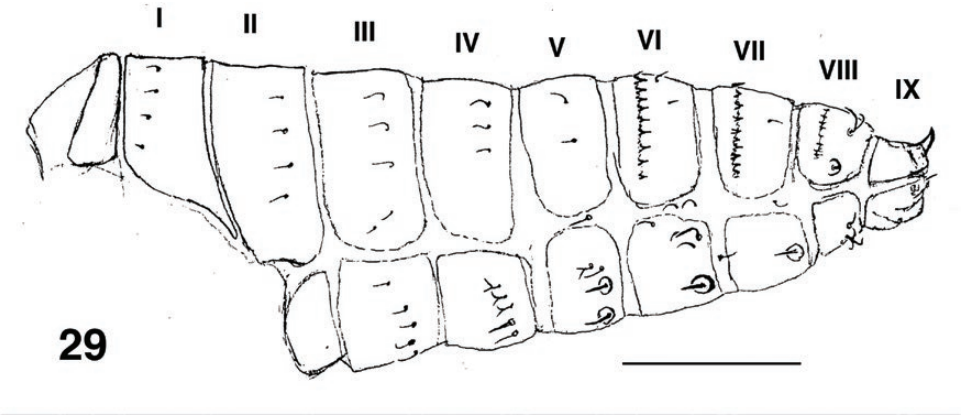
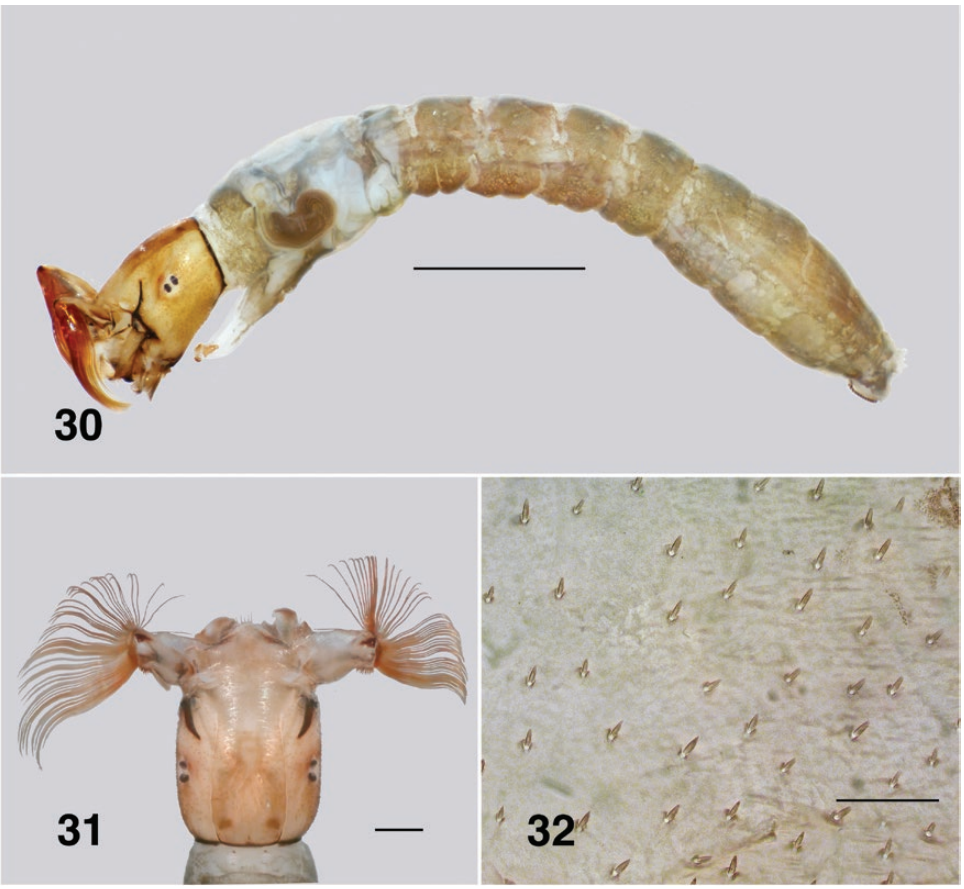


Fig. 29. *Ectemnoides umbratorum* pupal abdominal chaetotaxy and armature. Modified—original by H. Zwick. Used with permission. Scale bar = 0.5 mm.



Figs. 30–32. *Ectemnoides umbratorum* last instar larva (30) Habitus (Grampians). Scale bar = 1.0 mm. (31) Dorsal view of head (Grampians). Scale bar = 0.2 mm. (32) Cephalic setae. Scale bar = 0.05 mm.

examination, so exact label data is unknown, but no doubt as for the paratype.

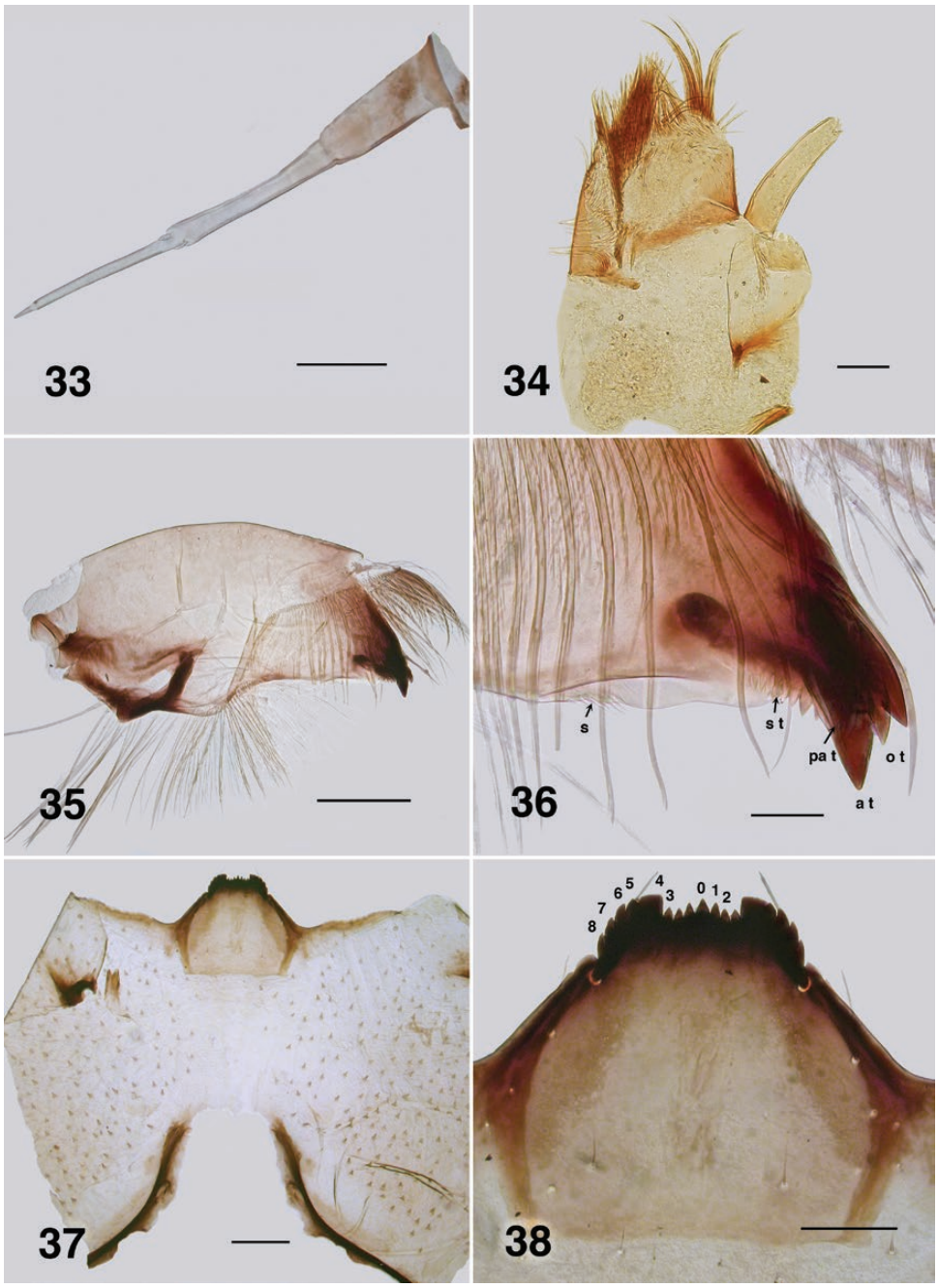
Tonnoir (1925) gave the type locality as Fern Tree Gully, Mt. Dandenong, (Melbourne), Victoria, 25. x. 1921. (*ca*. S37.8800° E145.3200° elev. 255 m). This site is southwest in the Dandenong Ranges National Park (east of Melbourne and adjacent to Upper Ferntree Gully suburb) and probably was Fern Tree Gully Creek. As are many of the earlier localities for Australian simuliids, the creek, albeit in a National Park, is now seriously impacted by human activities and there are no simuliids in the foul trickle of water exiting the Park. Tonnoir would weep!!!

Paratype

Label data: (Fern tree gy/ 25 October 1921/ A. Tonnoir/ Victoria) (PARATYPE. / Simulium umbratorum/ A. Tonnoir det.) (ANIC Database No./ 29 031820) (Aust. Nat./Ins. Coll.). Originally as pinned specimen (Fig. 1), now as slide mount. There was only this single paratype available in ANIC (D.A.C., personal observation 2014). Whereabouts of the other two is unknown.

Additional Material

Apart from the paratype, there were six other pinned females. Four slide mounts by H. Zwick of larval and female parts (ANIC

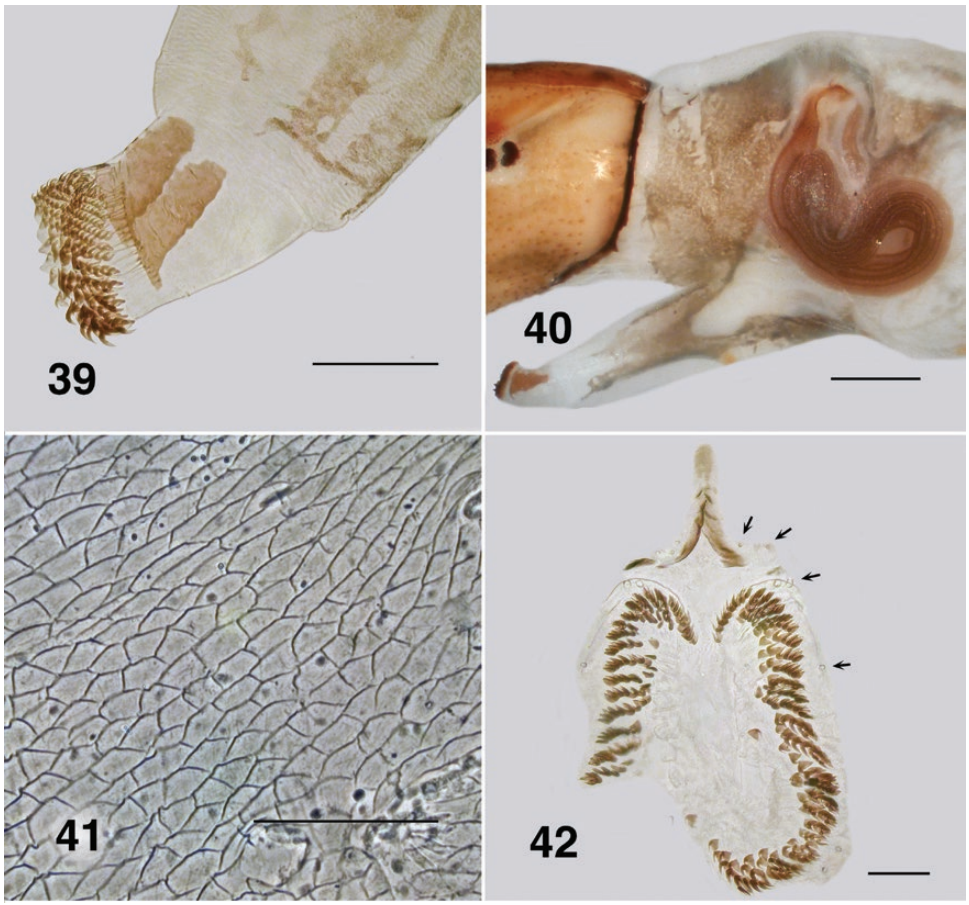


Figs. 33–38. *Ectemnoides umbratorum* last instar larva (Grampians). (33) Antenna. Scale bar = 0.05 mm. (34) Maxilla. Scale bar = 0.05 mm. (35) Mandible. Scale bar = 0.1 mm. (36) Mandible apex. Abbreviations: a t – apical tooth; o t – outer teeth; sub t – subapical teeth; s – serrations and sensillum; s t – spinous teeth. Scale bar = 0.02 mm. (37) Postgenal cleft. Scale bar = 0.1 mm. (38) Hypostoma. Numbers indicate teeth. Scale bar = 0.05 mm.

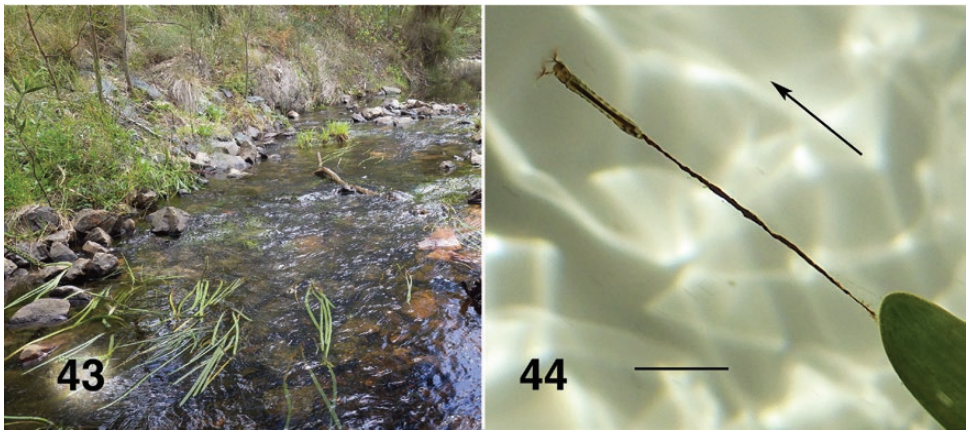
Database No./ 29 026699–29 026702) plus two alcohol tubes of larvae and adults (ANIC Database No./ 29 026703, 29 026704) of that 1972 material. Twelve other slides of various stages, locations and collectors (ANIC Database No./ 29 026716–726). Newer material in alcohol, from the present authors, is deposited in the Strickland Museum (UASM# 370858–370860).

Distribution (Fig. 229)

Victoria: Glenelg River (Upper), Red Hill Road, S37.3455° E142.3261°, elev. 293 m., larvae, adults, 10-XI-1994 to 3-X-2011, EPA; Jimmy Creek, Grampians Road, S37.3728° E142.5069°, elev. 322 m., larvae, adults, 13-X-1997, EPA; Fitzroy River, T and W Track, Drumborg, S38.0755° E141.4289°, elev. 95 m., adults, 17-X-1995, EPA; Betka River, Hard-to-Seek Track, Genoa, S37.5314° E149.5853°, elev. 80 m., adults, 17-XI-1994, EPA; Lerderberg River, O'Brien's Crossing, S37.4961°, E144.3611°, elev. 455 m., larvae, 8-X-1999, EPA; Aire River, Aire Valley (Binns) Road, Beech Forest, S38.6672° E143.5829°, elev. 321 m., larva, 27-III-2002, EPA; Acheron River, near Narbethong, S37.5000° E145.6000°, elev. 351 m., 4-VII-1972, larvae, pupae; 22-IX-1972, adults. Coll. Zwick (ANIC); Narbethong, female—biting, 15-X-1957, ANIC; Stream near Kinglake, S37.2600° E145.2700°, females, larvae, 22-IX-1972, Zwick, ANIC; Otway Ranges, Forrest Road, near Forrest, S38.5600° E143.6900°, female, 12-X-2002, A. Zwick,



Figs. 39–42. *Ectemnoides umbratorum* larva (Grampians). (39) Anterior thoracic proleg. Scale bar = 0.1 mm. (40) Lateral view of pupal gill histoblast. Scale bar = 0.2 mm. (41) Abdominal cuticle. Phase contrast. Scale bar = 0.05 mm. (42) Posterior proleg, circlet of hooks, anal sclerite. Arrows indicate campaniform sensilla. Scale bar = 0.05 mm.



Figs. 43 and 44. *Ectemnoides umbratorum* habitation and habitus. (43) Typical habitat. Wannon River, Grampians. November 2014. Note the Water Ribbons, *Cycnogeton procerum*. (44) Penultimate larval instar trailing on thread. Wannon River, Grampians. November 2014. Arrow indicates the direction of flow. See Supp Material for brief video.

cleared and mounted, ANIC; Otway Ranges, Barwon River, east branch, below Lake Elizabeth, S38.55067° E143.74622°, elev. 295 m., larvae, 21-IX-1986, Horne and Pettigrove (1989); Beaconsfield, East Melbourne, S38.0400° E145.3600°, elev. 56 m., females, 6-XI-1923, G. F. Hill; 6-XI-1923, female. A. L. Tonnoir, ANIC; Gould, S38.0100° E146.3500°, September, Douglas, ANIC; McKenzie Falls, Grampians National Park, S37.5310° E145.7730°, females, September, Neboiss, ANIC; King Parrot Creek, Kinglake West, S37.2690° E145.2713°, October, Neboiss, ANIC; Boho, nr. Benalla, S36.6790° E145.7736°, August, Douglas, Mackerras and Mackerras (1955: 105); Grampians. 27-IX-1953, female, Neboiss (ANIC); Grampians. McKenzie Falls. female, 26-IX-1953, Neboiss ANIC; Grampians, Rose Creek Road, S36.9637° E142.4460°, elev. 220 m., females, 27-IX-1996, J.K.M., UASM; Grampians, Lodge

Road, Earl's culvert, S37.1696° E142.3488°, elev. 240 m., larvae, pupae, 11-IX-2011, D. A. and R. E. G. Craig, UASM; Grampians, Roses Gap Road, Troopers Creek, S36.9579° E142.4631°, alt. 190 m., larva, adult, 14-IX-2011, D. A. and R. E. G. Craig, UASM; Grampians, Serra Road, Wannon River Bridge, S37.3486° E142.5065°, elev. 330 m., larvae, 11-IX-2014, D. A. and R. E. G. Craig, UASM; Grampians, Syphon Road Bridge, Glenelg River, 'Big Cord', S37.3123°, E142.3671°, elev. 260 m., 11-IX-2014; pupal exuviae, 26-XI-2014, D. A. and R. E. G. Craig, UASM; Grampians, Red Hill Road, Glenelg River, S37.3455°, E142.3262°, elev. 290 m., larvae, 29-IX-1996, J.K.M., UASM; larva, 15-IX-2014, D. A. and R. E. G. Craig, UASM; Grampians, Fyans Creek, Highway C261, south of Halls Gap, S37.2144° E142.4529°, elev. 280 m., larvae, 18-IX-2014, D. A and R. E. G Craig, ANIC.

Horne and Pettigrove (1989) suggested that the predilection by the larvae for a rather specialized habitat would determine the species distribution. We do not disagree. Still, it is unusual that *Ect. umbratorum* is known only from Victoria. Slow flowing streams with trailing vegetation occur elsewhere, so we suggest that winter and spring temperatures may be involved. Indeed, the distribution known so far falls within the overlapping terrestrial phytogeographical 'Victoria' subregion, the 'Southeastern Forest' terrestrial zoogeographic subregion and the 'Lessonian' freshwater zoogeographical region (Ebach et al. 2013). But, unless the Victoria subregion ecological conditions (Crisp et al. 1995) are those controlling distribution, the species should be expected to occur further north into ACT and NSW since the other ecoregions extend north of Sydney.

Etymology

Not given by Tonnoir (1925), but refers to 'from the shade'. Possibly in reference to the color of the head and thorax, described as 'testaceous' (brick colored), in contrast to the slightly yellower abdomen and legs, or, equally likely where the specimens were originally collected. The emendation by Crosskey and Howard (1997) of *umbratorum* to *umbratora* was unnecessary.

Bionomics

Tonnoir (1925) reported that the type material had been collected while sweeping plants. There are no published reports that the females feed on vertebrates, but two specimens from Narbethong (ANIC) are labeled 'biting'. The females collected by J.K.M. were netted while flying around his head.

Zwick (1979) gave an account of the life cycle, with which we fully concur. In short, larvae develop during the austral winter (July, August) with pupation and eclosion of adults in early spring—September and October. Larvae inhabit streams with sandy substrate, or with stones mixed in with sandy sections, but with steady gentle flow that allows growth of macrophytes (e.g., Fig. 43), as noted by Mackerras and Mackerras (1952) and Horne and Pettigrove (1989). Pupae (with widely spread and long thin filaments, Fig. 22) recovered from the Acheron River, were on submerged macrophytes covered by green algae. Zwick also suggested that larvae might feed by browsing the 'Aufwuch' (biofilm), a suggestion similar to that of Horne and Pettigrove (1989). The later account is puzzling given they appear to have actually reared larvae through pupae to adults. Additionally, they commented that the head and mouthparts of larvae of *Ect. umbratorum* were similar to non-filter feeding larvae of *Twinnia* Stone and Jamnback, which lack labral fans (Craig 1974, Adler et al. 2004). This is curious as larvae of *Ect. umbratorum* (Fig. 31) clearly have quite large delicate labral fans.

It was J.K.M. who drew attention to the unusual behavior of larvae attaching themselves to the substrate via a long thin thread (e.g., Fig. 44) and Moulton and Adler (1997) comment about this (as '*Cnephia*' *terebrans*—larvae of that species are still unknown) in relation to independently evolved stalks employed by larvae of the North American *Ectemnia*. Adler et al. (2004) similarly comment, again noting that larvae abandon the thread prior to pupation. Examination (J.K.M., D.A.C., D.C.C.) of the thread using scanning electron microscopy shows it to consist of apparent extraneous material and fecal pellets covered by a silk matrix. The larvae attach to the extreme apex of the thread, which can be upwards of 10 cm long, typically attached to the apex of an elongated leaf of Water Ribbons (*Cycnogeton procerum* (R. Br.) Buchenau—previously known as *Triglochin procera*. See von Mering and Kadereit 2010) and undulates in the current (Figs. 43 and 44) (see Supp Material for brief video). The thickness of the thread increases with length and shows distinct changes in diameter. This might indicate a molt to the next larger instar. We will report in detail on the attachment threads elsewhere.

Of note is that when alive the larvae are semitransparent with alimentary canal contents visible (Fig. 44). The body is held straight with the labral fans widespread—larvae do not twist the body as is typical for simuliid larvae attached to hard substrates (e.g., Chance and Craig 1986). When preserved, however, larvae assume a markedly more curved posture (e.g., Fig. 30) than typical of dead simuliid larvae. The behavior of attaching to a thread is no doubt integral to the unusual physiognomy of the larvae.

For the three main localities in the Grampians, namely Wannon River, Glenelg River, and Fyans Creek, all had Water Ribbon leaves trailing in the flow. While the Wannon site had a more rocky substrate (Fig. 43), there were stretches of sand. None of the sites had markedly deep water (ankle to knee deep), and temperatures ranged from 9.8 to 15.0°C and velocities from 44 to 80 cm/s. Of interest is that attempts in 2014 to recollect material from previously known sites failed. Similarly, although timing was appropriate, nothing was obtained from near Narbethong, neither the Acheron River, nor further south at The Otways.

The rarity of pupal material is of note. Moulton and Adler (1997) and Adler et al. (2004) comment that larvae abandon their thread prior to pupation. Apart from the pupal material obtained by the Zwicks, the only other specimen obtained was a partial exuviae from a kick sample of the sandy substrate of the Glenelg River (Syphon Road) site where there were numerous larvae. In agreement with the those statements, we are of the opinion that since pupae are not found on the attachment thread, pharate pupae detach and drift, either into vegetation (e.g., as for the Zwick pupae previously), or down to the substrate. Crosskey (1990) briefly mentions such pupation behavior in other simuliids. This is one aspect of the bionomics of *Ect. umbratorum* that needs closer examination.

We recovered larvae of *Austrosimulium furiosum* (Skuse) and *Aust. montanum* Mackerras and Mackerras from the same sites as *Ect. umbratorum*. *Aust. victoriae* (Roubaud) was recorded by Mackerras and Mackerras (1952).

Remarks

The original adults of *Ect. umbratorum* netted by Tonnoir (1925) were all female. Similarly for Mackerras and Mackerras (1950), who, however, in 1952 illustrated possible larvae of *Ect. umbratorum* (their Figs. 1–5). Rearing of larvae through to adults reported by Horne and Pettigrove (1989) is inconclusive since no details are given. Firm confirmation of that association was not until Zwick (1997) and in this study.

Although only minimal pupal material was available, there is no question that the pupae are those of *Ect. umbratorum*. This is confirmed

by pharate pupal gill structure from last instar larvae that fully agrees with the pupal stage, including the previously unnoticed unusual basal fenestral diverticulum (Figs. 24 and 25), as far as known, unique in Simuliidae and synapomorphic for *Ect. umbratorum*, *Ect. faecofilus*, *Ect. uvulatus*, and *Ect. acanthocranius*. Also unique for Australian Simuliidae are double setae on the pupal frontal plate (Figs. 26, 27, and 60) of *Ect. umbratorum* and *Ect. faecofilus*; synapomorphic for those two species. These setae are absent in other *Ectemnoides* species. Further, the pharate male that was recovered by Zwick (1997), while still the only male known, has wing characteristics that agree with the known female wing (Fig. 9), namely only moderately expressed spinous hairs on the costa, plus vein CuA barely sinuous. Other character states gleaned from the pharate female pupae, such as head proportions, calcipala, pedisulcus, claw tooth, genital fork, spermatheca with pigmentation partially down the seminal duct and lack of clear area at the junction, confirm the association to known *Ect. umbratorum* female adults and thence, via the pupal gill, fully confirming association to the larvae described by Makerras and Mackerras (1952).

The anal circlet of merely some 390 hooks is of interest and probably relates to the larval habit of attaching to a thread in moderate velocity water. Palmer and Craig (2000) give the lowest hook number for simuliid larvae, known at the time, as ca. 700. Moulton et al. (2004), reported some 400 hooks for last instar larvae of *B. gladiator*, similar to that of *Ect. umbratorum* larvae. As shown later, larvae of other *Ectemnoides* species have even fewer hooks. When not dissected, as shown in Fig. 42, the circlet is more angulate, not circular as more typical for simuliid larvae—no doubt to accommodate attaching to a tubular thread. Campaniform sensilla associated with the anal sclerite and circlet of hooks, for *E. umbratorum* and other larvae of the genus, have a common arrangement. The ventral arms of the anal sclerite have two sensilla dorsolaterally, with two more between that and the circlet of hooks. There is, then, one further around the circlet and another laterally halfway around. With the absence of an anal sclerite in other members of the genus, the sensilla while retained, are more evenly arrayed (e.g., Fig. 226).

Mouthparts of the female adult are well expressed, with the clypeus that houses muscles that work the blood-pumping cibarium, large and domed (Fig. 3) The mandible possesses teeth on each edge; however, these are markedly small (Fig. 6). The cibarium is well sclerotized. Character states that, overall, indicate blood feeding. The sensory vesicle on the maxillary palp is, however, small and this structure is generally assumed to be a CO^2 receptor (McIver 1987) involved in host detection. The expression of the abdominal tergites of the female are equivocal regarding blood feeding (Craig et al. 2012); i.e., while they are medium sized, indicating a tendency to non-blood feeding, they are not strongly sclerotized.

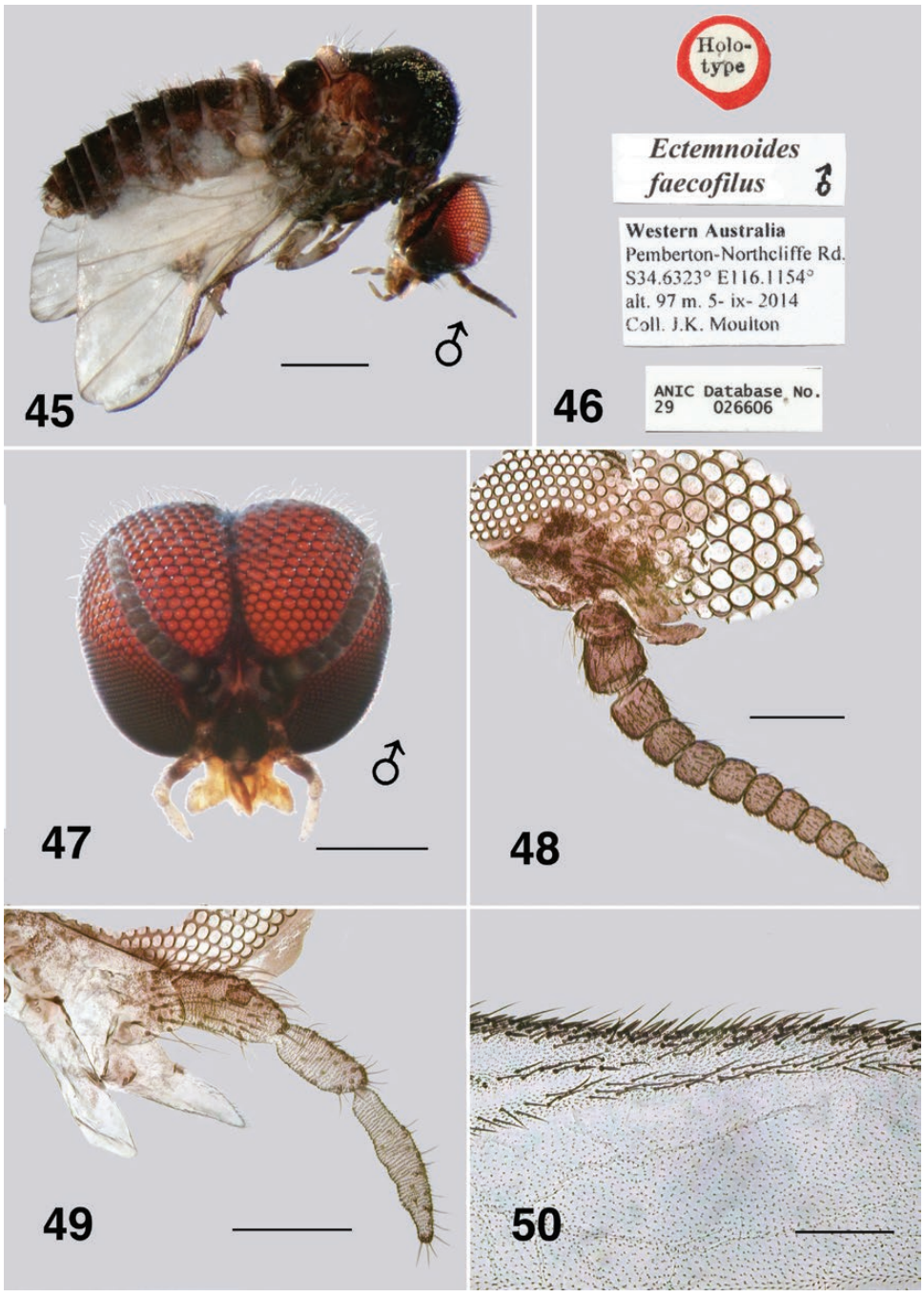
Ect. faecofilus n. sp. (Figs. 45–78)

(LSID: urn:lsid:zoobank.org:act:21B500EC-A3E7-48F7-BF0A-A82D6B341EC0)

Adult female. Unknown.

Adult male (one reared early teneral, plus one pharate specimen). *Body*: in alcohol, head dark, thorax evenly black, abdomen concolorous (Fig. 45); total length 2.6 mm. *Head* (Fig. 47): overall black when dried; width 0.68 mm, depth 0.57 mm. *Eyes*: large ommatidia ca. 23 up and across, diameter 0.029 mm; small ommatidia ca. 36 up and across, diameter 0.010 mm. *Antenna* (Fig. 48): total length 0.50 mm; overall dark brown and evenly tapered; scape short, pedicel as long as broad, larger than flagellomere I which is quadratic in shape, other flagellomeres bead-like, apical flagellomere IX cone-shaped. *Mouthparts*: black, markedly insubstantial; length 0.20× head depth; maxillary palp (Fig. 49) 0.35 mm long, two basal palpomeres small, palpomere III tubular and dark, palpomere IV shorter, palpomere V tapered distally, proportional lengths of III–V palpomere 1.0:0.9:1.5, sensory vesicle spherical and minute, occupying 0.33× palpomere width, opening half width of vesicle; lacinia and mandible small, teeth absent, with apical hairs. *Thorax*: markedly domed, semicircular in lateral view; length 0.96 mm; width 0.6 mm; postpronotal and antepronotal lobes with sparse fine dark hairs, proepisternum bare; scutum evenly black, vestiture of moderately sparse longish pale hairs, golden under some lighting, a few long and blackish hairs in scutellar depression; scutellum yellowish with long black hairs laterally, postpronotal lobe concolorous with scutum; pleurae blackish brown, anepisternal membrane without hairs; katepisternum angled (of Simuliini provenance), sulcus not markedly expressed; metathoracic furcasternum dorsal projections finely tapered, lacking projections (Fig. 52). *Wing* (Fig. 51): length 2.0 mm, width 1.3 mm; hyaline; basal hair tuft well expressed; basal cell small, but distinct; a:b ratio 1.0:2.8; anterior veins dark; costa with spiniform setae; r-m junction not pigmented; Rs not branched (Fig. 50); M_1 double; CuA not sinuous. *Haltere*: stem pale, knob tan. *Legs*: probably bicolorous, junctions dark; hind basitarsus (Fig. 53) margins parallel, irregular ventral row of sparse stout spines, calcipala moderately expressed; tarsomere II short, 2.0× as long as apical width; pedisulcus absent; tarsal claw small and finely expressed, with distinct basal tooth, grappling pad of ca. 23 teeth. *Abdomen*: black dorsally and posteriorly, vestiture marked anteriorly, decreased posteriorly, fine black hairs; basal scale (tergite I) black, hairs black and long, extended to posterior of tergite II, tergites well sclerotized, subequal in dimensions, ca. 2× wide as the length. *Genitalia* (Fig. 54): relatively small, probably not heavily pigmented; cerci well developed; gonocoxa in ventral view 1.5× longer than basal width, vestiture of long black sparse hairs, microtrichia; gonostylus in ventral view markedly curved, in lateral view straight along inner edge, markedly curved on outer apex (Fig. 56) ca. 2.0× longer than basal width, strengthened along inner edge, two substantial apical spines; ventral plate small, subequal in breadth and length, posteromedial apex blunt in ventral view, but is cone-shaped, broadly convex anteromedially, vestiture of markedly dense fine hairs, basal arms short and finely expressed; median sclerite well expressed with marked junction to ventral plate, broadly bifurcated apically and short sclerotized arms projected ventrally; paramere connector barely expressed; parameres plate-like, barely expressed, each with single elongated parameral spine, various (e.g., two on one side); adeagal membrane essentially bare (Fig. 55).

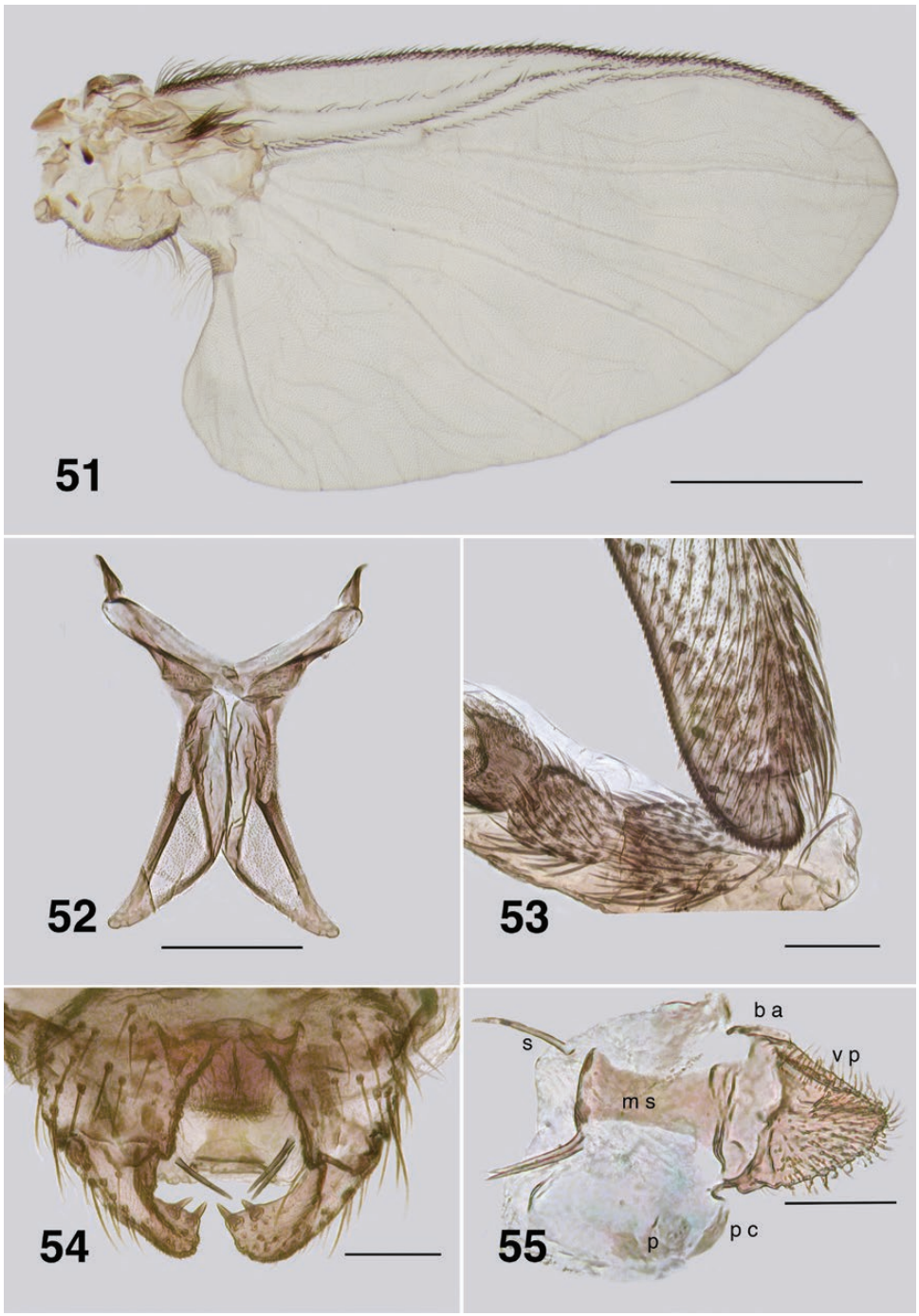
Pupa (based on two immature female pupae, one fully developed male pupa and one exuviae). Poorly known. *Body*: length; female 2.2 mm (Fig. 57), cuticle essentially colorless. *Head*: male frontal plate covered with barely visible minute clear tubercles; facial setae elongated and curled, frontal setae doubled (Fig. 60), ratio of basal width to length 1.0:2.1, basal width to maximum width 1.0:1.5. *Thorax*: anterior dorsal shield with tubercules as for frontal plate, dorsocentral setae long, curled apically (Fig. 61). *Gill* (Figs. 58, 59, and 61): total length 2.4–2.6 mm; as long as pupal body with two thin light-brown trunks arising close to base, various; fenestral diverticulum thin-walled, transparent (Fig. 59); trunks at approximately half-length further divided into 6 and 8 long thin filaments, respectively. Surface pseudoannulated to annulated proximally, finely annulated distally. *Abdomen* (Fig. 62): chaetotaxy and armature similar to *Ect. umbratorum* (Fig. 29); tergites and sternites with light tuberculation; tergite IX with two short blunt terminal spines and well-expressed spine comb; sternite IX with straight and bifurcated setae, with slightly curled tips, but not as grapnel hooks. *Cocoon*



Figs. 45–50. *Ectemnoides faecofilus* male adult. (45) Holotype male (teneral). Habitus. Scale bar = 0.5 mm. (46) Holotype labels. (47) Frontal view of pharate paratype male head (Northridge Creek). Scale bar = 0.25 mm. (48) Antenna. Paratype. Scale bar = 0.1 mm. (49) Maxilla, palp, mandible, lacinia. Scale bar = 0.1 mm. (50) Anterior wing veins (pharate) of paratype. Scale bar = 0.1 mm.

(based on a single pupa from Rosa Brook plus one from Northridge Creek). Sparse thin silk filaments over posterior abdomen; extraneous material from substrate incorporated.

Larva (based on four larvae from Carey Brook, two early last instar larvae from Rosa Brook). *Body* (Fig. 63): total length 5.5 cm, evenly light brown, anterior abdomen with lighter intersegmental regions. *Head* (Figs. 64 and 65): overall transparent yellowish brown with sclerotized structures dark; total length 0.87 mm, width 0.57 mm; distance between antennal bases 0.35 mm; antennal phragma markedly expressed posteromedially; anterior margins of head subparallel, narrowed posteriorly; apotome narrow, head spot pattern not obvious; ecdysial lines well visible, essentially parallel and straight until extreme posterior of head, then rounded; cervical sclerites not evident; postocciput darkly pigmented, but finely sclerotized; cephalic cuticle with short stout secondary setae producing roughened spotted appearance, posterior third of apotome bare, genae also with setae (Fig. 72). *Antenna* (Figs. 66 and 67): basal and medial antennomeres brown, apical antennomere pale and often hard to observe; extended to just beyond half length of labral fan stem; total length 0.32 mm; basal and medial antennomeres subequal, apical antennomere shorter than medial; proportional lengths of basal, medial, and apical antennomeres various 1.0:0.5:0.5 (Fig. 66, Carey Brook) and 1.0:1.4:1.0 (Fig. 67, Rosa Brook). *Labral fan*: stalk thin



Figs. 51–55. *Ectemnoides faecofilus* male adult. (51) Wing. Paratype. Pharate. Scale bar = 0.5 mm. (52) Metathoracic furcasternum. Scale bar = 0.1 mm (53) Hind basitarsus and tarsomere II. Partially encased in pupal exuviae. Scale bar = 0.05 mm. (54) Ventral view of genitalia. Scale bar = 0.05 mm. (55) Slide mount of genitalia. b a – basal arm; m s – median sclerite; p – paramere; p c – paramere connector; s – spines; v p – ventral plate. The ventral plate is flipped 90 degrees to the right. Scale bar = 0.05 mm.

and elongated, 48–51 markedly fine rays, length 0.79 mm, mid-ray width 0.008 mm; microtrichia 0.006 mm in length, 6–8 smaller microtrichia between longer ones, microtrichia only on distal half of rays; 10–12 aborted ray bases distinct, ca. 5 secondary fan rays. *Mandible* (Fig. 69): overall lightly pigmented and slightly elongated; brushes markedly reduced; apex (Fig. 70) of unusual configuration—outer apical teeth poorly developed; apical tooth distinct with subapical teeth small and occasionally not obvious; 6–8 spinous teeth with saw-toothed configuration; sensillum and serrations present merely as fine spine-like hairs well separated from spinous teeth by convex blade-like region. *Maxilla* (Fig. 71): distinctly directed away from mouthparts, maxillary lobe cone-shaped with distinct apical grouping of dark hairs, palp dark, 4.0× as long as basal width; elongated and curved, distinctly separated at base from lobe, tuft of hair at base of palp essentially absent (Rosa and Carey Brooks). *Postgenal cleft* (Fig. 72): well developed, U-shaped, sclerotized laterally with sclerotization well anterior of poorly expressed posterior tentorial pits; postgenal bridge lacking stout setae; ratio of hypostoma, postgenal bridge, and postgenal cleft 1.0:1.3:1.3; suboesophageal ganglion pigmented (Fig. 68). *Hypostoma* (Fig. 73):

well pigmented; tooth 0 (median) and teeth 1–3 (sublateral) in cone-shaped arrangement, small, subequal and depressed below extended other teeth, tooth 4 (lateral) sharp, protruded slightly and directed slightly medially, fused to broadly-based tooth 5, teeth 6–8 (paralaterals) teeth tips curved medially toward tooth 5; lateral serrations absent, edge of hypostoma markedly smooth and slightly curved; one main hypostomal seta high on each side; 2 to 3 smaller setae variously arrayed more basally. *Thorax* (Fig. 74): prothorax grayish brown, remainder of thorax lighter; the mature pharate pupal gill with the two main filament trunks directed ventrally then curved broadly posteriorly then rapidly dorsally and anteriorly then dorsally toward gill base and recurved back ventrally, to produce shallow U-shaped arrangement. *Prothoracic proleg* (Fig. 75): well extended; dorsal hooks markedly small; lateral plates distinct and elongated V-shaped. *Abdomen*: evenly mottled medium brownish gray (variable) almost transparent in Rosa Brook population; cuticle with hexagonal patterning (Fig. 76). *Ventral tubercles*: absent. *Rectal papillae*: three simple lobes. *Anal sclerite* (Fig. 77): markedly reduced, anterodorsal arms absent, posteroventral arms poorly expressed, campaniform sensilla typical. *Posterior circlet*: markedly directed ventrally; ca. 40 rows of hooks, six per row (total ca. 240).

Figs. 56. *Ectemnoides faecofilus* male adult gonocoxa and stylus. Paratype. Scale bar = 0.05 mm.

Type Material

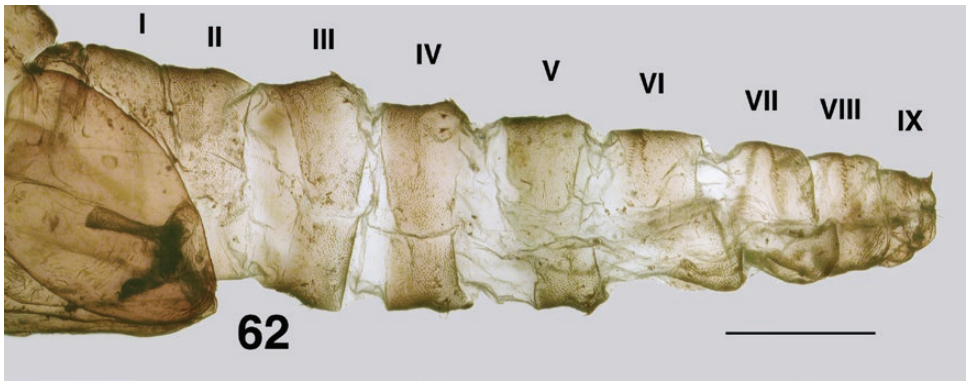
Holotype

Dried (Peldri II) from alcohol. Micro-pinned teneral male adult (Fig. 45). Label (Fig. 46), (Holo/type [red]) (*Ectemnoides/ faecofilus* [M]) (Western Australia/ Pemberton-Northcliffe Rd./ S34.6323° E116.1154°/ elev. 97 m. 5-ix-2014./ Coll. J.K.M.) (ANIC Database No./ 29 026606). Exuviae as subsidiary material in glycerine microvial on the pin. Both in good condition, adult lacking both hind tarsomeres (still in pupal exuviae) and with some extraneous material on surfaces.

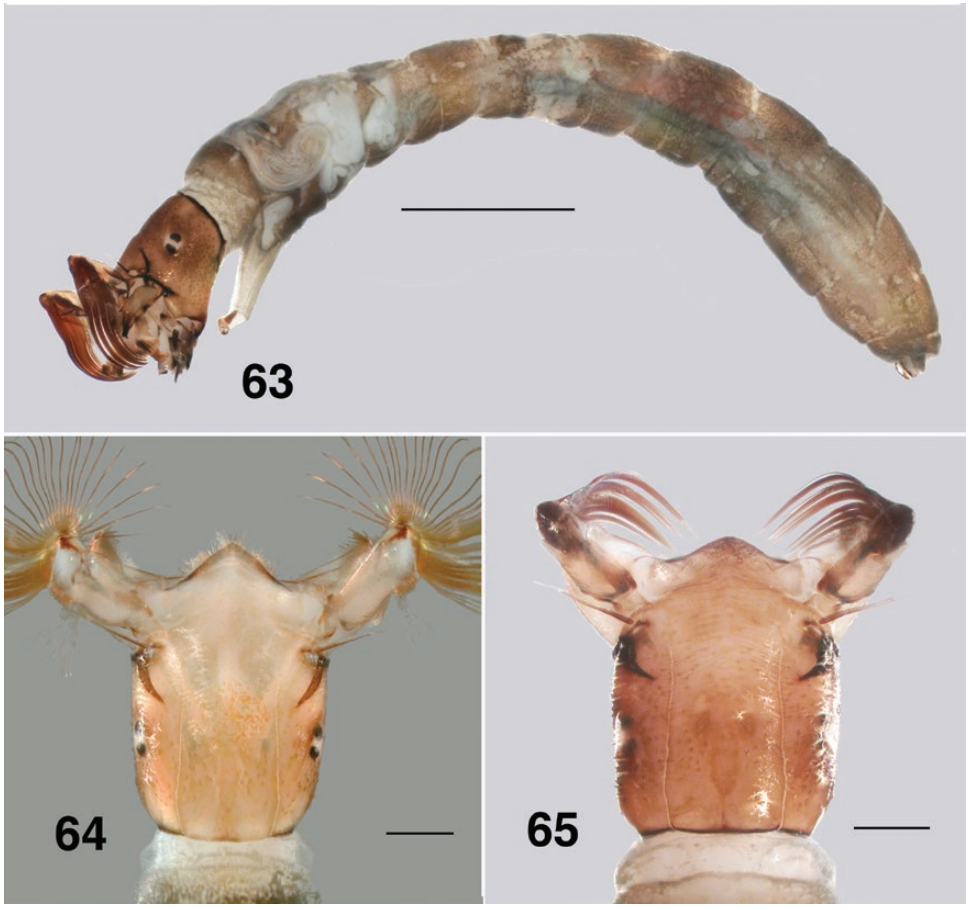
Paratype

Slide mount, pharate adult male. Label as for holotype, but with (Para/type [yellow]) (ANIC Database No./ 29 026607).

Figs. 57–61. *Ectemnoides faecofilus* pupa. (57) Dorsal view of female (Rosa Brook). Scale bar = 1.0 mm. (58) Gill (Rosa Brook). Arrow indicates fenestral diverticulum Scale bar = 0.5 mm. (59) Gill base (Rosa Brook). Arrow as for Fig. 58. Scale bar = 0.2 mm. (60) Male frontal plate. f s – facial setae; fnt s – frontal setae. Scale bar = 0.3 mm. (61)Thoracic cuticle and dorsocentral setae. Arrow as for Fig. 58. Scale bar = 0.2 mm.



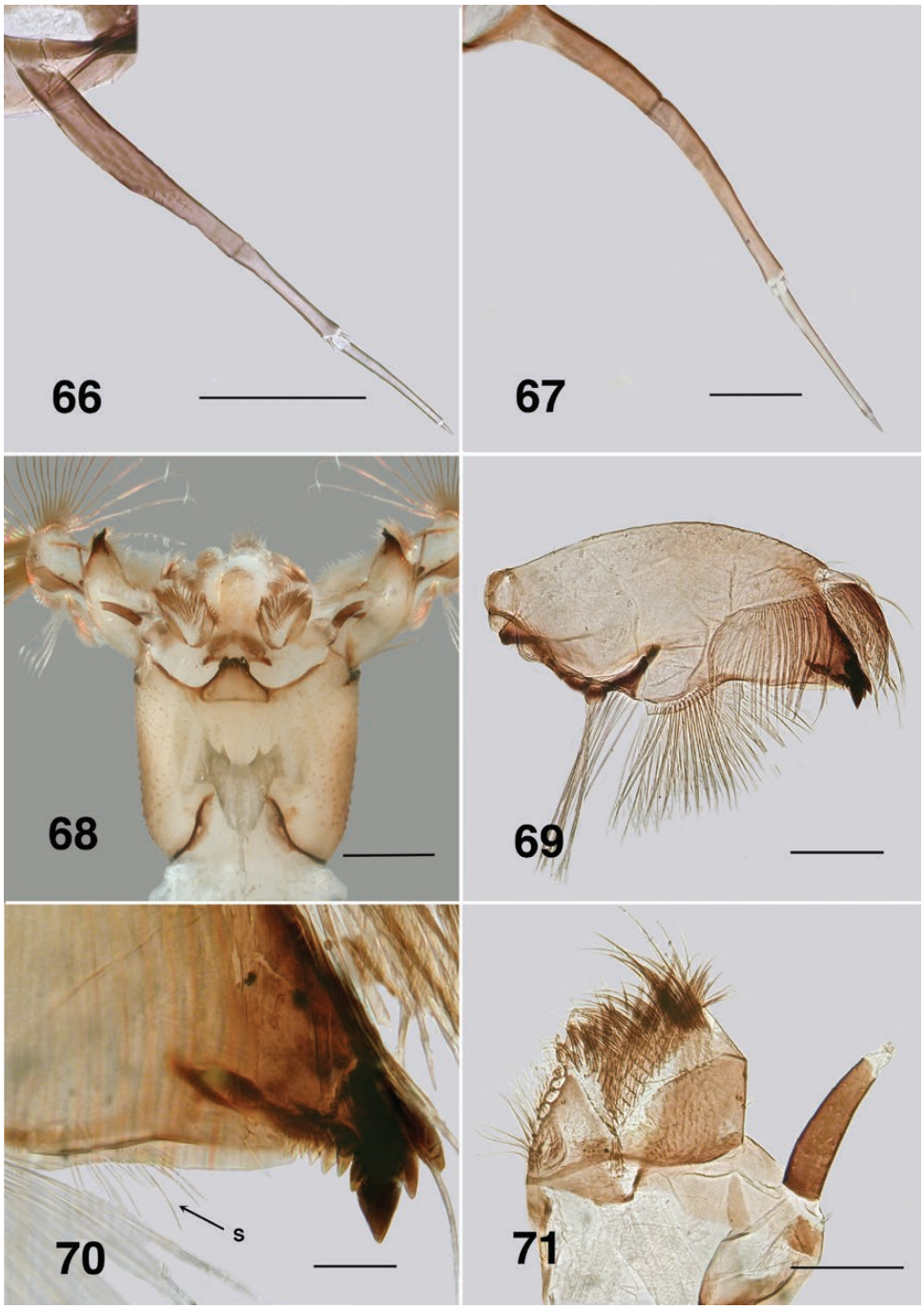
Figs. 62. *Ectemnoides faecofilus* pupal abdomen showing armature. Scale bar = 0.5 mm.



Figs. 63–65. *Ectemnoides faecofilus* larva. (63) Habitus early last instar. (Carey Brook). Scale bar = 1.0 mm. (64) Dorsal view of head (Rosa Brook). Scale bar = 0.2 mm. (65) Dorsal view of head (Carey Brook). Scale bar = 0.2 mm.

Additional Material

Alcohol; two penultimate instar larvae. Label (*Ectemnoides/ faecofilus*) (Western Australia/ second trib of Rosa Brook/on Mowen Rd. E of X-ing/with Sues Rd./ S33° 55′/E115° 26′/ 12–13 September 1996/ Coll. J.K.M.) (ANIC Database No./ 29 026611). Three penultimate instar larvae. Label (*Ectemnoides/ faecofilus*) (34.25S 115.49E/ [S34.4349° E115.7972°, elev. 37 m] s.w. Western Australia,/ Carey Brook, 16–19. viii. 1996, Coll. Cranston and Judd) (ANIC Database No./ 29 026612). Four last instar larvae. Label data: (*Ectemnoides/ faecofilus*) (Western Australia,/ Site 21: Carey Brook at Rt. 10 crossing,/ 34° 24.878′S 115° 48.722′E,/ 38 m, 5 m wide str., 17 September 2014,/ Coll. Currie and Moulton) (ANIC Database No./ 29 026613). Early pupa (*Ectemnoides/ faecofilus*) (AUSTRALIA: WA/ second trib of Rosa Brook/ on Mowen Rd. E of X-ing/ with Sues Rd./S 33°55′/E 115°262° [sic]/ 12–13 September1996/ Coll: J.K.M.) (UASM#/ 353368). Two early pupae (*Ectemnoides/ faecofilus*/ AUSTRALIA: WA/ ESE of/ Northcliffe, Loverock Rd/ S34.6500° E116.1300° 88m/ 9-vii-2014 Coll: J.K.M.) (UASM#/ 353369). *Slide material*: one, label as for Carey Brook, larva (ANIC Database No./ 29 026713), one, label as for Rosa Brook, larval attachment thread (ANIC Database No./ 29 026714). Last instar larva (ANIC Database No./ 29 026608) (*Ectemnoides/ faecofilus*/ Western Australia,/ Carey Brook, Vasse Hwy/ S34.41464° E115.81256°/ elev. 38 m, 17-ix-2014/ Coll. J.K.M. &/ D.C.C.). Early last instar larva



Figs. 66–71. *Ectemnoides faecofilus* larva. (66) Antenna (Carey Brook). Scale bar = 0.1 mm. (67) Antenna (Rosa Brook). Scale bar = 0.05 mm. (68) Ventral view of head (Rosa Brook). Scale bar = 0.2 mm. (69) Mandible (Rosa Brook). Scale bar = 0.5 mm. (70) Mandible tip (Rosa Brook). s – serrations and sensillum. Scale bar = 0.02 mm. (71) Maxilla (Rosa Brook). Scale bar = 0.5 mm.

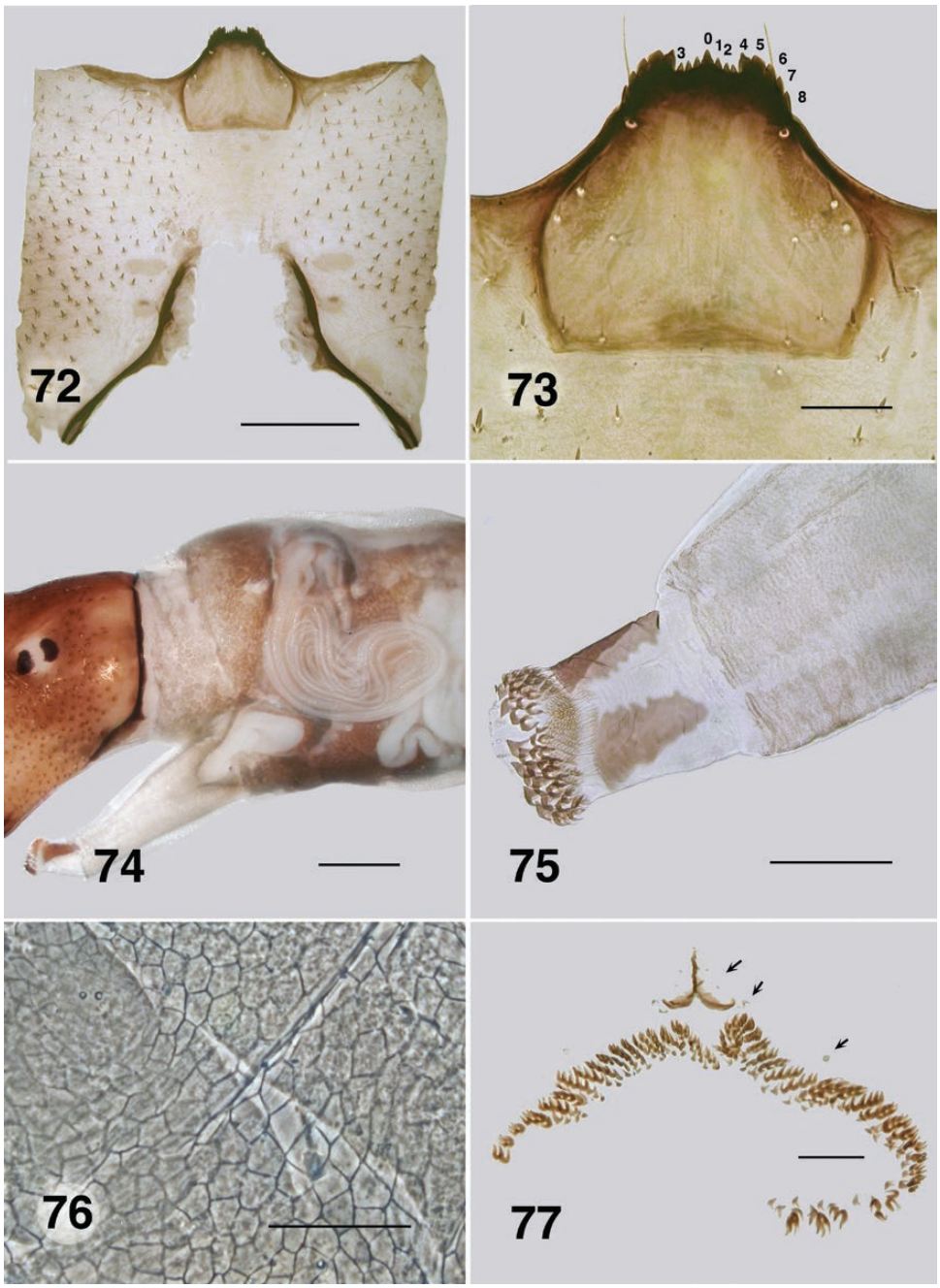
(ANIC Database No./ 29 026610) (*Ectemnoides/ faecofilus/* Western Australia/ Rosa Brook, Mowen Rd/ S33.91865° E115.43884°/ elev. 136. 12-13-ix-1996/ Coll. J.K.M.). Pupal gills and thorax (exuviae), as previous, but with (ANIC Database No./ 29 026609).

Etymology

Named for behavior of the larvae in attaching to a thread containing fecal material.

Distribution (Fig. 229)

Western Australia: Carey Brook, S34.4349° E115.7972°, elev. 40 m., larvae, 16–19-VIII-1996, Cranston and Judd; second trib. of Rosa Brook on Mowen Rd., East of X-ing with Sues Rd., S33.9183° E115.4408°, elev. 130 m., larvae, 12–13-IX-1996, J. K.M.; Carey Brook, 5-m-wide stream crossing Vasse Highway (Rt. 10), S34.4146° E115.8125°, elev. 40 m., larvae, 17-IX-2014, Currie and Moulton; Northcliffe, 0.5- to 1.0-m-wide stream crossing Pemberton-Northcliffe Road, S34.6323° E116.1154°, elev. 100 m., larvae, pupae, reared adults, 5-IX-2014, Currie and Moulton; South of Northcliffe, 5- to 8-m-wide stream crossing Northcliffe Log Road, S34.6751° E116.1601°, elev. 65 m., larvae, 5-IX-2014, Currie and Moulton; Carey Brook at Rt. 10 crossing, S34.4163° E115.8120°, elev. 38 m., larvae, 17-IX-2014, Currie and Moulton.



Figs. 72–77. *Ectemnoides faecofilus* larva. (72) Postgenal cleft (Carey Brook). Scale bar = 0.2 mm. (73) Hypostoma (Carey Brook). Scale bar = 0.05 mm. (74) Pharate pupal gill (Carey Brook). Scale bar = 0.2 mm. (75) Prothoracic proleg (Carey Brook). Scale bar = 0.1 mm. (76) Abdominal cuticle. Paratype. Phase contrast. Scale bar = 0.05 mm. (77) Anal sclerite and circlet of hooks. (Rosa Brook). Arrows indicate campaniform sensilla. Scale bar = 0.05 mm.

Bionomics

Behavior of the larvae is similar to those of *Ect. umbratorum* that tend to attach to submerged plant material, such as leaves and twigs on the end of a thread (e.g., Fig. 44). Other simuliids known to co-occur with *Ect. faecofilus* are *Austrosimulium* spp. and *Paracnephia tonnoiri* (Drummond). Given the dates of collection of *Ect. faecofilus*, plus that streams inhabited are definitely ephemeral, the species is likely a late winter, univoltine species.

Carey Brook (Fig. 78) is a typical stream in southwestern Western Australia, with brown low-velocity water, sandy substrate, and trailing macrophytes, namely *C. procerum* (Water Ribbon).

Remarks

There are differences in larval head proportions, coloration (Figs. 64 and 65), antennal proportions (Figs. 66 and 67) and hypostoma between Rosa Brook and Carey Brook material, all indicative that there is more than a single species. The types of *Ect. faecofilus* from Northcliffe Road correspond to the Rosa Brook form. Since we did not have a full suite of stages from Carey Brook, we refrain from erecting separate entities.

The low number of hooks (ca. 240) in the posterior circlet, plus that of *Ectemnoides* sp. A, with some 220 (see description) are probably records for Simuliidae. All species dealt with in this work

Fig. 78. Carey Brook, Snottygobble Loop Camp Ground, WA. 6-VI-2014. Habitat for *Ectemnoides faecofilus* immatures. Image by D.C.C.

inhabit slow to moderate velocity water and possess extremely low numbers of hooks in the circlet; synapomorphic for them all.

Of interest is that the apparently delicate fenestral diverticulum at the base of the pupal gill does not necessarily become detached or damaged during the pupal stage. It can still be observed, whole, on pupal exuviae (Fig. 59). This is in contrast to *Ect. acanthocranius* (Figs. 106 and 120), albeit there, exuviae were obtained via rearing.

In Western Australia, the known distribution of *Ect. faecofilus* is restricted to and well within the Warren bioregion (Kauri Forest bioregion). This region is mainly coastal sand plains between Cape Naturaliste and Albany, and for most of its extent it is within 10 kilometers of the coast. North of Point D'Entrecasteaux it extends farther inland. To the north and east is the Jarrah Forest bioregion. Trayler et al. (1996), in discussing conservation of aquatic fauna of the Warren Bioregion, note that rivers of the southwestern corner of Australia arise on an ancient flat semi-arid plateau and flow sluggishly toward the coast. Then there is steeper topography and increased rainfall, coastal lowlands, and lagoons. For simuliids, they list only *Aust. furiosum* (Skuse) and *P. tonnoiri* as occurring in the region.

Ect. acanthocranius and other species of the genus occur further north in the Jarrah Forest bioregion, east of Perth.

Ect. acanthocranius n. sp. (Figs. 79–121)

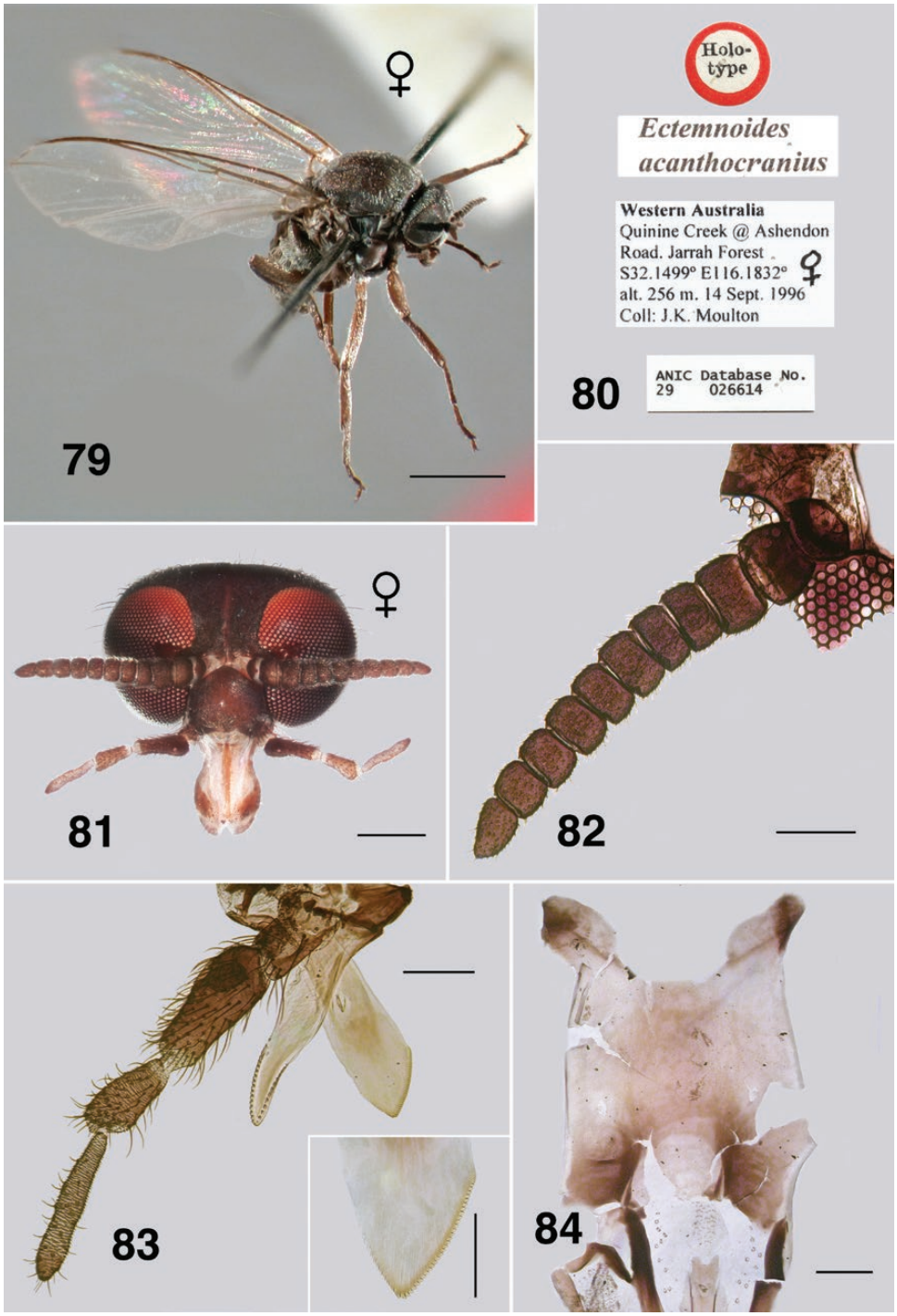
(LSID: urn:lsid:zoobank.org:act:AD2E5D5A-E55B-4D48-8D87-B946FD65D328)

'*Cnephia*' sp. nr. *terebrans* Tonnoir (= 'GKW2'), Moulton 2000: 86. Moulton 2003: 47.

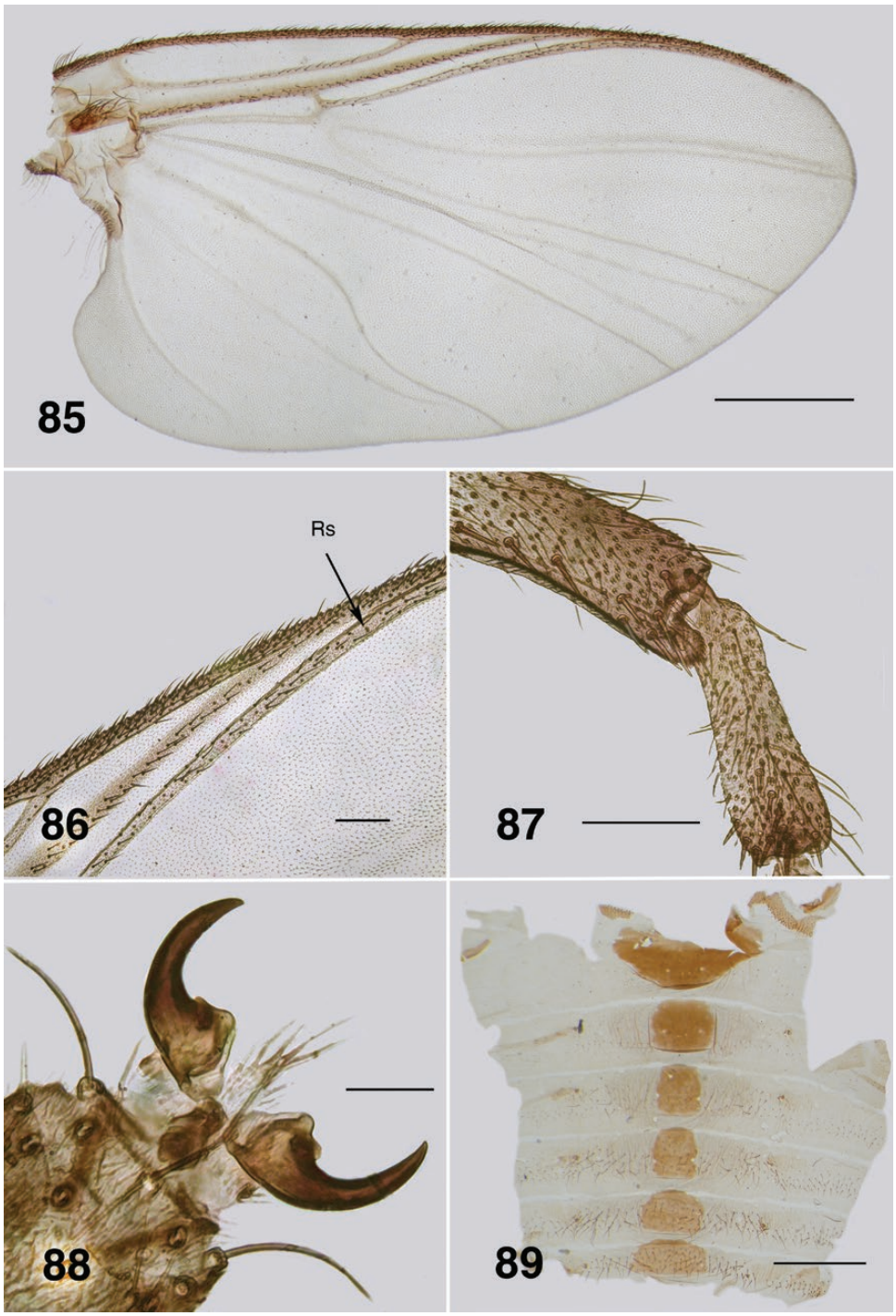
Adult female (based on five reared specimens). *Body* (Fig. 79): overall black to dark brown; total length 2.4–2.5 mm, legs lighter brown. *Head* (Fig. 81): overall dark brown; width 0.78 mm; depth 0.49 mm; postocciput markedly hirsute with long pale hairs, frons markedly broad, margins splayed dorsolaterally, dark brown-black, sparse pale hairs; frons:head width ratio 1.0:4.1. *Eyes*: interocular distance 0.19 mm; ommatidia dark red, diameter 0.016 mm; ca. 30 rows across and 36 down at mid-eye. *Clypeus*: substantial, width 0.26 mm; markedly dark brown with hairs anterolaterally. *Antenna* (Fig. 82): long, tapered, extended well beyond head; evenly dark brown; total length 0.55 mm; scape small, pedicel larger and similar in size to flagellomere I, remainder subequal in size, apical flagellomere IX small, cone-shaped. *Mouthparts*: markedly substantial, ca. 0.6× length of head depth; mandible (Fig. 83) with ca. 31 small inner teeth, 11 outer teeth; lacinia with 13 and 18 teeth; maxillary palp (Fig. 83), total length 0.68 mm, palpomeres I & II markedly small, palpomere III darker brown than remainder and expanded basally, dense vestiture, IV small, V (distal) not markedly elongated; proportional lengths of palpomeres III–V 1.0:0.6:1.1; sensory organ small and spherical, 0.25× length of palpomere III, opening 0.5× vesicle width; cibarium (Fig. 84) median depression broad and shallow, cornuae not markedly flared, pigmented. *Thorax*: evenly dark brownish black; length 1.1–1.3 mm, width 0.8–1.2 mm; scutum with sparse fine short hairs; pronotal lobe well developed but virtually bare; scutellar depression with sparse long dark hairs; scutellum concolorous with scutum, vestiture of sparse very fine yellowish hairs centrally, darker laterally; postnotum concolorous with scutellum; antepronotal lobe (propleuron) proepisternum and fore coxa with sparse pale hairs; pleuron and anepisternal (plural) membrane yellowish brown, without hairs; katepisternum dark brown, sulcus shallow and broad. *Wing* (Fig. 85): hyaline and clear, lacking all pigmentation except anal lobe slightly dusky; total length 2.7–2.9 mm; width 1.3–1.5 mm; anterior veins dark; basal cell present, but small; a:b ratio 1.0:2.8; costa lacking spiniform hairs, hairs dense apically, Rs not branched (Fig. 86); M_1 double; CuA markedly sinuous, almost contacting vein CuP. *Haltere*: stem clear, knob tan. *Legs*: overall lighter brown than body, slightly yellowish, hind basitarsus (Fig. 87) with regular row of stout spines, parallel-sided, 6.2× as long as mid-width; calcipala markedly small, with clump of stout spines; hirsute intersegmental plate ventrally between basitarsus and tarsomere II apparently absent; pedisulcus only faintly indicated; tarsomere II 3.0× longer than distal width; claws (Fig. 88), finely curved and tapered, basal tooth poorly expressed, heel well developed. *Abdomen* (Fig. 89): overall blackish brown; basal scale dark brown, vestiture of long dense hair extended to segment IV; tergites well sclerotized, tergite II broadly V-shaped, III–V quadratic, VI and VII broader than long. *Genitalia*: sternite VIII lacking distinct median region, vestiture of microtrichia, large strong hairs posterolaterally; hypogynial valves (Fig. 90), markedly divergent, well strengthened along median edges, slightly convex, triangulate apically; genital fork (Fig. 91) well expressed, anterior arm fine and markedly curved ventrally, no indication of membranous lateral areas, posterolateral arms broad, knee-bend extreme, lateral apodeme expressed as ridge at beginning of triangular posterolateral expansions, those not markedly developed, medial space broadly

expressed; cerci in lateral view broadly rounded, slightly angulate dorsally, anal lobes smaller, slightly angulate with vestiture of longer hairs (Fig. 93); spermatheca ovoid (Fig. 92), externally smooth, internal fine spines (acanthae) present, distinct clear region surrounding junction with spermathecal duct, edge slightly raised.

Adult male (single reared specimen, three pharate specimens). *Body* (Fig. 94): in alcohol, head dark, thorax evenly dark brown, abdomen concolorous; total length 2.2 mm. *Head* (Fig. 95): width 0.76 mm; depth 0.58 mm. *Eyes*: upper ommatidia color dark red, diameter 0.036 mm, 20 across, 23 down; lower ommatidia blackish red, markedly smaller, diameter 0.016 mm, ca. 26 across and down. *Clypeus*: black; width 0.17 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 96): overall dark brown and slightly tapered; total length 0.60 mm; scape short, pedicel as long as broad, flagellomeres II–VII quadratic in shape, flagellomeres VIII & IX slightly longer

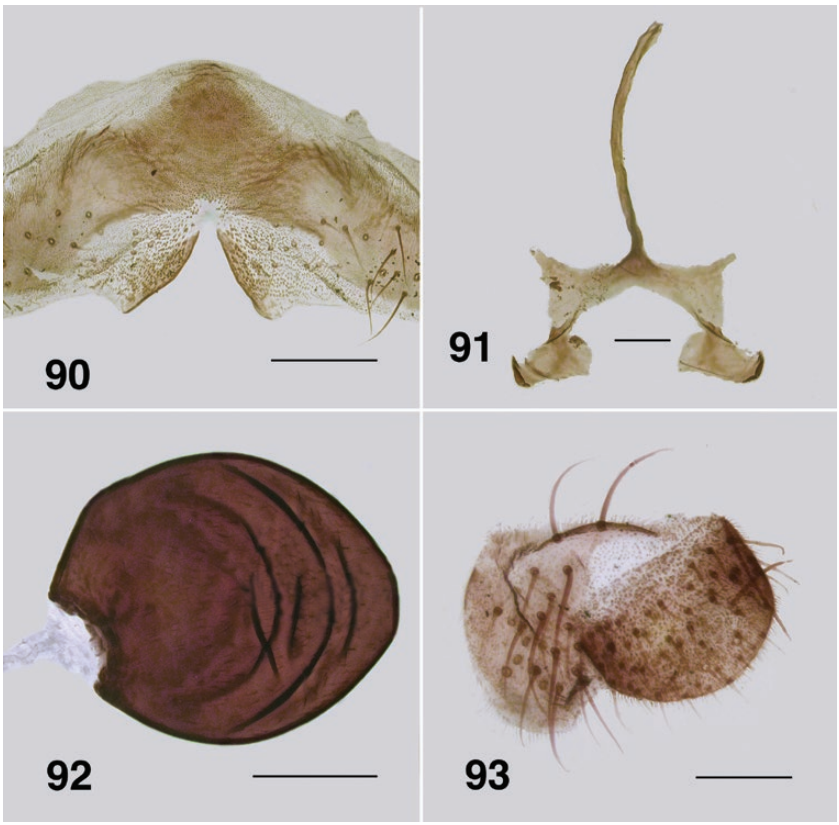


Figs. 79–84. *Ectemnoides acanthocranius* female. (79) Holotype. Habitus. Scale bar = 1.0 mm. (80) Holotype labels. (81) Frontal view of head. Scale bar = 0.2 mm. (82) Antenna. Scale bar = 0.1 mm. (83) Maxilla, palp, mandible, lacinia. Scale bar = 0.1 mm. Insert: mandible tip. Scale bar = 0.05 mm. (84) Cibarium. Scale bar = 0.05 mm.



Figs. 85–89. *Ectemnoides acanthocranius* female. (85) Wing. Scale bar = 0.5 mm. (86) Wing veins. Rs – radial sector vein. Scale bar = 0.1 mm. (87) Hind basitarsus and tarsomere II. Scale bar = 0.1 mm. (88) Tarsal claw. Scale bar = 0.02 mm. (89) Abdominal tergites. Scale bar = 0.5 mm.

than wide. *Mouthparts*: insubstantial; length 0.25× head depth; maxillary palp (Fig. 97) 0.38 mm long, palpomeres I & II small, palpomere III tubular and dark, IV shorter and expanded distally, V fine and insubstantial, proportional lengths of III–V palpomeres 1.0:0.7:1.0, sensory vesicle spherical and minute, occupying 0.33× palpomere width, opening full width of vesicle; lacinia and mandible small, teeth absent, apical hairs. *Thorax*: well domed; length 0.8 mm; width 0.7 mm; postpronotal lobe with fine pale hairs, antepronotal lobe with sparse fine pale hairs, proepisternum bare; scutum evenly blackish brown, vestiture of evenly sparse small fine pale hairs, long and black in scutellar depression; scutellum yellower than scutum with long black hairs laterally, postpronotal lobe concolorous with scutum; pleurae blackish brown, membrane without hairs, katepisternum dark brown, sulcus distinct, but shallow. *Wing*: hyaline; total length 2.8 mm, width 1.3 mm; veins not colored, a:b ratio 1.0:2.3, costa lacking spiniform hairs (Fig. 98), r-m junction not pigmented, Rs not branched, M_1 double, CuA markedly sinuous, CuP not. *Haltere*: stem pale, knob tan. *Legs*: paler than body, hind leg lighter than fore and mid legs; hind basitarsus margins parallel, irregular ventral row of sparse stout spines, calcipala barely expressed;

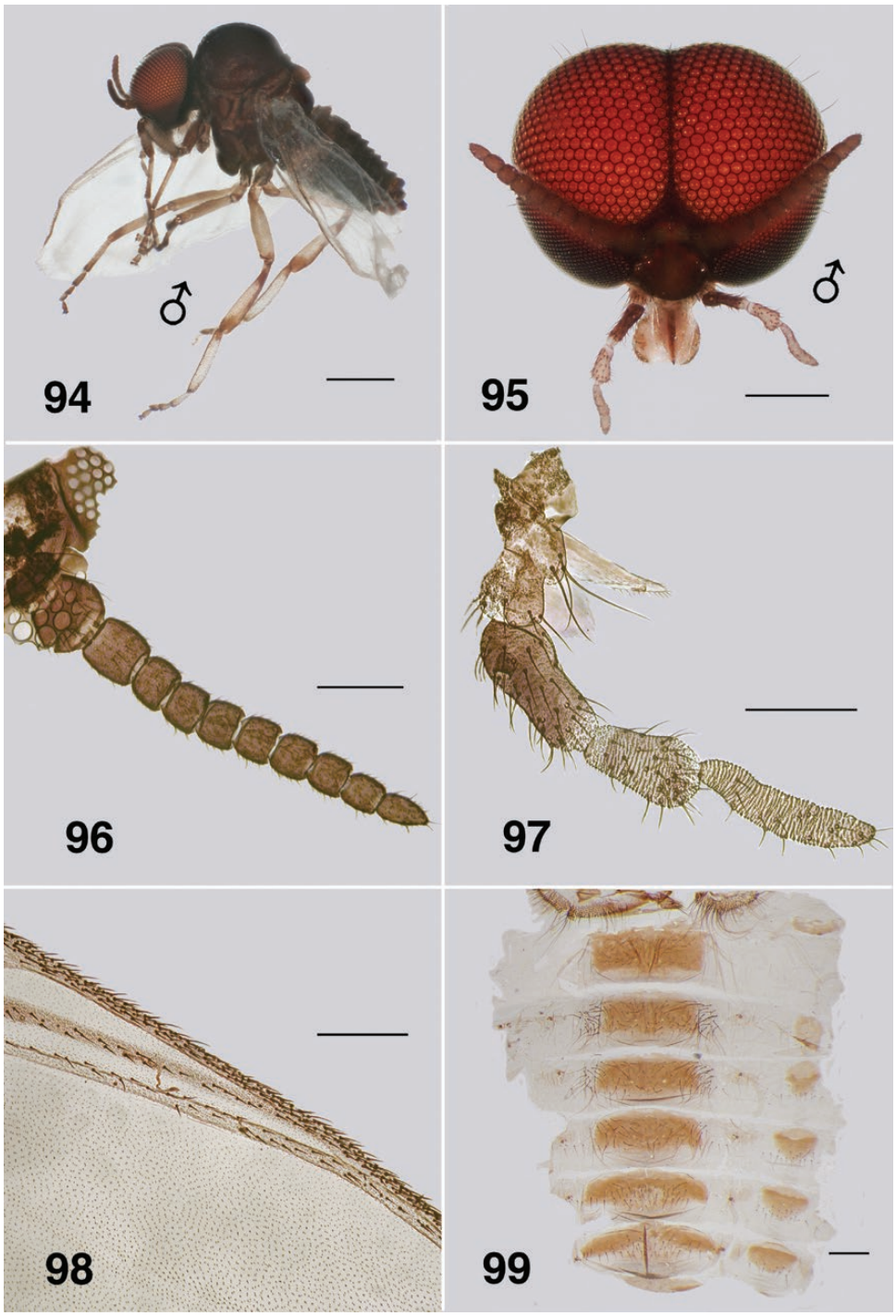


Figs. 90–93. *Ectemnoides acanthocranius* female. (90) Hypopygial valves. Scale bar = 0.1 mm. (91) Genital fork. Scale bar = 0.05 mm. (92) Spermatheca. Scale bar = 0.05 mm. (93) Cercus and anal lobe. Scale bar = 0.05 mm.

tarsomere II 2.8× as long as apical width; pedisulcus absent; tarsal claw small and finely expressed, with distinct basal tooth, grappling pad of ca. 23 teeth. *Abdomen* (Fig. 99): black dorsally and posteriorly, pale anteroventrally, vestiture not marked, sparse fine black hairs; basal scale (tergite I) black, hairs black and long, extended to posterior of tergite II, tergites well sclerotized, subequal in dimensions, ca. 2× wide as the length, pleural cuticle not markedly concertinaed; sternite II absent, others well developed. *Genitalia* (Fig. 100): relatively enlarged, not heavily pigmented; cerci well developed but not markedly distinct; gonocoxa in ventral view 1.6× longer than basal width, vestiture of long black sparse hairs, microtrichia, posteromedial margin scalloped; gonostylus in ventral view markedly curved, in lateral view scimitar sword-shaped (Fig. 101) approximately 2.3× longer than basal width, strengthened along inner edge, two short, blunt, apical spines plus one or two substantial setae adjacent, various; ventral plate small, 2.0× wider than long, posteromedial apex bluntly pointed with small keel and directed slightly ventrally producing appearance of shallow posteromedial concavity, laterally concave, broadly shallow convex anteromedially with strengthened edge, vestiture of sparse fine hairs (Fig. 102), basal arms broadly expressed; median sclerite well expressed with marked junction to ventral plate, broadly bifurcated apically and short sclerotized arms projected ventrally; parameral connector markedly expressed and curved; paramere plate-like, lightly expressed, slightly strengthened along inner edge, with single separated elongated parameral spine; adeagal membrane with dense microtrichia.

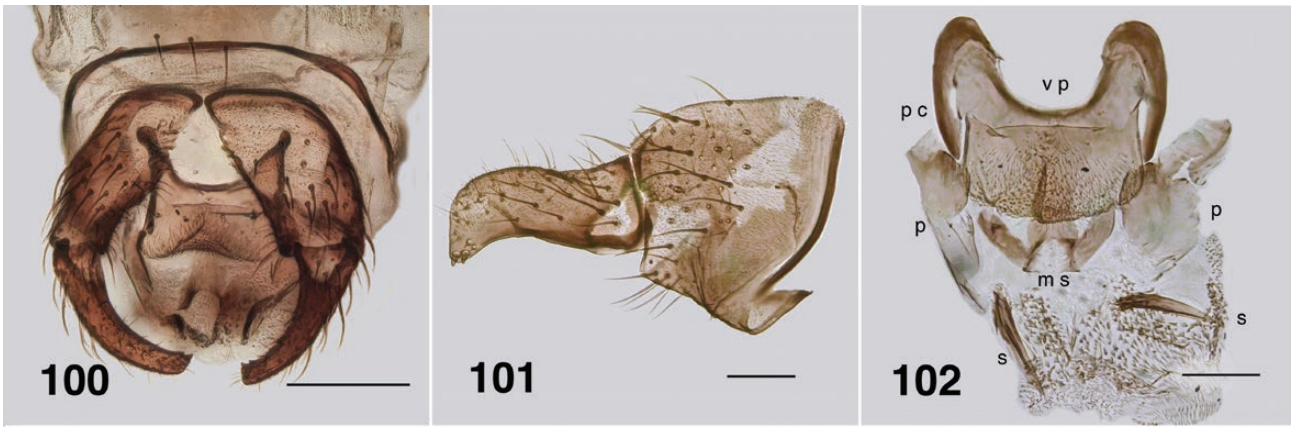
Pupa (based mainly on exuviae from reared adults). *Body*: length, female 2.9–4.3 mm, male 3.3–3.7 mm, clear yellow cuticle. *Head*: frontal plates with small regular dark tubercles; female markedly broad and truncated apically, ratio of frons basal width to vertex width 1.0:1.5 and height 1.0:1.6 (Fig. 103); male ovoid; ratios of 1.0:1.3 and 1.0:2.0, respectively (Fig. 104), frontal setae absent, facial setae present, substantial, and curved apically; antenna of female extended to and beyond edge of ocular shield, in male markedly not extended (cf. Figs. 103 and 104). *Thorax*: notum not markedly domed, cuticle with evenly spaced small darker tubercles, dorsocentral setae elongated, curled at apex (Fig. 105). *Gill* (Fig. 106): total length ca. 2.5 mm; fenestral diverticulum typically absent in exposed gill, but present and poorly expressed when pharate (e.g., Fig. 120), basal gill of two trunks, distal of half-length are 15–20 markedly fine filaments arising at random; trunk surfaces reticulate, filament surfaces finely annulated (Fig. 107). *Abdomen* (Fig. 108): overall, cuticle clear and yellow, with small tubercles, sclerites not markedly distinct; armature markedly poorly developed; terminal spines on tergite IX, short, stout, sharply tapered, grapnel hooks present; segment IX expanded ventrally; tergites II–IV with small anteriorly directed hooks; tergites V–IX with spine combs directed posteriorly; segment VI with minute pleurite posterad of lateral hook, absent from other segments; sternites II–VII with anteriorly-directed spicules. *Cocoon*: Pupae reared from larvae in a Petri dish by J.K.M. spun only a few criss-crossed threads.

Larva (based on numerous last instar larvae). *Body* (Fig. 109): total length 6.8–7.3 mm, abdomen color evenly mottled light grayish orange. *Head* (Fig. 110): overall pale yellow with transparent cuticle, head spot pattern startlingly positive; length 1.0–1.1 mm, maximum width 0.74–0.77 mm; margins parallel, then broadly curved behind stemmata to postocciput, producing narrow connection to thorax; distance between antennal bases 0.54–0.57 mm; apotome not markedly narrowed, ecdysial lines distinct, slightly divergent, straight, broadly rounded posteriorly, cephalic sensilla

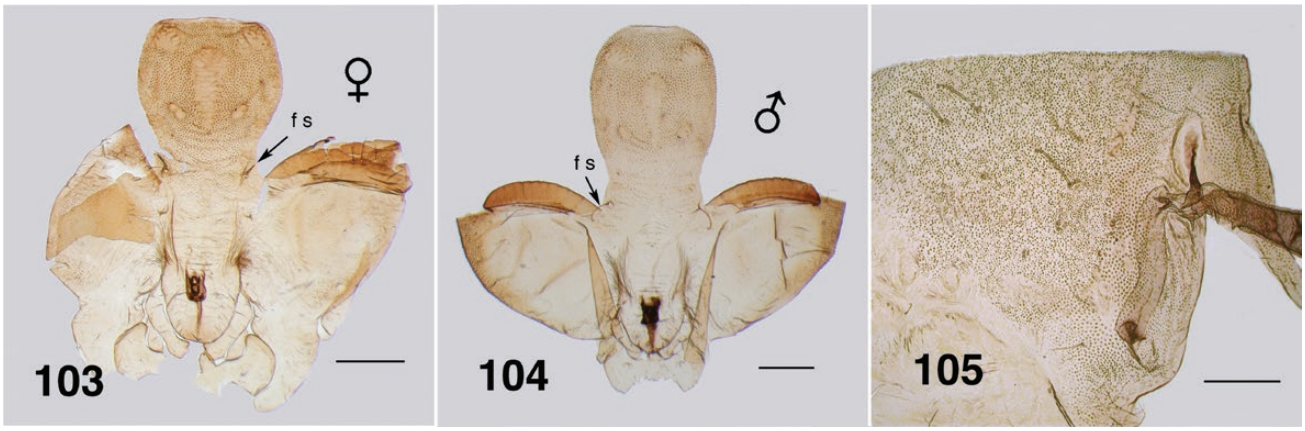


Figs. 94–99. *Ectemnoides acanthocranius* male (94) Habitus. Alcohol. Scale bar = 0.5 mm. (95) Frontal view of head. Scale bar = 0.2 mm. (96) Antenna. Scale bar = 0.1 mm. (97) Maxilla, palp, lacinia, mandible. Scale bar = 0.1 mm. (98) Wing veins. Scale bar = 0.2 mm. (99) Abdominal tergites. Scale bar = 0.2 mm.

not obvious on the apotome or dorsal genae, but distinct and pigmented elsewhere; cervical sclerites poorly expressed, distinctly separate from postocciput. *Antenna* (Fig. 112): elongated, but not extended to end of labral fan stem; total length 0.51 mm, brown; basal antennomere subequal in length to medial article, both pale along one side, distal antennomere evenly brown, proportional lengths of basal, medial, and apical antennomeres 1.0:1.0:1.8. *Labral fan*: stalk elongated, broad, pale and transparent, 63–67 fine medium brown rays, length 1.1 mm, mid-ray width 0.014 mm; microtrichial pattern of 7 or 8 smaller decreasing in size, longer microtrichia ca. 0.012 mm in length; three aborted fan ray bases. *Mandible* (Figs. 113 and 114): overall pale; brushes typical; apical teeth heavily pigmented; outer teeth short; apical tooth moderately developed; subapical teeth small, one larger than others; ca. seven short spinous teeth with serrated tips, serrations and sensillum on raised convex region, serration as single anterior structure, sensillum trichoid; blade region flat. *Maxilla* (Fig. 115): heavily pigmented; palp curved, shorter than maxillary lobe, 3.0× as long as basal width; markedly separated from lobe, hair tuft at base of palp not developed. *Postgenal cleft* (Fig. 116): angulate with irregular



Figs. 100–102. *Ectemnoides acanthocranius* male. (100) Ventral view of genitalia. Scale bar = 0.1 mm. (101) Lateral view of gonocoxa and gonostylus. Scale bar = 0.05 mm. (102) Genitalia—slide mounted. m s – median sclerite; p – paramere; p c – paramere connector; s – spines; v p – ventral plate. Scale bar = 0.05 mm.



Figs. 103–105. *Ectemnoides acanthocranius* pupa. (103) Female cephalic capsule. Arrow indicates facial seta (f s). Scale bar = 0.25 mm. (104) Male cephalic capsule. Arrow as for Fig. 103. Scale bar = 0.2 mm. (105) Thoracic cuticle and dorsocentral setae. Scale bar = 0.2 mm.

edges; posterior tentorial pits and postocciput markedly substantial and pigmented; postgenal bridge lightly pigmented posteriorly; genae colorless except for dark brown muscle scars and cephalic sensilla bases; ratio of hypostoma, postgenal bridge and postgenal cleft 1.0:1.5:0.5; ventral nerve cord and suboesophageal ganglion heavily pigmented (Fig. 111). *Hypostoma* (Fig. 117): darkly pigmented; all 17 teeth of subequal expression, inverted V-shaped array, tooth 8 obscured by ventral edge of hypostoma; flanked laterally by two marked cone-shaped protrusions of the hypostoma; one distinct hypostomal seta on each protrusion, three less substantial setae posteriorly; anterolateral edge of head capsule serrate (Fig. 116). *Thorax* (Fig. 119): yellowish gray; gill spot overall L-shaped, filaments forming broad U-shape below pharate adult thoracic spiracle (black spot); fenestral diverticulum present, albeit minimalistic (Fig. 120). *Prothoracic proleg*: well developed, elongated with V-shaped lateral plates, two sizes of hooks, dorsal small, ventral hooks of typical size (Fig. 118). *Abdomen*: cuticle smooth, hexagonal patterning not obvious. *Ventral tubercles*: absent. *Anal sclerite*: absent; typical campaniform sensilla complement present. *Rectal papillae*: three simple lobes, well developed. *Posterior circlet* (Fig. 121): small and poorly developed, directed posteriorly, surrounded with clear cuticular band, unique low numbers of hook rows and hooks per row, ca. 37 rows, with five or six hooks per row (total ca. 200)—of note is that the inner hooks are markedly reduced and triangular in shape.

Type Material

Holotype

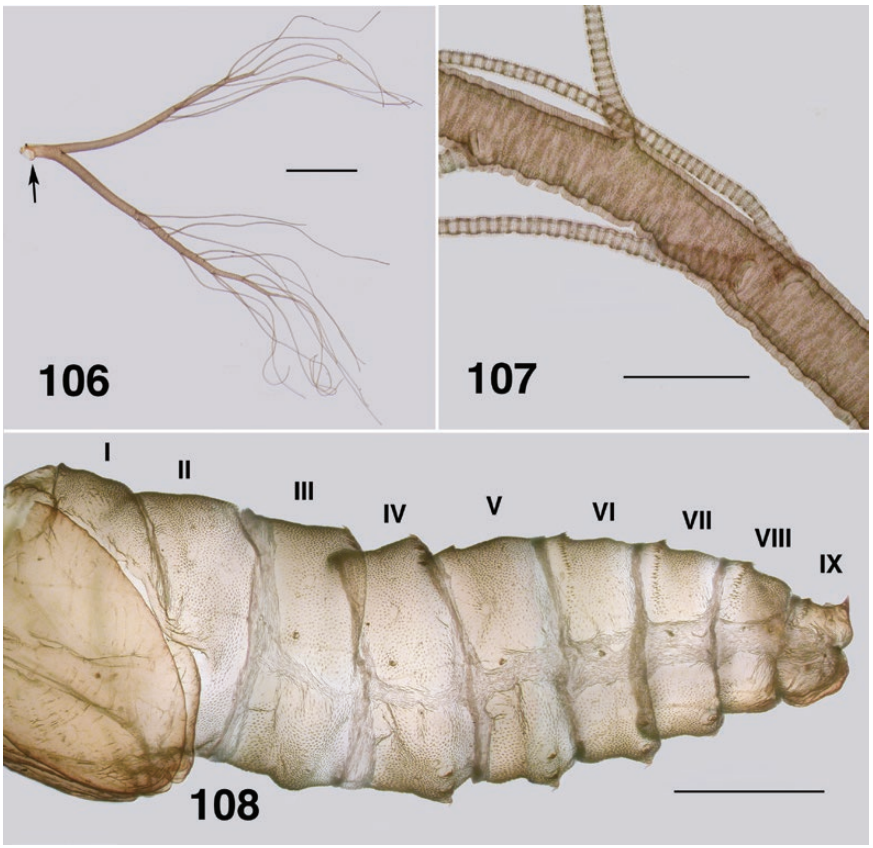
Pinned material; reared female (Fig. 79). Label (Fig. 80), (Holo-/type [Red]) (*Ectemnoides/ acanthocranius* [F]) (Western Australia/ Quinine Creek @ Ashendon/ Road. Jarrah Forest/ S32.1499° E116.1832°/ elev. 256 m. 14 September 1996/ Coll: J.K.M.) (ANIC database No./ 29 026614). Pupal exuviae on cardboard point as subsidiary material. Originally in alcohol, dried with Peldri II. Colors slightly muted. Condition excellent.

Paratypes

Pinned material; two females, labels as for holotype, but with (Para-/type [Yellow]) (ANIC database No./ 29 026615) and (ANIC database No./ 29 026616). Condition excellent. *Alcohol material*: three female pupae. Label as for holotype, but: (Para-/type [Yellow]) (ANIC Database No./ 29 026624). Five larvae, three last instar, two penultimate. Label as for holotype (ANIC Database No./ 29 026625). *Slide material*: two last instar larvae. Label as for holotype (ANIC Database No./ 29 026633 and -634).

Additional Material

Alcohol material; four vials of larva, pupae, and exuviae deposited Strickland Museum (UASM# 370862–370865). *Slide material*: nine of all stages (ANIC Database No./ 29 026728–736).



Figs. 106–108. *Ectemnoides acanthocranius* pupa. (106) Pupal gill. Arrow indicates position of broken diverticulum (cf. Fig. 120). Scale bar = 0.5 mm. (107) Gill surface. Scale bar = 0.1 mm. (108) Pupal abdomen showing armature. Scale bar = 0.5 mm.

Fig. 109. *Ectemnoides acanthocranius* habitus, last instar larva. Scale bar = 1.0 mm.

Etymology

In reference to the numerous short substantial setae on the larval cranium.

Distribution (Fig. 229)

Western Australia: Western Australia, Quinine Creek, Ashendon/ Road, Jarrah Forest, S32.1499° E116.1832°, elev. 256 m., 14-IX-1996, larvae, pupae, reared adults, J.K.M. Known, so far, from only this locality.

Bionomics

This species occurs in a low-lying, small, first-order stream with sand and rock substrate, slow to moderate velocity, and trailing vegetation. Although the body form and ventrally directed posterior abdominal proleg and circlet of hooks are markedly similar to *Ect. umbratorum* and *Ect. faecofilus*, larvae of *Ect. acanthocranius* attach directly to trailing plant material in typical simuliid fashion. However, one fecal thread is included in the collections—perhaps from *Ect. faecofilus*? Pupation does not occur on the plant—presumably in the substrate as incompletely known for *Ect. umbratorum*. Larvae from Quinine Creek reared (J.K.M.) to adult stage in Petri dishes spun only a few criss-crossed silken strands that served to anchor the pupa.

Associated with this species at Quinine Creek were *Austrosimulium* spp., *B. gladiator*, *Ect. absitus*, *Ect. faecofilus*, and *P. tonnoiri*.

Figs. 110–115. *Ectemnoides acanthocranius* last instar larva. (110) Dorsal view of head. Scale bar = 0.5 mm. (111) Ventral view of head. Scale bar = 0.2 mm. (112) Antenna. Scale bar = 0.1 mm. (113) Mandible. Scale bar = 0.1 mm. (114) Mandible apex. Scale bar = 0.05 mm. (115) Maxilla. Scale bar = 0.1 mm.

Remarks

The wing shows considerable differences from those of *Ect. umbratorum* and *Ect. faecofilus,* where for those, vein CuA is essentially straight and the a:b ratio is different (cf. Figs. 8, 9, 85, and 86). *Ect. acanthocranius* wing also lacks the spiniform setae on the costa that are present in *Ect. umbratorum* and *Ect. faecofilus*. The expression of the fenestral diverticulum on the pupal gill is of some interest. While present, albeit poorly so in the pharate state (Fig. 120), it appears absent in the fully exposed gill (Fig. 106); an assumption is, being so delicate, it is easily broken off. Molecular data (J.K.M., unpublished) show that *Ect. acanthocranius* is the sister species to *Ect. princeae* + *Ect. absitus*, in agreement with distribution of some character states—discussed later.

Ect. uvulatus n. sp. (Figs. 122–137)

(LSID: urn:lsid:zoobank.org:act:D88C04C2-42D3-4677-8CAA-F4371598C64A)

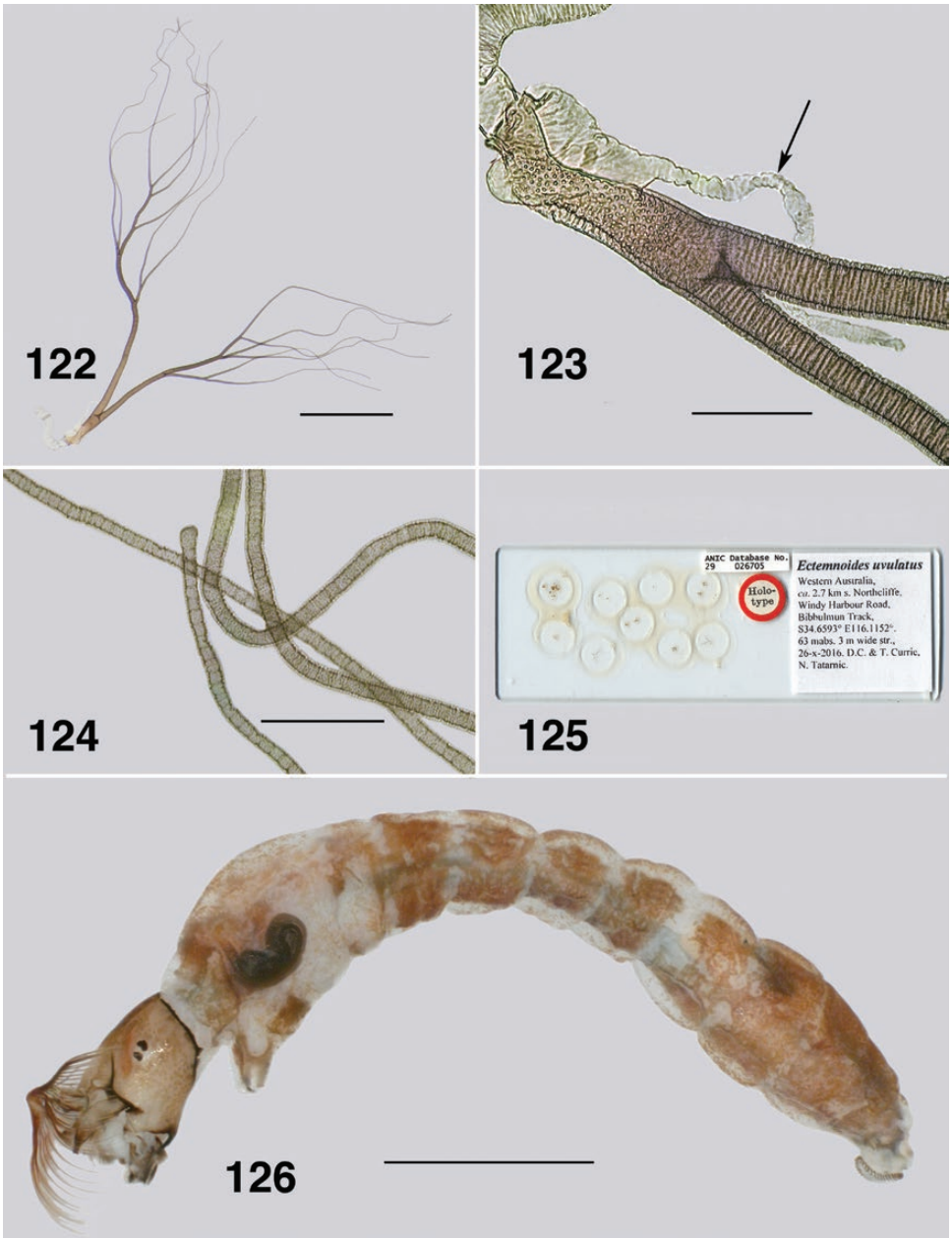
Adults: unknown.

Pupa: Unknown except for pharate pupal gill (Figs. 122–124). *Gill*: Total length 2.5 mm; basal stem short, two main filaments, branching irregularly into eight and six fine filaments respectively; surface pseudoannulated basally, annulated apically; stem and basal length of filaments moderately pigmented, distal filaments darker; fenestral diverticulum present, but poorly expressed.

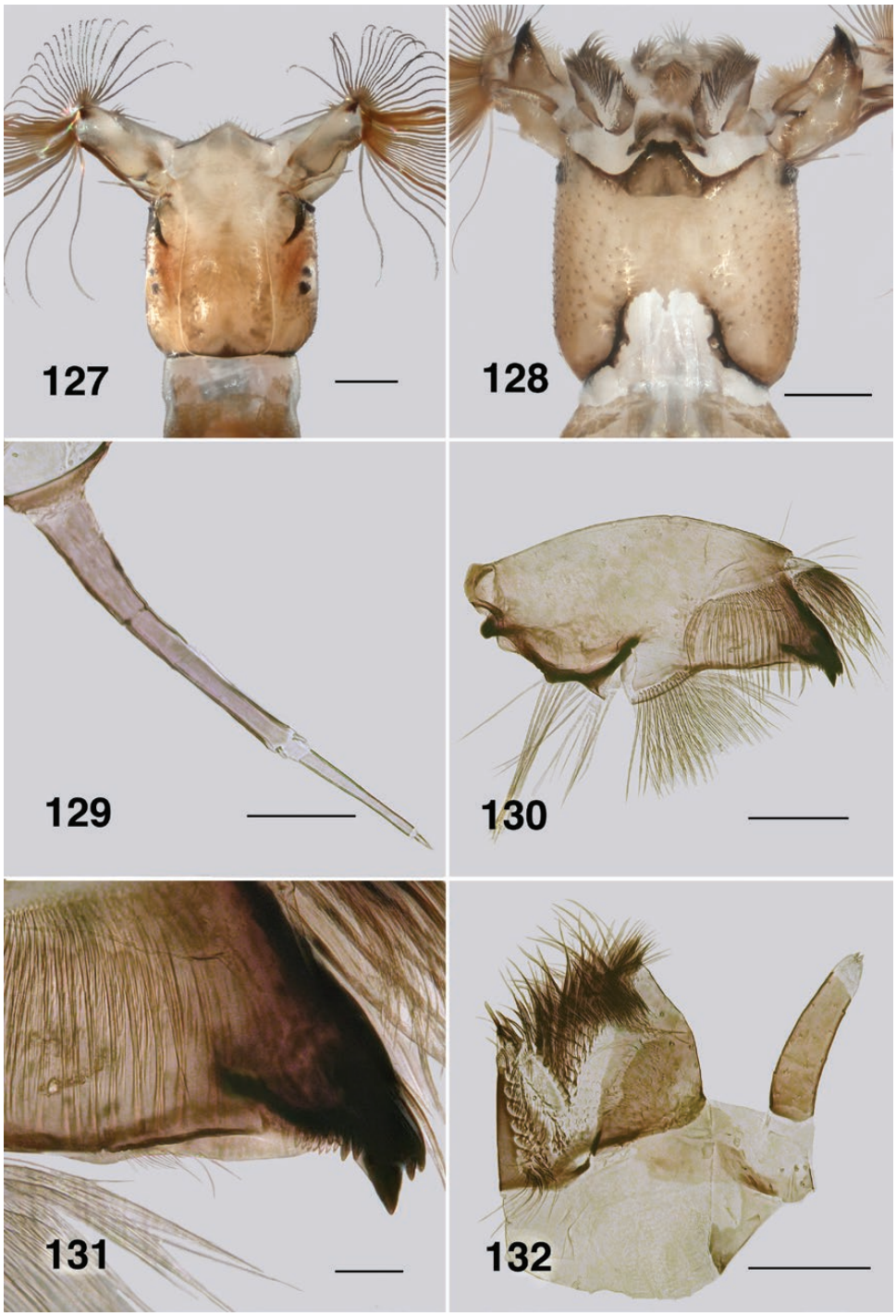
Figs. 116–121. *Ectemnoides acanthocranius* last instar larva. (116) Postgenal cleft. Scale bar = 0.2 mm. (117) Hypostoma. Scale bar = 0.1 mm. (118) Anterior proleg. Scale bar = 0.2 mm. (119) Pharate pupal gill. Scale bar = 0.5 mm. (120) Pharate pupal gill base. Scale bar = 0.5 mm. Arrow indicates fenestral diverticulum. (121) Circlet of hooks. Arrows indicate campaniform sensilla. Scale bar = 0.1 mm.

Larva: (Based on one last instar and two penultimate larvae). *Body* (Fig. 126): total length of last instar, 5.4 mm; brown with marked segmental banding. *Head* (Figs. 127 and 128): evenly pale anteriorly with sclerotized structures dark, lightly pigmented posteriorly; total length 0.7 mm, width 0.5 mm; distance between antennal bases 0.4 mm; posteromedial antennal phragma arm markedly expressed; anterior margins of head subparallel, convergent posterior of stemmata; apotome narrow, head spot pattern positive, but barely obvious; reddish brown 'eyebrow' over stemmata; ecdysial lines well visible, essentially parallel and straight until extreme posterior of head, then rounded; cervical sclerites, small, pale, well separate from darkly pigmented and narrow postocciput; apotome with short stout secondary setae producing roughened spotted appearance, posterior third bare, genae also with setae (Figs. 128 and 133); suboesophageal ganglion not pigmented. *Antenna* (Fig. 129): basal and medial antennomeres light brown, distal antennomere pale; extended to 3/4 length of labral fan stem; total length 0.25 mm; proportional lengths of basal, medial, and apical antennomeres 1.0:1.3:1.0. *Labral fan*: stalk elongated, ca. 50 markedly fine rays, length 0.7 mm, mid-ray width 0.006 mm; longer microtrichia 0.004 mm in length, separated by ca. 6 shorter. *Mandible* (Figs. 130 and

131): lightly pigmented with apical teeth dark; brushes reduced; outer apical teeth poorly developed; apical tooth not markedly produced; subapical teeth small and subequal to spinous teeth; ca. eight cone-shaped spinous teeth; sensillum and serrations present merely as fine hairs posterior of slightly convex blade-like region. *Maxilla* (Fig. 132): maxillary lobe broadly cone-shaped, palp dark, elongated, curved, 4.0× as long as basal width; palp markedly separated from lobe; tuft of hair at base of palp apparently absent. *Postgenal cleft* (Fig. 133): well developed, deeply U-shaped, sclerotized laterally anterior of posterior tentorial pits, medial uvula-like projection, larger in immature larvae; postgenal bridge lacking stout setae; posterior tentorial pits not markedly expressed; ratio of hypostoma, postgenal bridge, and postgenal cleft 1.0:1.9:1.5; suboesophageal ganglia not pigmented. *Hypostoma* (Fig. 134): darkly pigmented; tooth 0 (median) and teeth 1, 2, 3 (sublateral) small, subequal, in slightly convex lineage, depressed below other teeth, tooth 4 (lateral) larger, tooth 5 slightly protrusive, teeth 6, 7, 8 (paralaterals) teeth subequal in size; serrations variable and poorly expressed; one main hypostomal seta on each side; 2 or 3 other small setae variously arrayed posteriorly. *Thorax* (Fig. 135): prothorax brown, remainder of thorax lighter; mature pharate pupal gill with basal trunk directed ventrally then filaments curved broadly posteriorly, then dorsally and anteriorly to produce shallow U-shaped structure. *Prothoracic proleg*: elongated, lateral plates distinct, V-shaped (not shown in figure). *Abdomen*: brown, intersegmental regions pale, producing distinct banding effect; cuticle with hexagonal patterning (e.g., Fig. 41). *Ventral tubercles*: absent. *Anal sclerite* (Fig. 136): markedly reduced, anterodorsal arms absent, posteroventral arms small and broad, clear cuticular ring around circlet of hooks present, better expressed adjacent to posteroventral arms, less so



Figs. 122–126. *Ectemnoides uvulatus* last instar larva. (122) Pharate pupal gill. Scale bar = 0.5 mm. (123) Pharate pupal gill base showing diverticulum (arrow). Scale bar = 0.1 mm. (124) Pupal gill filament structure. Scale bar = 0.05 mm. (125) Holotype slide mount. (126) Last instar larva. Habitus of holotype. Scale bar = 1.0 mm.



Figs. 127–132. *Ectemnoides uvulatus* last instar larva. (127) Dorsal head. Scale bar = 0.2 mm. (128) Ventral head. Scale bar = 0.2 mm. (129) Antenna. Scale bar = 0.05 mm (130) Mandible. Scale bar = 0.1 mm. (131) Mandible apex. Scale bar = 0.02 mm. (132) Maxilla. Scale bar = 0.1 mm.

elsewhere. *Posterior circlet*: markedly directed ventrally; ca. 45 rows of hooks, six or seven per row (total ca. 290).

Type Material

Holotype

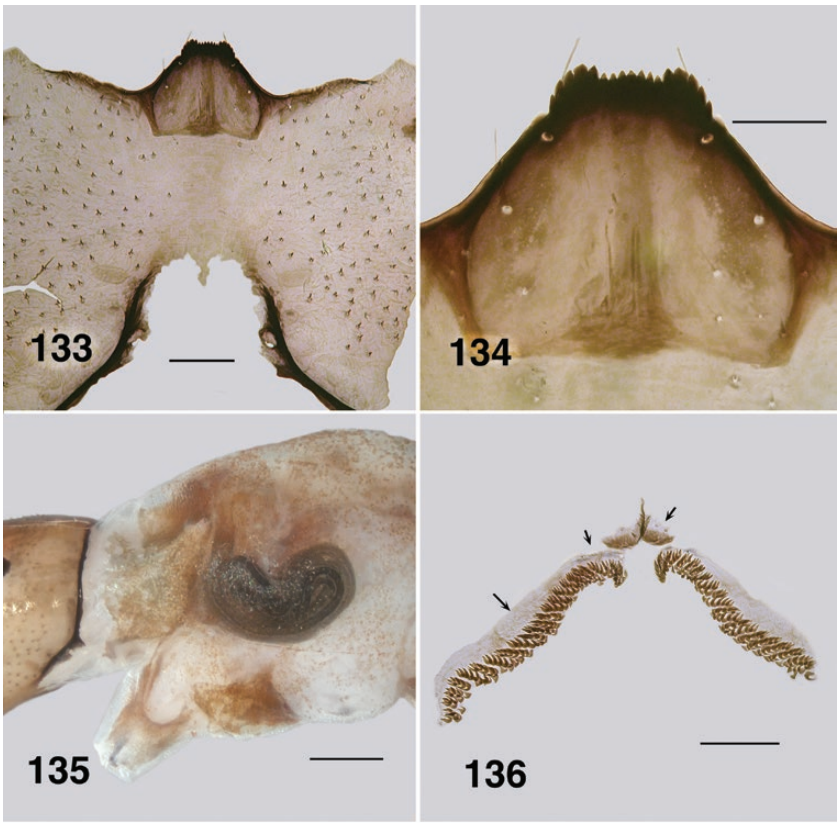
Slide mount; last instar larva. Label (Fig. 125) (Holo-/ type) (*Ectemnoides uvulatus*/ Western Australia,/ *ca*. 2.7 km s. Northcliffe,/ Windy Harbour Road,/ Bibbulmun Track,/ S34.6593° E116.1152°./ 63 mabs. 3 m wide str.,/ 26-x-2016. D.C. & T. Currie,/ N. Tatarnic.) (ANIC Database No./ 29 026705).

Paratypes

Slide mount; penultimate instar larva. Label as for holotype, but with (Para-/ type) (ANIC Database No./ 29 026706). *Alcohol material*; penultimate instar larva, label the same, but with (ANIC Database No./ 29 026707).

Etymology

In reference to the 'uvula'-shaped structure (derived from Latin 'uvae' for 'grape') on the postgenal cleft apex.



Figs. 133–136. *Ectemnoides uvulatus* last instar larva. (133) Post genal cleft. Scale bar = 0.1 mm. (134) Hypostoma. Scale bar = 0.05mm (135) Pharate pupal gill. Scale bar = 0.2 mm. (136) Anal sclerite, circlet of hooks. Arrows indicate campaniform sensilla. Scale bar = 0.1 mm.

Distribution (Fig. 229)

Western Australia: ca. 2.7 km s. Northcliffe, Windy Harbour Road, Bibbulmun Track, 3 m wide stream, S34.6593° E116.1152°, elev. 63 m., pupae, larvae, 26-X-2016. D. C. and T. Currie, N. Tatarnic. Known from only this locality (Fig. 137).

Bionomics

Little is known. The date of collection is later (October) than those recorded for other Western Australia species of *Ectemnoides*, that are generally assumed to be univoltine austral late winter-early spring (early September) species. *Ect. uvulatus* occurs with *Aust. furiosum*.

Remarks

Body shape, head structures, and pupal gill expression, among other characters, are synapomorphic for *Ect. uvulatus*, *Ect. acanthocranius*, *Ect. faecofilus*, and *Ect. umbratorum*. However, *Ect. uvulatus* has a distinctive postgenal cleft (cf. Figs 37, 72, and 133) and hypostomal teeth (cf. Figs. 38, 73, and 134).

Ect. princeae n. sp. (Figs. 138–179)

(LSID: urn:lsid:zoobank.org:act:FC963009-77A6-4009-9CC3-1FFFFEA192A9)

'*Cnephia*' 'y'. Moulton 2000: 86. Moulton 2003: 47.

Adult female (based on five reared specimens). *Body*: dried; overall black to dark brown; total length 2.4–2.7 mm (Fig. 138). *Head* (Fig. 140): width 0.74–0.77 mm; depth 0.52–0.53 mm; frons tapered slightly toward antennae; pollinose; postocciput black, vestiture of sparse, short black hairs; frons:head ratio 1.0:5.4. *Eyes*: interocular distance 0.13–0.16 mm; ommatidia, black, diameter 0.016 mm; ca. 40 rows across and down at mid-eye. *Clypeus*: width 0.22–0.24 mm; dark brown; vestiture of sparse pale hairs. *Antenna* (Fig. 141): overall, blackish brown; total length 0.7 mm; scape and pedicel bead-like, nine flagellomeres, first not markedly expressed, remainder slightly tapering, distal flagellomere small. *Mouthparts* (Figs. 140 and 142): moderately substantial, ca. 0.5× length of head depth, labrum pale; cibarium cornuae broadly flared and well sclerotized, median depression broadly V-shaped (Fig. 143); mandible with ca. 16 outer and 39 inner teeth; lacinia with ca. 15 teeth on each side; maxillary palp, total length 0.65 mm, palpomeres I & II small, palpomere III darker brown than remainder, not extended laterally at distal articulation, palpomere IV extended slightly, palpomere V slightly elongated; proportional lengths palpomeres III–V 1.0:0.8:1.4; sensory organ not elongated, 0.5× length of palpomere III, opening 0.5× vesicle width. *Thorax*: length 1.2–1.4 mm; width 0.87–0.88 mm; markedly blackish brown; postpronotal lobe with sparse fine hair longer than scutal vestiture, of even sparse fine small hairs; scutellar depression black with vestiture of sparse fine hairs; postpronotal lobe concolorous with scutellum, vestiture sparse; antepronotal and proepisternum lobes hirsute; fore coxa markedly hirsute; pleuron and anepisternal membrane dark brown, without hair; katepisternal sulcus well expressed and deep. *Wing* (Figs. 144 and 145): hyaline, lacking color; length 3.0–4.0 mm; width 1.4–1.5 mm; small but distinct basal cell; a:b ratio 1.0:3.3; costa with hairs only; Rs not branched, but slightly thickened distally; CuA markedly sinuous. *Haltere*: stem grayish, knob tan. *Legs* (Fig.146): blackish-brown, markedly hirsute, fore coxa in particular; hind basitarsus with ventral row of stout spines; calcipala expressed as small projection with clump of stout spines; small hirsute intersegmental plate ventrally between basitarsus and tarsomere II; pedisulcus absent; claws small, basal tooth generally absent, but

Fig. 137. Bibbulmun Track Stream, Windy Harbour Road, WA. 26-X-2016. *Ectemnoides uvulatus* habitat. Image by D.C.C.

present occasionally, various on either side, rounded heel substantial (Fig. 147). *Abdomen* (Fig. 148): overall dark brown; basal scale dark gray, with creamy-yellow hairs; remaining segments generally dark gray, paler at posterior of segment, with short creamy-yellow hairs, posteriorly; tergite II bowl-shaped, tergites III–V rectangular, essentially bare, more vestiture on posterior segments; cuticle corrugated lateral of tergites. *Genitalia*: hypogynial valves triangular, slightly divergent, inner edges strengthened, sparse vestiture except for microtrichia (Fig. 149); genital fork with narrowed anterior arm, lateral arms with knee-bend triangular, posterolateral expansions of irregular expression and lateral apodeme apparent as fine ridge only (Fig. 150); spermatheca spherical (Fig. 151), medium brown, externally smooth with internal acanthae, length 2.7–4.1 µm, width ca. 0.27 µm, region surrounding junction with spermathecal duct sculpted; cerci in lateral view broadly rounded with slight apical protrusion, anal lobes small, but with distinct anteroventral projection (Fig. 152).

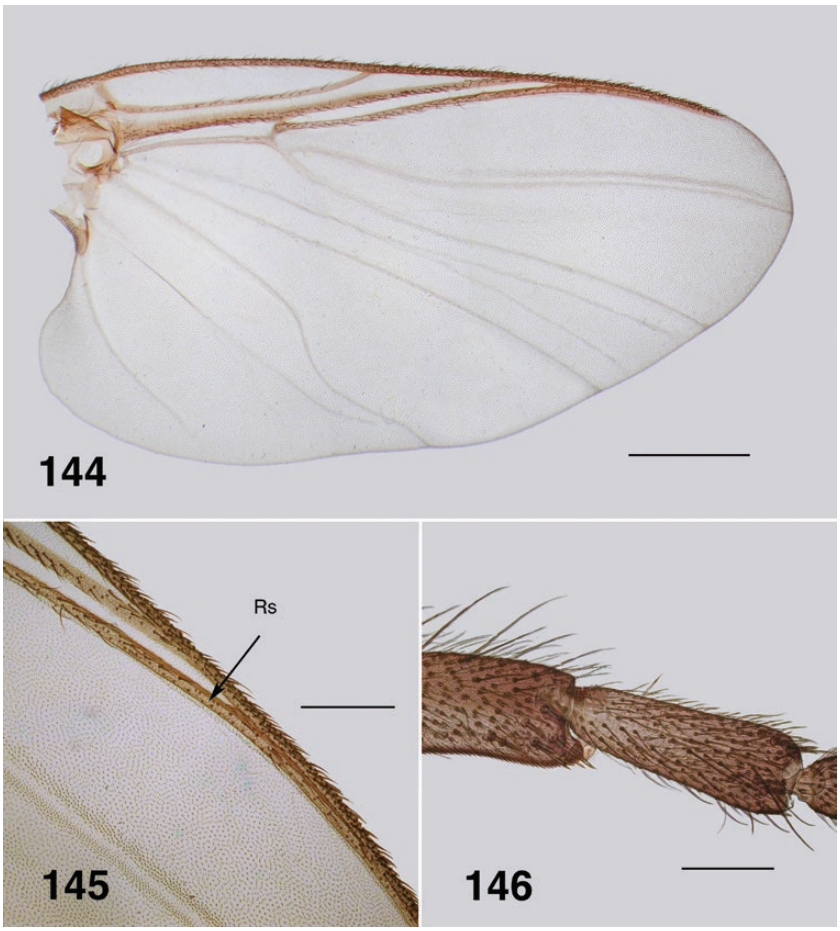
Adult male (based on single pharate and five reared specimens). *Body*: in ethanol or dried, overall color black (Fig. 153); total length 3.7 mm. *Head* (Fig. 154): width 1.0 mm; depth 0.8 mm. *Eyes*: upper ommatidia dark reddish, diameter 0.037 mm, ca. 24 across and 27 down; lower small ommatidia darker, diameter 0.016 mm, ca. 24 across and 28 down. *Clypeus*: black; width 0.19 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 155): total length 0.70 mm; overall black, pedicel small, scape twice as long and rounded distally, flagellomere I slightly narrower than scape, remaining flagellomeres tapered slightly to apical flagellomere. *Mouthparts* (Fig. 156): length 0.3× head depth; maxillary palp 0.55 mm long, palpomeres I & II small, proportional lengths of palpomeres III–V, 1.0:0.8:1.6; palpomere IV expanded distally; sensory vesicle irregular spherical shape, occupying 0.45× palpomere III width, opening 0.3× vesicle width. *Thorax*: domed; length 1.1–1.2 mm; width 0.73–0.75 mm; postpronotal lobe, antepronotal lobe and proepisternum markedly haired; scutum evenly velvety black, vestiture of dense fine pale hairs, dense and long in scutellar depression; postpronotal lobe vestiture dense and long; scutellum concolorous with scutum, bare medially, with dense long black hairs laterally; postnotum concolorous with scutum, bare; pleurae dark brown, membrane without hair. *Wing* (Fig. 157): hyaline; length 3.3 mm, width 1.6 mm; a:b ratio 1.0:2.8; Rs slightly branched at apex (Fig. 158). *Haltere*: base of stem black, knob tan. *Legs*: markedly hirsute, front leg black, femur with long fine hairs; mid-leg mainly black to blackish brown; hind leg with proximal segments hirsute, black, basitarsus yellowish brown as are other tarsomeres; basitarsus with ventral row of stout spines, calcipala present, small, with clump of stout spines ventrally, triangular inter-article sclerite present; pedisulcus absent, but cuticle slightly irregular at that position, tarsomere II apical width to length ratio 1.0:3.0; tarsal claw grappling pad of ca. 25 teeth. *Abdomen*: overall black, basal scale hairs black, extended to posterior of segment III, tergites blackish brown, 3 to 4× as wide as long, tergites II–IV with long hairs laterally, remainder with more evenly arrayed vestiture; sternites present, but small. *Genitalia* (Fig. 159): heavily pigmented; gonocoxa 1.7× longer than basal width, vestiture of sparse hairs, microtrichia in rows, hairs accentuated anterolaterally and medially; gonostylus ca. 2.2× longer than basal width, flattened in lateral view, strengthened along medial edge, vestiture of shorter hairs, two apical spines (Fig. 160); ventral plate complex, 1.7× wider than length, median keel-like projection directed ventrally, broadly rounded laterally, broadly concave anteromedially; vestiture of coarse hairs; basal arms massive and well sclerotized, paramere connectors as markedly thin curved arms (Fig. 161); median sclerite well developed, substantial insertion anteromedially on ventral plate, distinct distal bifurcation with reflexed apices; parameres broadly rounded, with marked articulations to connector, anteromedial edge marked, body of the paramere thin with slightly crenulated posterolateral extremity; parameral spines absent; adeagal membrane with microtrichia.

Pupa (based on six mature pupae and exuviae). *Body* (Fig. 162); length, male 3.6–3.7 mm, female 3.4–36 mm, dark brown. *Head*: frontal plate of female quadratic (Fig. 166), basal width ratio of frons to vertex 1.0:1.3, male more ovoid ratio 1.0:1.5 (Fig. 167), male apparently smooth, but covered with barely visible minute tubercles; muscle scars positive and distinct; female with pitting and corrugations; frontal setae absent, facial setae present, stiff and curled apically. *Thorax*: anterior dorsal shield with crinkled cuticle, dorsocentral setae neither markedly developed nor with curled tips (Fig. 165). *Gill* (Fig. 163): markedly longer than pupa, total length 4.3–5.3 mm; fenestral diverticulum absent, three fine trunks arising directly from base, ca. 10 short fine filaments arising from basal third of main trunks. Surface reticulated on main trunks, finely pseudoannulated on filaments (Fig. 164). *Abdomen* (Fig. 168): overall yellowish brown, cuticle substantial, covered with minute tubercles and corrugations; armature poorly developed; terminal spines on

Fig. 138–143. *Ectemnoides princeae* female. (138) Habitus of female holotype. Scale bar = 1.0 mm. (139) Holotype labels. (140) Frontal view of head. Scale bar = 0.25 mm. (141) Antenna. Scale bar = 0.1 mm. (142) Maxilla, palp, lacinia, mandible. Insert: mandible apex. Scale bar = 0.1 mm. (143) Cibarium. Scale bar = 0.05 mm.

tergite IX short, substantial, sharply tapered, curved anteriorly, grapnel hooks present; spine combs essentially absent, present only as sporadic spines well lateral on posterior tergites; pleurites essentially absent, small one present on segment VI, that on segment V closely attached to extended tergite; concertinaed pleural cuticle markedly brown. *Cocoon* (Fig. 162). Silk fibers fine; close-fitting shapeless bag covering the abdomen, occasionally reaching anteriorly to mid thorax, anterior edge not well formed; two layers, inner one coarsely woven, outer one finer with extraneous material from substrate variously incorporated.

Larva (based on twelve final instar larvae). *Body* (Fig. 169): total length 7.3–8.1 mm, evenly mottled yellowish gray. *Head* (Figs. 170 and 171): evenly medium to moderate brown with darker regions (various); anterior apotome paler, posterolateral regions and upper genae darker; total length 1.1–1.2 mm, width 0.77–0.83 mm; distance between antennal bases 0.53–0.64 mm; anterior of head expanded, narrower posteriorly; head spot pattern slightly positive; ecdysial lines well visible, divergent until near posterior of head, then markedly curved; cervical sclerites



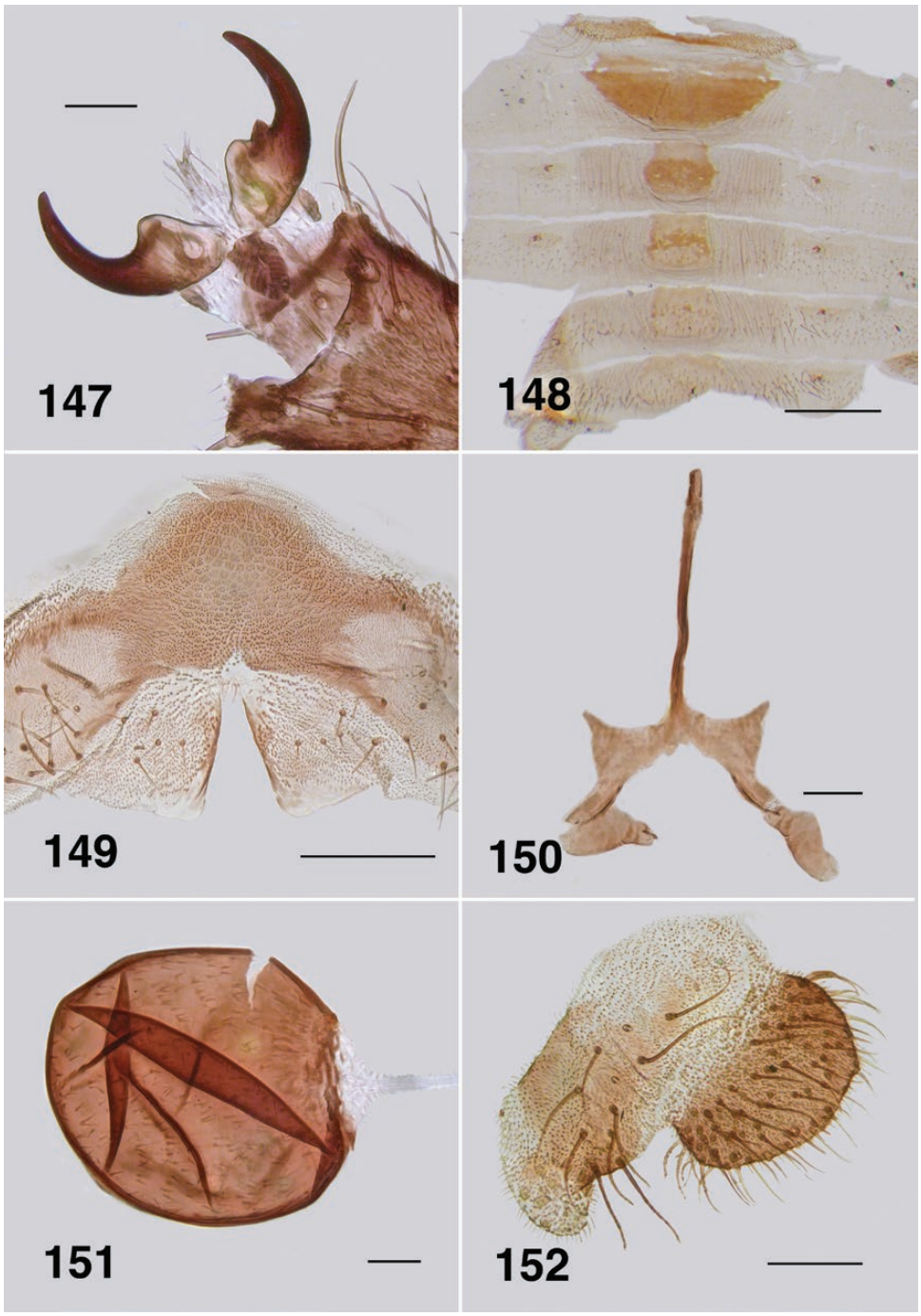
Figs. 144–146. *Ectemnoides princeae* female. (144) Wing. Scale bar = 0.5 mm. (145) Wing veins. Rs – radial sector. Scale bar = 0.2 mm. (146) Hind basitarsus and tarsomere II. Scale bar = 0.1 mm.

poorly expressed, not fused to postocciput; upper genae anterior of stemmata markedly dark brown, cephalic sensillae slightly elongated, fine with clear sockets. *Antenna* (Fig. 172): subequal in length to labral fan stem, apex often missing in available material; total length ca. 0.60 mm; antennomeres dark brown, basal antennomere with narrow clear band laterally; basal, medial and distal antennomeres subequal in length, apical antennomere slightly longer; proportional lengths 1.0:1.0:1.4. *Labral fan*: markedly expressed; stalk light brown, ca. 75 rays, all rays more or less equally developed, length 1.05 mm, mid-ray width 0.012 mm; microtrichia small, but with pattern of longer microtrichia, length 0.007 mm, interspersed with 6–8 smaller. *Mandible* (Figs. 173 and 174): not markedly pigmented; outer teeth short, broad, poorly developed; apical tooth substantial; subapical teeth markedly small; ca. 8 spinous teeth, small and saw-toothed in expression; sensillum and serration complex, on well developed raised base; blade region smooth and slightly convex. *Maxilla* (Fig. 175): lobe cone-shaped, palp markedly elongated, longer than lobe, 2.7× as long as basal width, black, well separated from lobe; tuft of hair at base of palp not markedly developed. *Postgenal cleft* (Fig. 176): poorly developed, roughly U-shaped, moderately sclerotized; posterior tentorial pits small; postgenal bridge darker brown posteriorly, otherwise concolorous with genae; posteroventral muscle spots small, ratio of hypostoma, postgenal bridge and postgenal cleft 1.0:1.5:0.5; suboesophageal ganglion not markedly pigmented (Fig. 171). *Hypostoma* (Fig. 177): darkly pigmented apically; tooth 0 neither well developed nor protrusive; teeth 1, 2, 3 minute, barely visible, teeth 4, 5, 6 equally developed and larger than tooth 0, teeth 7, 8 obscured by hypostoma edge; lateral edge of hypostoma forming serrated cone-shaped projection, other lateral serrations various; single hypostomal seta situated anterolaterally on the hypostoma; 3 or 4 smaller setae variously arrayed more basally. *Thorax* (Fig. 178): prothorax brown, remainder of thorax lighter; the mature pharate pupal gill shallowly L-shaped, the three main filaments directed ventrally then broadly posteriorly to turn dorsally then anteriorly and curled centrally; fine filaments sometimes showing. *Prothoracic proleg*: when extended, elegant, anterolateral plates small and V-shaped. *Abdomen*: evenly mottled medium yellowish brown, gradually expanded posteriorly and rounded, cuticle smooth. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 179): markedly absent, campaniform sensilla array typical. *Posterior circlet*: directed posteriorly ca. 45 rows of hooks, seven or eight per row (total ca. 340).

Type Material

Holotype

Pinned material; reared female (Fig. 138) with subsidiary of pupal exuviae in microvial. Label (Fig. 139), (Holo-/type [Red]) (*Ectemnoides/ princeae*) (AUSTRALIA:WA/ Spice Brook @ Whitaker Rd./ Jarrah Forest, SEE of Perth/ S 31° 27′/ E 116° 12′/ elev. 307 m/ 7 September 1996 [F]/ Coll: J.K.M.) (ANIC Database No./ 29 026594). Condition excellent.



Figs. 147–152. *Ectemnoides princeae* female. (147) Tarsal claws. Note basal tooth variation. Scale bar = 0.02 mm. (148) Abdominal tergites. Scale bar = 0.5 mm. (149) Hypogynial valves. Scale bar = 0.1 mm. (150) Genital fork. Scale bar = 0.05 mm. (151) Spermatheca. Scale bar = 0.02 mm. (152) Cercus and anal lobe. Scale bar = 0.05 mm.

Paratypes

Pinned material; three females, labels as for holotype, but with (Para-/type [Yellow]) (ANIC Database No./ 29 026595) to (ANIC Database No./ 29 026597). Five males labeled as for holotype (ANIC Database No./ 29 026598) to (ANIC Database No./ 29 026602). *Alcohol material*: nine last instar larvae (ANIC Database No./ 29 026603), six pupae, (ANIC Database No./ 29 026604), labeled the same.

Addtional Material

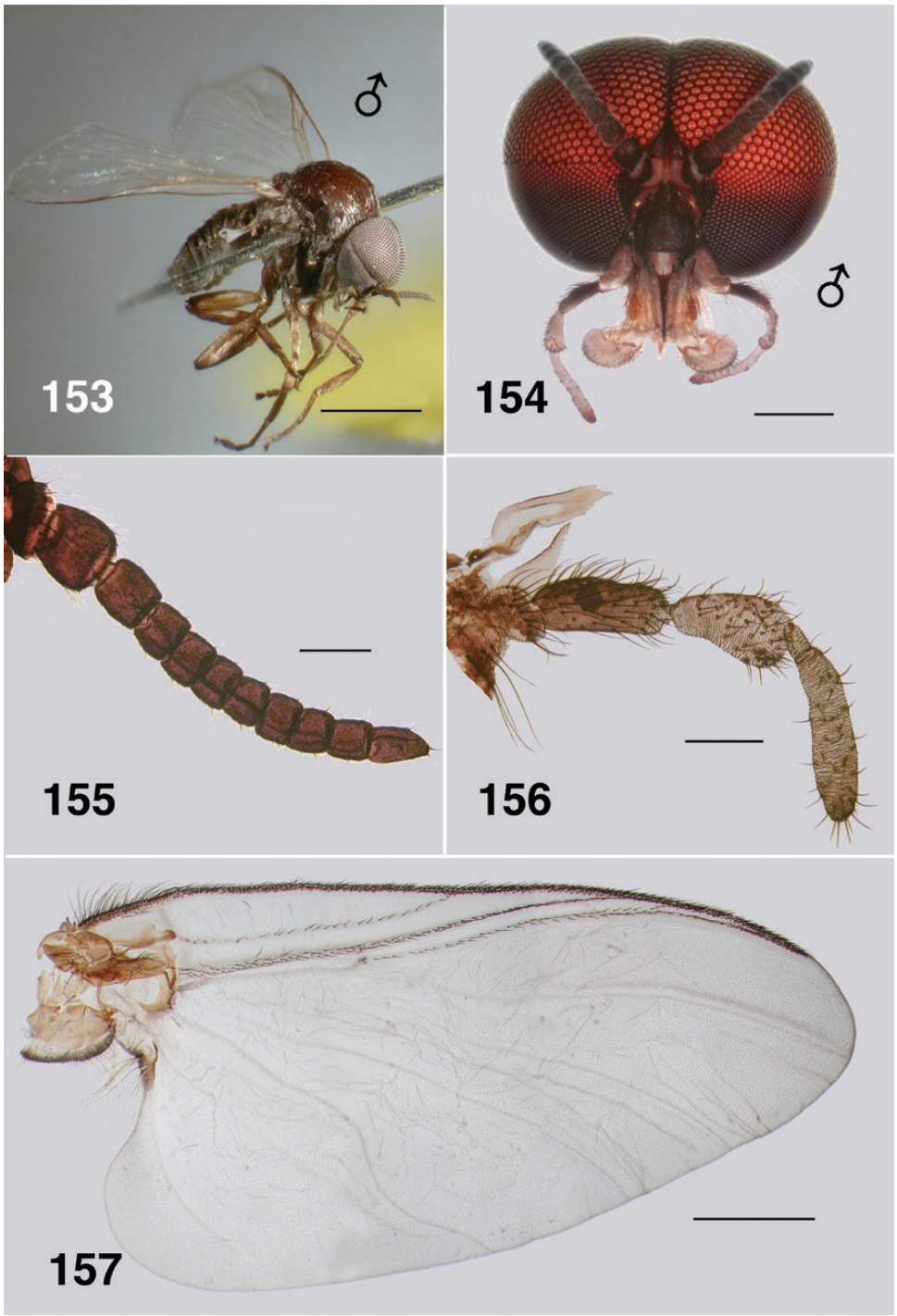
Slide material; five slides; labels as for holotype, one pharate male, two females, two last instar larvae (ANIC Database No./ 29 026708–712); one slide, last instar larva, label (Western Australia/ Hotham River Trib./S32.8708° E116.4524°/ elev. 200 m. 10-iv-96/ Coll. J.K.M./ Last instar larva) (ANIC Database No./ 29 026715).

Etymology

Named in honor of Jane Prince, who first discovered the species while conducting ecological studies (Prince 1980) in the Jarrah Forest.

Distribution (Fig. 229)

Western Australia: Spice Brook at Whitaker Road, Jarrah Forest, SEE of Perth, S32.4499° E116.1999°, elev. 330 m., larvae, pupae,



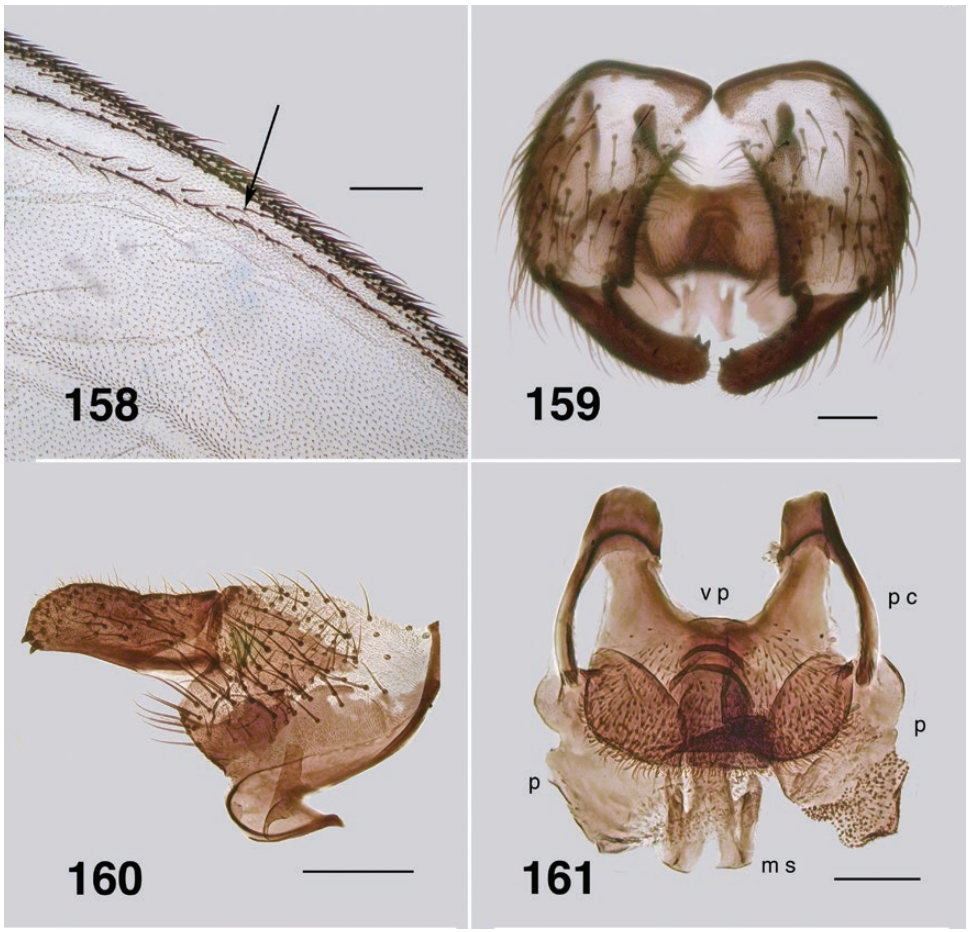
Figs. 153–157. *Ectemnoides princeae* male. (153) Habitus of paratype. Scale bar = 1.0 mm. (154) Frontal view of head. Alcohol. Scale bar = 0.25 mm. (155) Antenna. Scale bar = 0.1 mm. (156) Maxillary palp, mandible, lacinia. Scale bar = 0.1 mm. (157) Wing (pharate). Scale bar = 0.5 mm.

7-IX-1996, J.K.M.; Dale River tributaries, S32.3584° E116.4583°, elev. 300 m. and S32.2000° E116.1167°, elev. 350 m.; Hotham River tributary, S32.8708° E116.4524°, elev. 200 m., larvae, 10-IV-1996, J.K.M.

Bionomics

Ect. princeae is known only from small first-order streams in the Jarrah Forest SE of Perth. The type locality of Spice Brook was a shallow seepage stream strewn with fallen leaves on which the larvae and pupae were found in great abundance. The other localities, with smaller populations, were more stream-like, with trailing grasses, leaf packs and snags.

There were no other simuliids present at the type locality, but at the other two sites *Ect. princeae* was associated with *Ect. absitus* and *Nothogreniera occidentalis* (Makerras and Mackerras) (Craig et al. 2018b).



Figs. 158–161. *Ectemnoides princeae* male. (158) Wing veins. Arrow indicates branch of Rs. Scale bar = 0.1 mm. (159) Ventral view of genitalia. Scale bar = 0.05 mm. (160) Lateral view of gonocoxa and gonostylus. Scale bar = 0.1 mm. (161) Genitalia—slide mounted. m s – median sclerite; p c – paramere connector; p – paramere; v p – ventral plate. Scale bar = 0.05 mm.

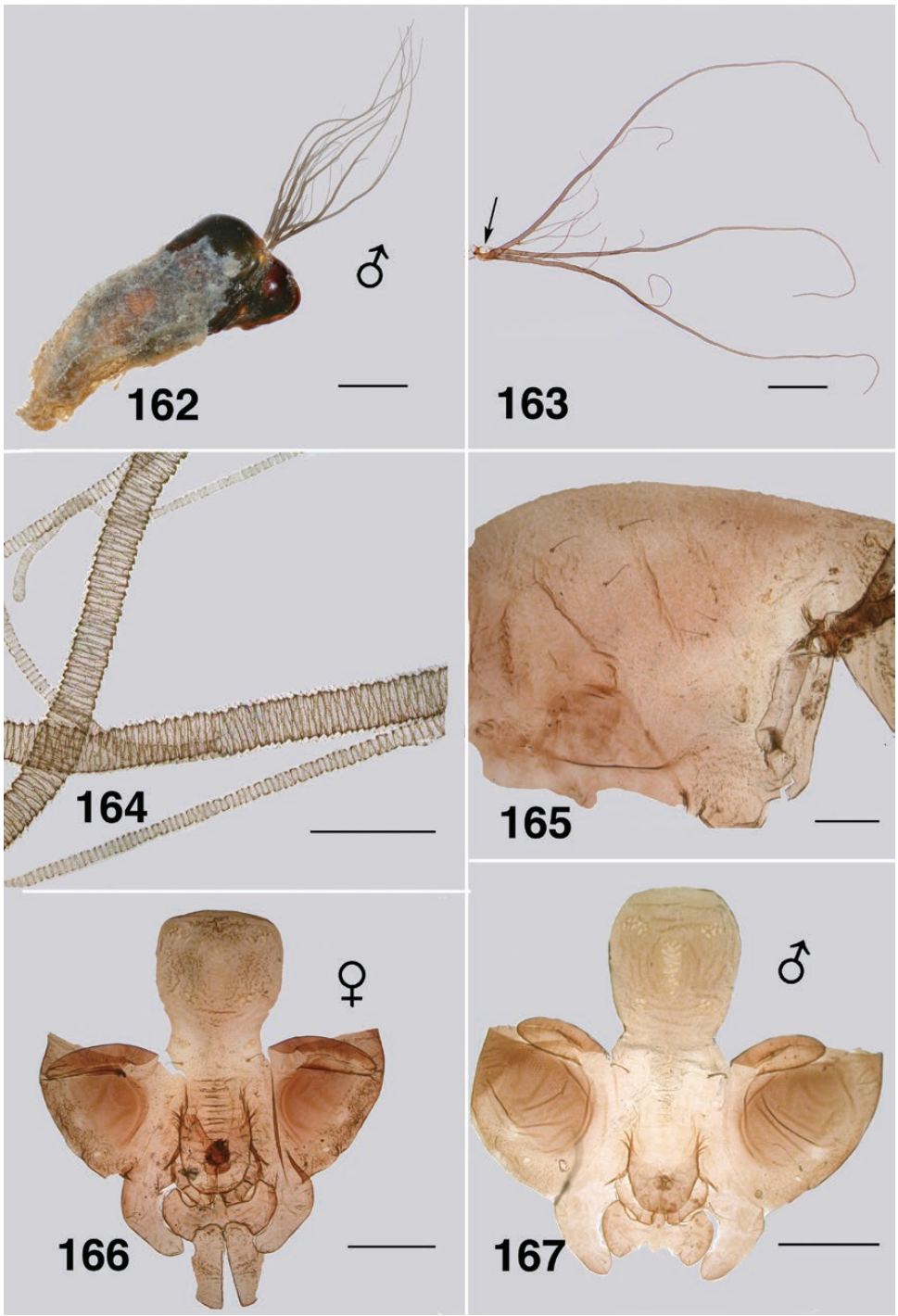
Remarks

The female has substantial mouthparts with mandibles toothed on both edges. This, in conjunction with the poorly expressed abdominal tergites, suggest that *Ect. princeae* females probably blood feed. There is, however, no information on that. Lacking a tooth on the claw indicates that (Adler et al. 2004), if a blood feeder, *Ect. princeae* is probably not ornithophilic. The male is unusual in that it shows a slight branching of the Rs vein (Fig. 158). Further, the paramere connector is markedly curved and expressed, and parameral spines are absent. The pupal gill while of similar overall expression to those of *Ect. acanthocranius, Ect. faecofilus, Ect. umbratorum*, and *Ect. uvulatus*, has three long trunks and lacks the fenestral diverticulum. As noted elsewhere, this suggests that the diverticulum, when present, is a poorly expressed third trunk. While the larval body is somewhat similar to those other four species in being slightly elongated, the posterior proleg is directed posteriorly, not ventrally. Similar to *Ect. absitus* described next, the larval mandibular serration and sensillum are cone-like and distinct on a raised base. The hypostomas of these species are also similar to *Ect. absitus* with the anterolateral edges of the 'hypostoma' not formed by teeth.

Ect. absitus n. sp. (Figs. 180–222)

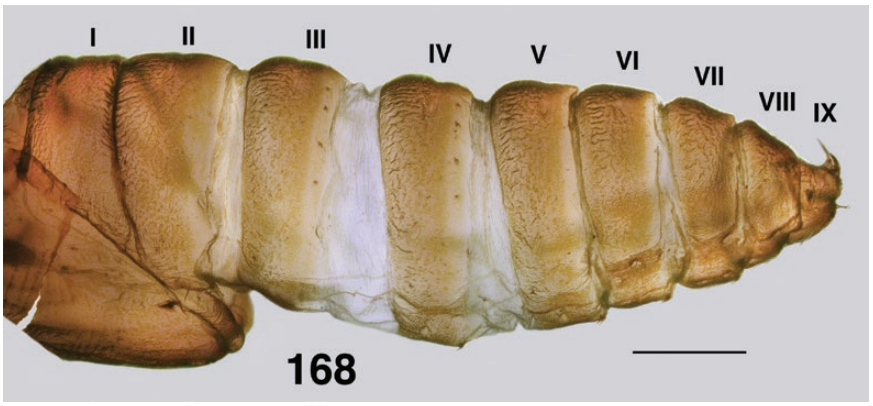
(LSID: urn:lsid:zoobank.org:act:35C55EE4-1D1D-4719-9C64-9085BD0C0E45)

Adult female (based on eight reared specimens). *Body* (Fig. 180): dried; overall black to dark brown; total length 2.4–2.9 mm. *Head* (Fig. 182): black; width 0.87–0.89 mm; depth 0.61–0.63 mm; frons broad, narrowest just above antennae; slightly pollinose; postocciput black, vestiture of sparse, short black hairs; frons:head ratio 1.0:5.5. *Eyes*: interocular distance 0.13–0.16 mm; ommatidia black, diameter 0.016 mm; ca. 34 rows across and down at mid-eye. *Clypeus*: width 0.19 mm; dark brown; vestiture of sparse dark hairs. *Antenna* (Fig. 183): overall, blackish brown; total length 0.72 mm; scape and pedicel segments bead-like, flagellomere I broad, remainder slightly tapering, apical flagellomere IV small. *Mouthparts*: moderately substantial, ca. 0.3× length of head depth, labrum pale; maxillary palp (Fig. 184), total length 0.76 mm, palpomeres I & II small, palpomere III darker brown than remainder, not extended beyond articulation with palpomere IV; proportional lengths of palpomeres III–IV 1.0:0.7:1.5; sensory organ ovoid, 0.3× palpomere III length, opening 0.3× vesicle width; lacinia with ca. 16 teeth on each side; mandible expanded apically with ca. 16 outer and 34 inner teeth, fine and subequal in size (Fig. 185); cibarium cornuae broadly flared and substantially sclerotized, median depression with central projection (Fig. 186). *Thorax*: length 0.9–1.4 mm; width 0.9–1.1 mm; markedly blackish brown; postpronotal lobe with sparse fine hair longer than vestiture on scutum, scutum overall with even sparse fine small hairs; scutellar depression black; scutellum with vestiture of sparse very fine hairs; postnotum concolorous with scutellum, vestiture absent; postpronotal and antepronotal lobes and proepisternum haired; pleuron and anepisternal membrane dark brown, latter without hairs; katepisternal sulcus well expressed and deep. *Wing* (Fig. 188): hyaline, lacking color;

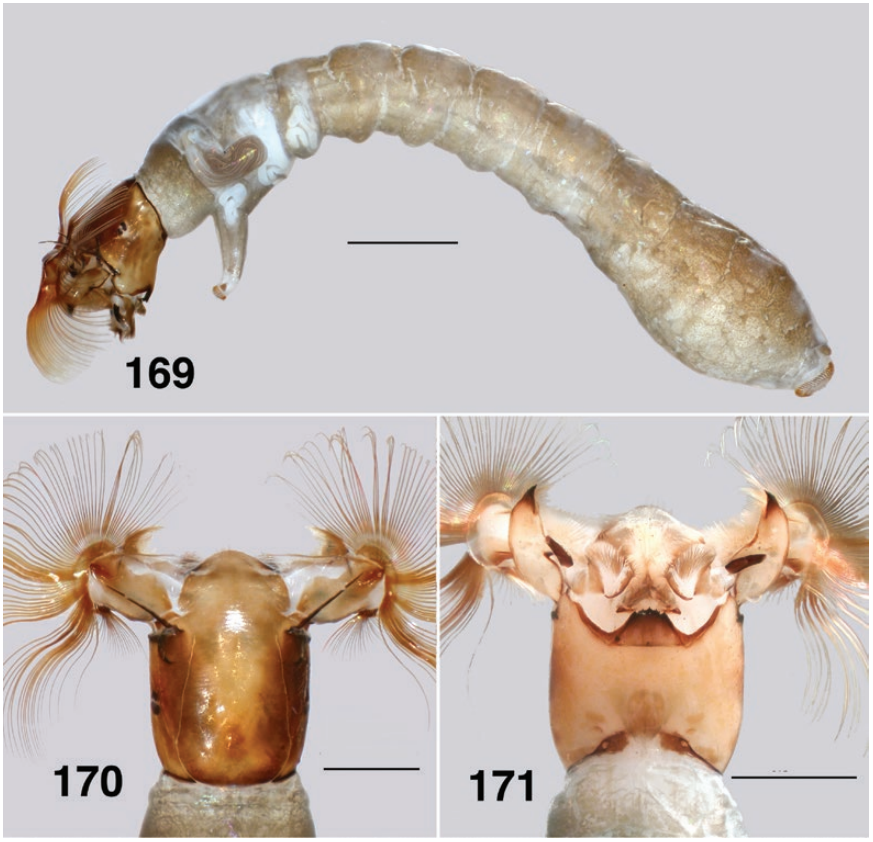


Figs. 162–167. *Ectemnoides princeae* pupa. (162) Habitus, male. Scale bar = 1.0 mm.(163) Gill. Arrow indicates fenestra. Note absence of diverticulum. Scale bar = 0.5 mm. (164) Gill surface structure. Scale bar = 0.1 mm. (165) Thoracic cuticle. Scale bar = 0.25 mm. (166) Female cephalic capsule. Scale bar = 0.5 mm. (167) Male cephalic capsule. Scale bar = 0.5 mm.

length 3.2–4.0 mm; width 1.4–1.6 mm; anterior veins dark; a:b ratio 1.0:2.8; costa lacking spiniform setae; Rs not branched; M_1 double, but not markedly so; CuA markedly sinuous. *Haltere*: stem pale with dark base, knob tan. *Legs*: evenly dark brown, not markedly hirsute, but in particular hairs long on the fore coxa; hind basitarsus with marked row of ventral stout spines; calcipala present as small projection with clump of stout spines (Fig. 187); intersegmental plate ventrally between basitarsus and tarsomere II small; pedisulcus absent, tarsomere II elongated, variable, ratio of apical width to length 1.0:2.8–3.7; claws small, basal tooth merely as small knob, if at all, rounded heel substantial (Fig. 189). *Abdomen* (Fig. 190): overall dark brown, vestiture sparse; basal scale (tergite I) dark gray; remaining segments generally dark gray; tergites dark brown, tergite II, 3× wider than long, tergite III twice as wide as long, tergites IV–VI quadratic, tergite VII twice as wide as long, curved anteriorly. *Genitalia*: sternite VIII evenly pigmented; hypogynial valves triangular, inner margins slightly sinuous and diverged, markedly strengthened edges (Fig. 191); genital fork with narrowed



Figs. 168. *Ectemnoides princeae* pupal abdomen showing armature. Scale bar = 0.5 mm.



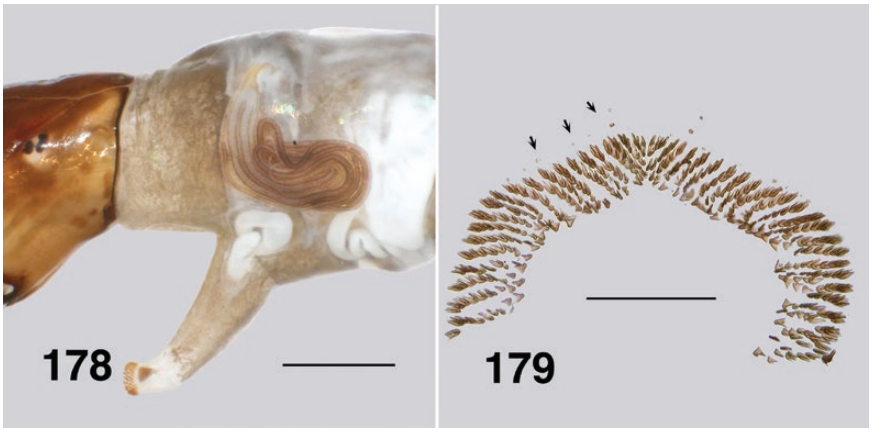
Figs. 169–171. *Ectemnoides princeae* last instar larva. (169) Habitus. Scale bar = 1.0 mm. (170) Dorsal view of the head. Scale bar = 0.5 mm. (171) Ventral view of the head. Scale bar = 0.5 mm.

straight anterior arm, knee-bend on lateral arm well expressed, lateral apodeme as elongated ridge, posterolateral expansions rounded laterally, angular medially (Fig. 192); cerci as for *Ect. princeae* (e.g., Fig. 152); spermatheca ovoid, dark brown, externally smooth, internal acanthae (length ca. 4.6–9.0 µm, width ca. 0.11 µm), region surrounding junction with spermathecal duct not markedly enlarged or sculpted (Fig. 193).

Adult male (based on single pharate and five reared specimens). *Body* (Fig. 194): overall color black; total length 3.5 mm. *Head* (Fig. 195): width 1.0 mm; depth 0.8 mm. *Eyes*: upper ommatidia dark reddish, diameter 0.04 mm, ca. 22 across and down; lower small ommatidia darker, diameter 0.016 mm, ca. 28 across and down. *Clypeus*: black; width 0.22 mm; vestiture of sparse fine black hairs. *Antenna* (Fig. 196): total length 0.75 mm; finely expressed, overall black, pedicel small, scape twice as long and rounded distally, flagellomere I slightly narrower and longer than scape, remaining flagellomeres tapered smoothly to slightly extended apical flagellomere IX. *Mouthparts*: more insubstantial than typical; length 0.2× head depth; maxillary palp (Fig. 197) length 0.61 mm, palpomeres I & II small, palpomere IV slightly expanded distally; palpomere V slightly elongated, proportional lengths of palpomeres III–V 1.0:0.9:1.7; sensory vesicle small, irregular spherical shape, occupying 0.25× palpomere III length, opening 0.3× vesicle width. *Thorax*: length 1.3 mm; width 0.9 mm; postpronotal lobe, anteprontal lobe and proepisternum vestiture of sparse fine pale hairs, fore

Figs. 172–177. *Ectemnoides princeae* larva. (172) Antenna. Scale bar = 0.1 mm. (173) Mandible. Scale bar = 0.1 mm. (174) Mandible apex. Scale bar = 0.05 mm. (175) Maxilla. Scale bar = 0.1 mm. (176) Postgenal cleft. Scale bar = 0.2 mm. (177) Hypostoma. Scale bar = 0.05 mm.

coxa densely so; scutum evenly velvety black, vestiture of dense fine pale hairs, long in scutellar depression; dense and longer on postpronotal lobe; scutellum concolorous with scutum, bare medially, with dense long black hairs laterally; postnotum concolorous with scutum, bare; pleurae dark brown, anepisternal membrane without hairs. *Wing* (Figs. 198 and 199): hyaline, length 2.7 mm, width 1.5 mm, veins slightly yellowish; basal cell small but distinct; a:b ratio 1.0:2.9; costa lacking spiniform hairs; Rs not branched. M_1 doubled, CuA markedly sinuous. *Haltere*: stem pale with black base, knob tan. *Legs*: evenly dark brown, not markedly hirsute, front femur with long fine hairs; hind leg with tibia slightly expanded; hind basitarsus with ventral row of stout spines, calcipala and pedisulcus as for female, tarsomere II noticeably elongated, ratio of apical width to length 1.0:3.5; tarsal claw grappling pad of ca. 25 teeth. *Abdomen* (Fig. 200): overall black, basal scale hairs black, markedly extended to posterior of segment III, tergites blackish brown, 2.5× as wide as long, tergites II–IV with long hairs laterally, remainder with more evenly arrayed vestiture; sternites present, distinct. *Genitalia* (Fig. 201): heavily pigmented; gonocoxa subequal in basal width and length, vestiture of sparse long and short hairs; gonostylus approximately 2.5× longer than basal width, flattened in lateral view, strengthened along medial edge, vestiture of short hairs, two apical spines (Fig. 202); ventral plate complex, 1.7× wider than length, no median keel as such, posteromedial edge undulated, broadly rounded laterally, broadly concave anteromedially; vestiture of even fine hairs; basal arms massive and well sclerotized apically,

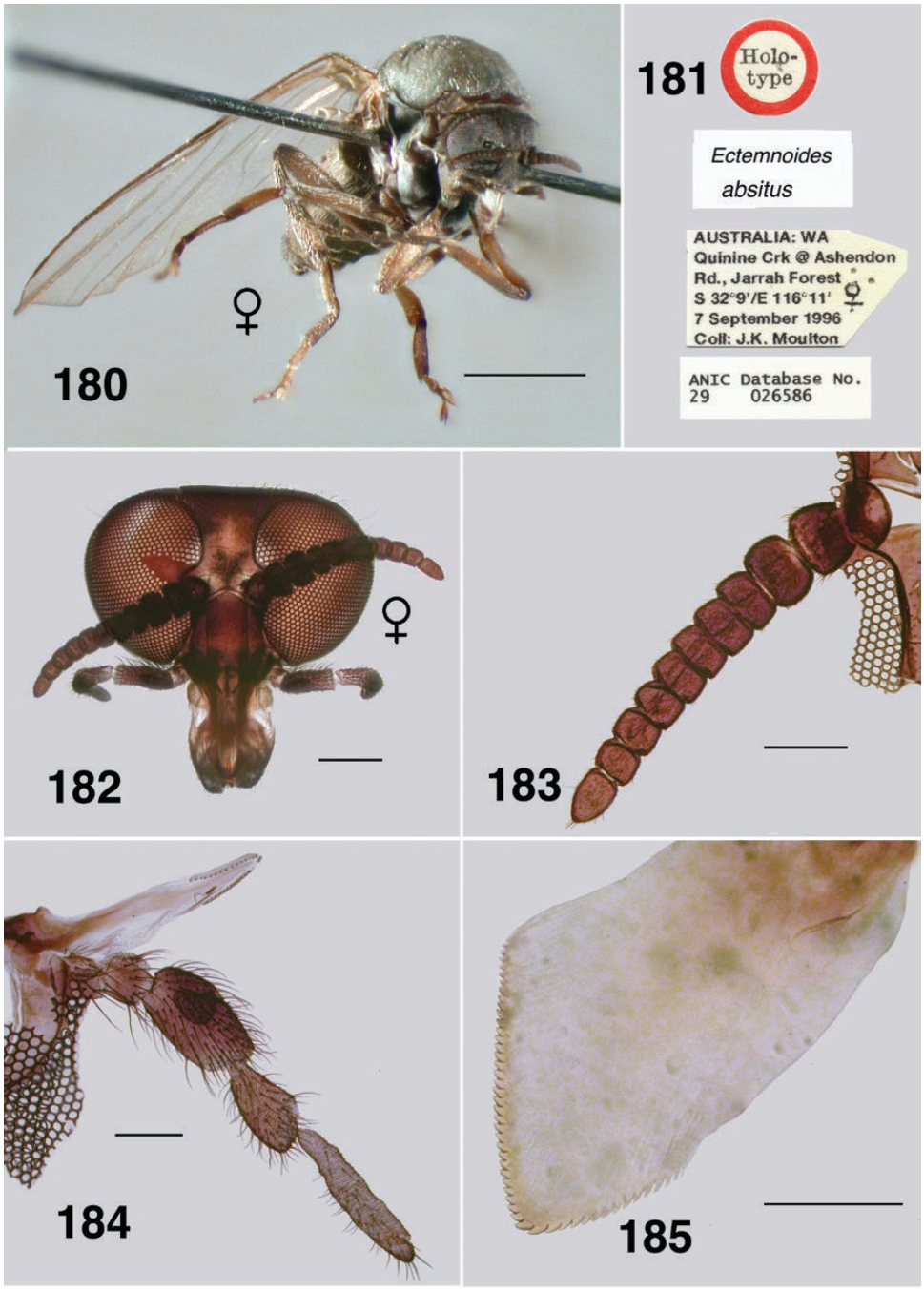


Figs. 178–179. *Ectemnoides princeae* larva. (178) Pharate pupal gill. Scale bar = 0.5 mm. (179) Circlet of hooks. Note absence of anal sclerite. Arrows indicate campaniform sensilla. Scale bar = 0.2 mm.

paramere connectors markedly thin and curved (Fig. 203); median sclerite well developed, substantial insertion anteromedially on ventral plate, distinct distal bifurcation with reflexed apices; parameres well developed, with distinct articulations to connectors, anteromedial edge marked, body of paramere thin with slightly crenulated posterolaterally; parameral spines absent; adeagal membrane with microtrichia. Cerci well developed, pigmented and hirsute.

Pupa (based on six specimens). *Body*: length; male 3.6–4.4 mm, female 3.4–3.9 mm, cuticle clear yellowish brown (Fig. 204). *Head*: frontal plate of female angulate, frons width to vertex width ratio 1.0:1.7 (Fig. 207), male ovoid; ratio of 1.0:2.3 (Fig. 208); male cuticle covered with barely visible minute tubercles and fine corrugations; muscle scars positive and distinct; female cuticle with dense, clear, low tubercles, and corrugations; frontal setae absent, facial setae present, curled apically. *Thorax*: anterior dorsal shield densely covered with small clear tubercles and crinkled cuticle, dorsocentral setae, fine, not markedly extended (Fig. 205). *Gill* (Fig. 206): not markedly longer than pupa, length 2.0–2.5 mm; three trunks arising directly from base, middle one massive; ventral trunk slightly longer, 13–15 terminal filaments, dorsal branch often with shorter filament, various even on same specimen; surface pseudoannulated on all filaments, finely annulated apically. *Abdomen* (Fig. 209): overall cuticle covered with minute clear tubercles and corrugations; armature poorly developed; two terminal spines on tergite IX short, sharply tapered, curved anteriorly, grapnel hooks present; spine combs present, but poorly expressed; pleurites essentially absent, present only as markedly small plates, posterior pleural cuticle extensively concertinaed. *Cocoon* (Fig. 204): silk fibers fine; coarse irregular weave, close-fitting shapeless bag covering the posterior of the abdomen, occasionally reaching to thorax, anterior edge absent; often extended laterally onto substrate, fine extraneous material from substrate sparingly incorporated.

Larva (based on 13 last instar larvae). *Body* (Fig. 210): total length 7.3–8.0 mm, evenly granular gray. *Head* (Figs. 211 and 212): evenly light to moderate brown; anterior apotome slightly paler, posterolateral regions and upper genae slightly darker; length 1.0–1.2 mm, width 0.83–0.86 mm; distance between antennal bases 0.59–0.64 mm; margins of head subparallel; head spot pattern positive; ecdysial lines not markedly distinct, slightly divergent until near posterior of head, then broadly curved medially; cervical sclerites finely connected to postocciput; cephalic setae fine, slightly elongated with clear sockets; suboesophageal ganglion not markedly pigmented; two distinct pigment spots anterolaterally to posterior tentorial pits. *Antenna* (Fig. 213): various, from subequal in length to labral fan stem, or extended beyond apex; total length ca. 0.50 mm; basal antennomere clear at junction with head and narrowly on one side, basal and medial antennomeres dark brown laterally, apical antennomere completely blackish brown; basal and medial antennomeres subequal in length, apical antennomere slightly longer; proportional lengths 1.0:1.0:1.3. *Labral fan*: not markedly expressed; stalk light brown, ca. 58 rays, all rays more or less equally developed, length 1.4 mm, mid-ray width 0.016 mm; microtrichia shorter than ray width, but with a pattern of longer microtrichia, length 0.012 mm, interspersed with 8 to 9 smaller. *Mandible* (Figs. 214–216): not markedly pigmented, shortened; brushes not markedly developed; outer teeth short, broad, poorly developed; apical tooth substantial, but not elongated; subapical teeth markedly small, differing between Hotham and Quinine populations; ca. eight spinous teeth small, saw-toothed in expression; sensillum and serrations complex, on raised base (marked in Hotham population); blade region short, smooth, convex. *Maxilla* (Fig. 217): lobe cone-shaped, rounded; palp elongated, subequal in length to lobe, 3.0× as long as basal width, well separated from lobe (Hotham), in Quinine population palp shorter than lobe, 2.7× as long as wide, slightly curved, not markedly separated from lobe; tuft of hair at base of palp not markedly developed. *Postgenal cleft* (Fig. 218): U-shaped but minute, well sclerotized with markedly irregular edges; posterior tentorial pits small and distinct; postgenal bridge evenly pale and concolorous with genae; ratio of hypostoma, postgenal bridge and postgenal cleft 1.0:1.6:0.4; suboesophageal ganglion pigmented, but not markedly obvious (Fig. 212). *Hypostoma*: darkly pigmented apically; teeth variable between Hotham and Quinine populations, for the latter (Fig. 219), tooth 0 slightly protrusive, teeth 1–3 markedly small, tooth 4 distinct with teeth 5, 6 distinct, 7 minute, hypostoma plus seta forming substantial lateral cone-shaped structure; for the Hotham population (Fig. 220), teeth 0–3 small and largely hidden by ventral edge of hypostoma, teeth 4–6 subequal in size with tooth 7 minute, lateral hypostomal structure lightly serrated; hypostoma edge angled smoothly posterolaterally, edge slightly irregular; single main hypostomal setae situated well anteriorly on hypostoma; three or four other small setae variously arrayed more basally. *Thorax*: prothorax gray, remainder of thorax lighter; slightly wider than head; the mature pharate pupal gill (Fig. 221) with up to six filaments showing basally, directed slightly posteroventrally then broadly posteriorly to recurve dorsally and curl centrally. *Prothoracic proleg*: anterolateral plates small and bluntly V-shaped. *Abdomen*: evenly granular grayish, narrower than



Figs. 180–185. *Ectemnoides absitus* female. (180.) Holotype. Habitus. Scale bar = 1.0 mm. (181) Holotype labels. (182) Frontal view of head. Cleared. Scale bar = 0.1 mm. (183) Antenna. Scale bar = 0.1 mm. (184) Maxillary palp, lacinia. Scale bar = 0.1 mm. (185) Mandible apex. Scale bar = 0.05 mm.

thorax, expanded evenly at sixth segment; cuticle lacking sculpture. *Ventral tubercles*: absent. *Anal sclerite* (Fig. 222): absent, campaniform sensilla array typical. *Posterior circlet*: noticeably small and circular, directed posteriorly, ca. 48 rows of hooks, seven or eight per row (total ca. 360).

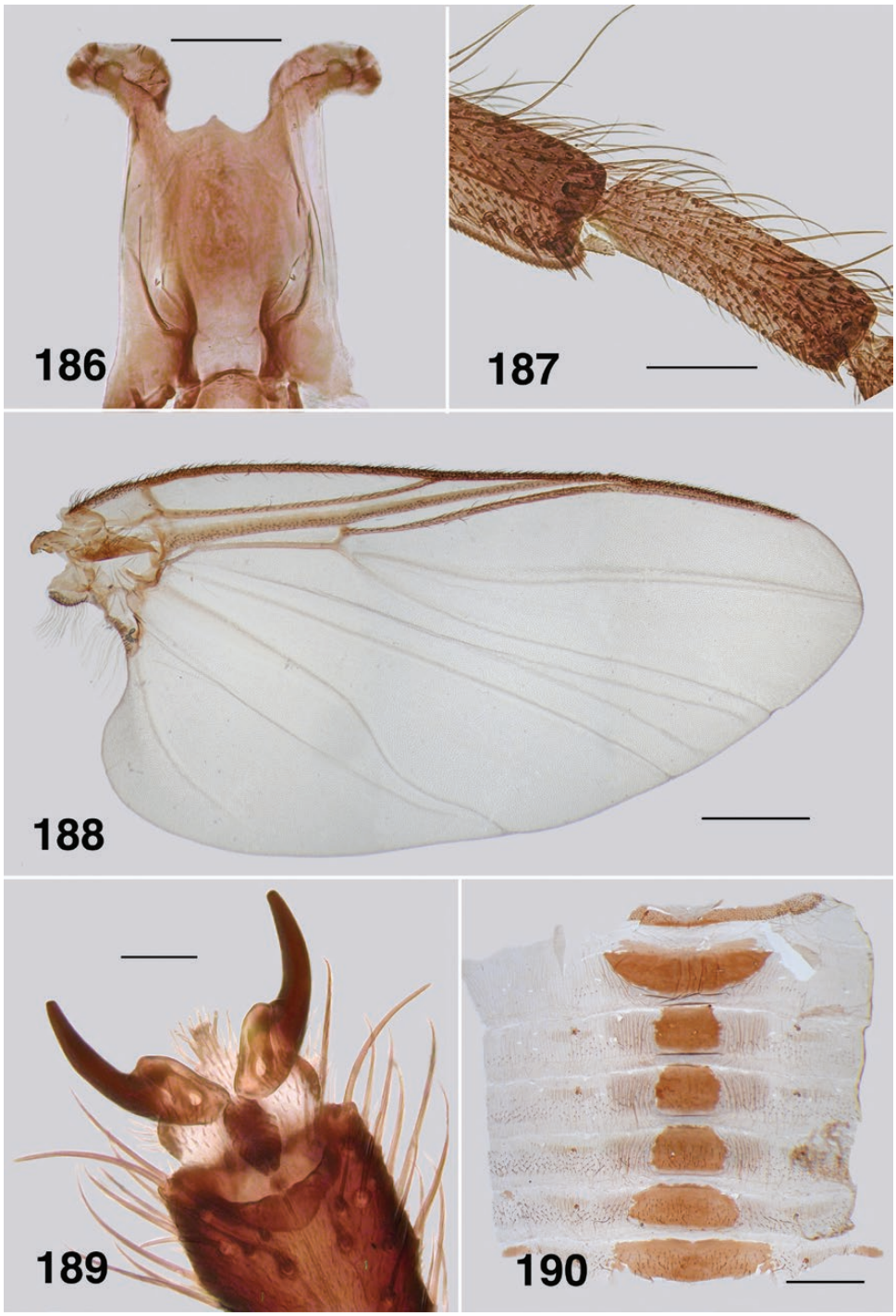
Type Material

Holotype

Pinned material; reared female (Fig. 180). Label (Fig. 181) (Holo-/type [red]) (*Ectemnoides*/ *absitus*) (AUSTRALIA: WA/ Quinine Creek @ Ashedon/ Rd. Jarrah Forest/ S 32° 9′/E E 116° 11′/ 7 September 1996/ Coll: J.K.M./ [F]) (ANIC Database No./ 29 026586). Subsidiary material of pupal exuviae plus cocoon, in microvial on the pin.

Paratypes

Pinned material; three reared females with associated pupal exuviae in microvial, labeled as for holotype: (Para-/type [yellow]). (ANIC Database No./ 29 026587) to (ANIC Database No./ 29 026589). Four reared males, as for holotype, with male symbol: (ANIC Database No./ 29 026590) to (ANIC Database No./ 29 026593). *Alcohol material*: seven last instar larvae, five pupae, one exuviae and cocoon, label as for holotype: (ANIC Database No./ 29 026605). *Slide material*: one slide each of male and female adult, label as for holotype, but with (ANIC Database



Figs. 186–190. *Ectemnoides absitus* female. (186) Cibarium. Scale bar = 0.1 mm. (187) Hind basitarsus and tarsomere II. Scale bar = 0.1 mm. (188) Wing. Scale bar = 0.5 mm. (189) Tarsal claws. Scale bar = 0.02 mm. (190) Abdominal tergites. Scale bar = 0.5 mm.

No./ 29 026619) and (ANIC Database No./ 29 026620). Two of pupal exuviae, label as for holotype (ANIC Database No./ 29 026621) and (ANIC Database No./ 29 026622). One last instar larva from Quinine Creek, as for holotype (ANIC Database No./ 29 026635).

Additional Material

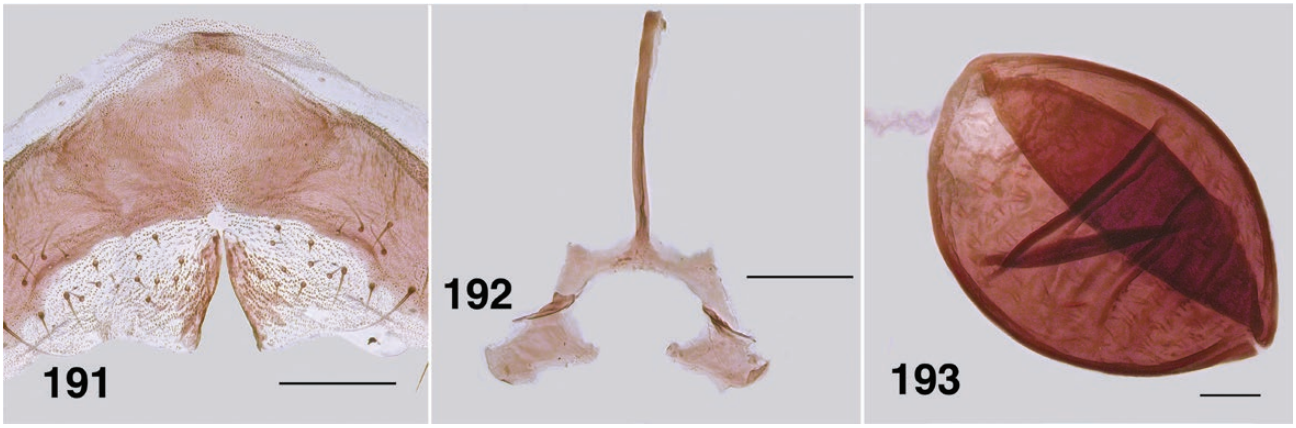
Alcohol; four last instar larvae, label as (WA. Hotham Trib./ *Cnephia* Z from/ Carnoys [too mature]/ 10-iv-1996/ J.K.M.) (Paratype) (ANIC Database No./ 29 026617). (S32.8708° E116.4524°). *Slide material*: one last instar larva from Hotham River Trib., label with (ANIC Database No./ 29 026623).

Etymology

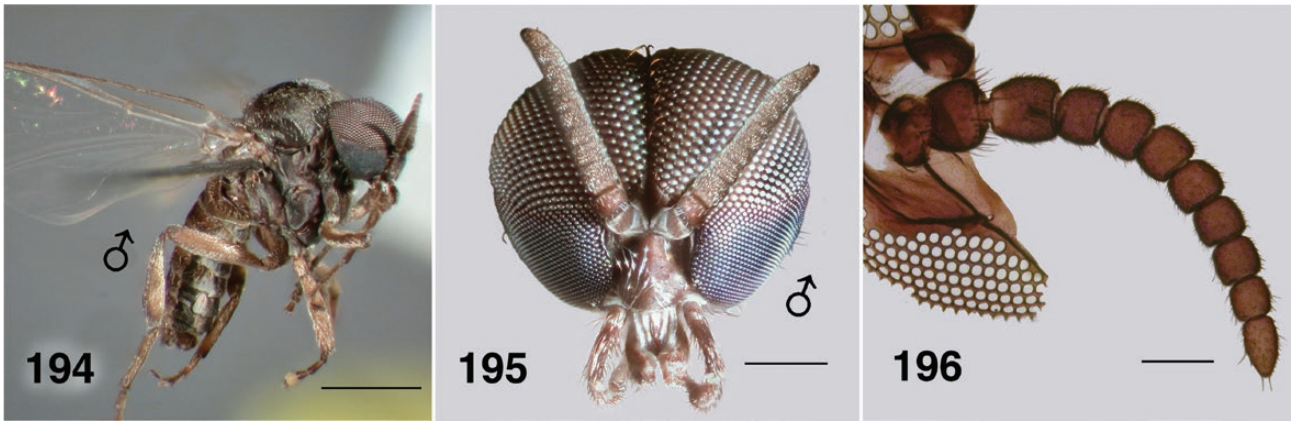
In reference to absence of spine-like setae on the larval cranium, plus absence of the anal sclerite.

Distribution (Fig. 229)

Western Australia: Quinine Creek, Ashedon Rd, Jarrah Forest, S32.14255° E116.19196°, elev. 250 m., larvae, pupae, 14-IX-1996,



Figs. 191–193. *Ectemnoides absitus* female. (191) Hypogynial valves. Scale bar = 0.1 mm. (192) Genital fork. Scale bar = 0.1 mm. (193) Spermatheca. Scale bar = 0.02 mm.



Figs. 194–196. *Ectemnoides absitus* male. (194) Habitus, paratype. Pinned. Scale bar = 0.02 mm. (195) Head, frontal view. In ethanol. Scale bar = 0.25 mm. (196) Antenna. Scale bar = 0.1 mm.

J.K.M.; Hotham River tributary, S32.8708° E116.4524°, elev. 200 m., larvae, 10-IV-1996, J.K.M.

Bionomics

Immatures are found in small streams with intermittent riffle areas where they use trailing grasses, sticks, and fallen leaves as substrate. Pupation occurs on that substrate and the cocoon is well developed. Associated with *Ect. absitus* were the following simuliids: *Austrosimulium* sp., *B. gladiator*, *Ect. acanthocranius*, *Ect. faecofilus*, *Ect. princeae*, *Ect.* sp. A, *N. occidentalis* and an undescribed *Paracnephia* sp.

Remarks

Differences in expression of the larval mandible (Figs. 215 and 216) and hypostoma (Figs. 219 and 220), between populations from Quinine Creek and the Hotham tributary indicate the latter is distinct. Without more material, however, we decline to erect a new species.

Ectemnoides sp. A (Figs. 223–226)

Not given full species rank because of lack of material. Based on a single partial exuviae of female pupa and attached larval cuticle, including hindgut intima.

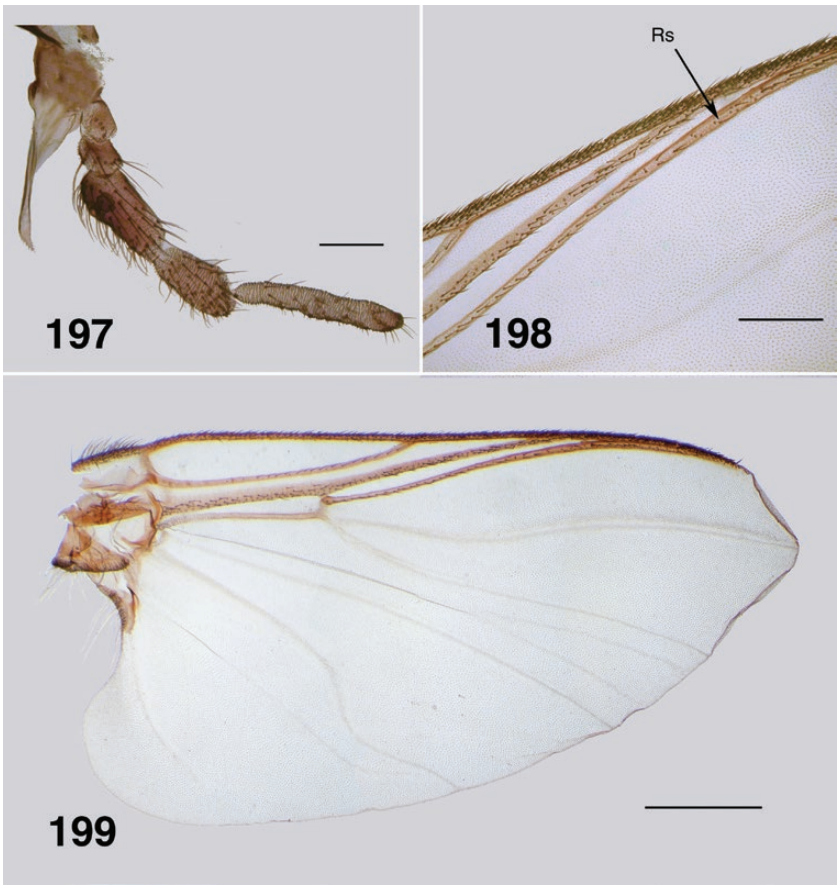
Pupa (female partial exuviae): frontal plate with tubercles absent, but slightly roughened, frontal setae long with markedly curled tips, facial setae absent, plate broad and angulate, basal width-to-length ratio 1.0:1.4, maximum width-to-basal width 1.0:1.3. (Fig. 223), thoracic cuticle roughened (Fig. 225), gill (Fig. 224) with short base, branching into three trunks, one thinner than others, total of 15 filaments (six each on the two thicker branches, three on the thinner), maximum length 3.6 mm, filament surface pseudoannulated. *Larva* (based on single partial exuviae attached to pupal exuviae). *Abdomen*: cuticle apparently smooth. *Anal sclerite*: absent; campaniform sensilla typical in number, but evenly arrayed around circlet (Fig. 226). *Posterior circlet*: markedly small, ca. 37 rows with six hooks each (Total ca. 220).

Material Examined

Single partial exuviae. Microscope slide. Label data: (*Ectemnoides* sp. A) (AUSTRALIA: WA/ Quinine Creek @/ Ashedon Road. Jarrah/ Forest/ S32.14255° E116.19196°/ elev. 250 m. 14 September 1996/ Coll: J.K.M./ Trichomycetes/ Euparal DAC. 2016) (ANIC Database No./ 29 026618).

Distribution (Fig. 229)

Western Australia: A single locality; Quinine Creek.



Figs. 197–199. *Ectemnoides absitus* male. (197) Maxillary palp. Scale bar = 0.1 mm. (198) Wing veins. Rs – radial sector vein. Scale bar = 0.2 mm. (199) Wing. Scale bar = 0.5 mm.

Bionomics

Of all larvae examined in total for this study, only this specimen (larval hindgut still attached to pupal exuviae) was noted to contain fungal trichospores. There appear to be two forms—a longer one (Fig. 227) that is perhaps *Furculomyces westraliensis* (Harpalles, Trichomycetes), described for chironomid larvae from Western Australia (Lichtwardt and Williams 1992). The broader shorter ovoid one (Fig. 228) is perhaps *Zancudomyces culisetae* (previously known as *Smittium*; Wang et al. 2013). Numbers of trichomycetes from eastern Australian *Austrosimulium* have been described by Lichtwardt and Williams (1990) and such are also known for New Zealand species (Williams and Lichtwardt 1990). Moulton et al. (2004) reported presence of the trichomycete *Harpella* Léger & Duboscq, plus an unidentified form, in larvae of the Western Australia simuliid *B. gladiator*.

Remarks

This specimen, not given full species designation, was part of a larger collection of material, mainly of *Ect. absitus* and *Ect. acanthocranius* from Quinine Creek. The pupal gill is intermediate in form between those two species. The characters that allow association to *Ectemnoides* are the angulate frontal plate of the female pupa, general gill structure, lack of anal sclerite in the larva, plus the remarkably small circlet of hooks.

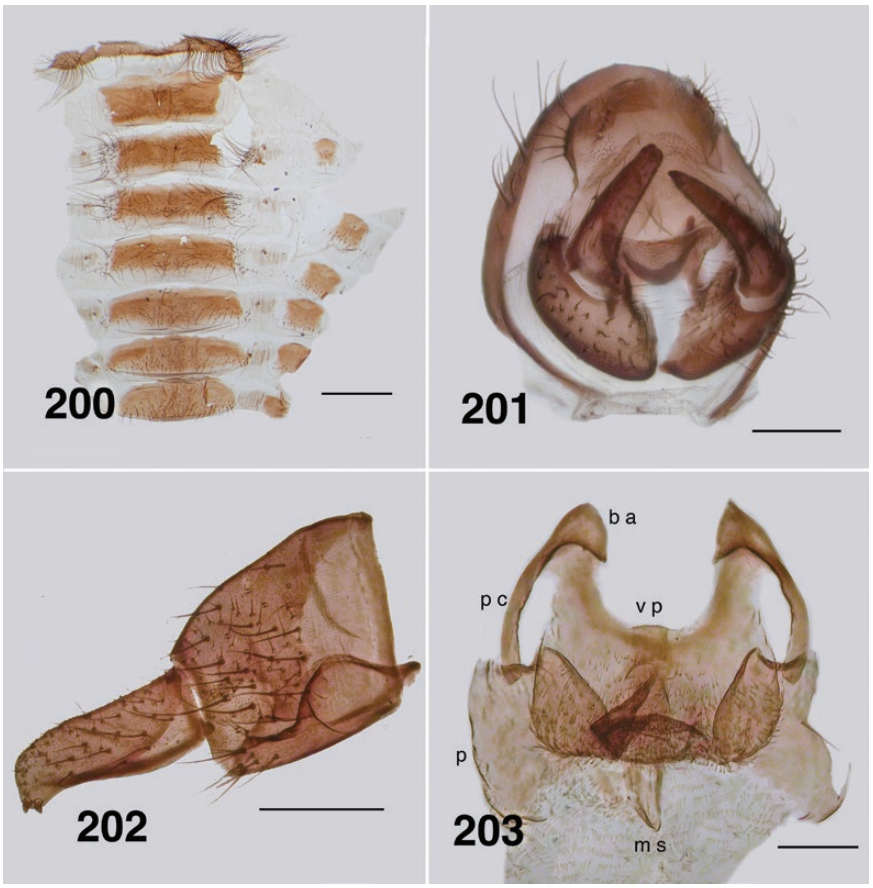
Discussion

We have refrained from establishing species segregates within *Ectemnoides*. Molecular evidence (J.K.M., unpublished) indicates that *Ect. umbratorum* + *Ect. faecofilus* is sister to *Ect. acanthocranius* + (*Ect. princeae* + *Ect. absitus*) and certain morphological character combinations do not disagree. Others do, however, indicating that *Ect. acanthocranius* is sister to *Ect. umbratorum* + *Ect. faecofilus*. Indeed it is probable, given our experience with the ephemeral nature of suitable *Ectemnoides* localities in Western Australia, where the time window for collection of material is short and easily missed, that there are yet-to-be-discovered species intermediate within *Ectemnoides* that might clarify this conundrum. The pupal gill of the single partial specimen of *Ectemnoides* sp. A, is a good example of this.

Following is a brief inter-generic comparison of morphological characters we consider phylogenetically important.

Adults Wings of *Ect. umbratorum* (Figs. 8 and 9) and *Ect. faecofilus* (Figs. 50 and 51) have spiniform setae on the distal half of the costal vein, Rs is not branched and CuA not sinuous. *Ect. acanthocranius* (Figs. 85 and 86), *Ect. princeae* (Fig. 145) and *Ect. absitus* (Fig. 188) are all similar with poorly-expressed to absent spiniform setae on the costa, with CuA markedly sinuous and in the female, Rs unbranched. One male of *Ect. princeae* (Fig. 158) showed rudimentary Rs branching.

Ect. umbratorum adults have a small, well-formed calcipala and wrinkled cuticle at the pedisulcus position (Fig. 11), *Ect. faecofilus* has a smaller calcipala and little sign of a pedisulcus (Fig. 53) and *Ect. acanthocranius* has virtually no calcipala and no evidence of a pedisulcus (Fig. 87). *Ect. princeae* shows little evidence of a calcipala (Fig. 146), similar to *Ect. absitus* (Fig. 187). For the last three species with the reduced calcipala, there is an aggregation



Figs. 200–203. *Ectemnoides absitus* male. (200) Abdominal tergites. Scale bar = 0.5 mm. (201) Posterior view of genitalia. Scale bar = 0.1 mm. (202) Gonocoxa and stylus. Scale bar = 0.1 mm. (203) Genitalia—slide mount. b a – basal arm; m s – median sclerite; p c – paramere connector; p – paramere; v p – ventral plate. Scale bar = 0.05 mm.

of spines (continuation of the ventral row of stout spines along the basitarsus) on the calcipala; similar to that known for *N. fergusoni*, previously the only known Australian simuliid to exhibit such a condition (see Tonnoir 1925: 221, his Fig. 2, F, G. H; Craig et al. 2018b). The two species of *Ectemnoides* that possess a calcipala, albeit small, lack the spine aggregation—indicating perhaps that, whatever is the function of the calcipala, when too small, it is assumed by the spines?

The claws of *Ect. umbratorum* female have a small but distinct tooth and minor heel (Fig. 12), that for *Ect. faecofilus* is unknown, whereas *Ect. acanthocranius* claw has a barely evident tooth with a heel similar to *Ect. umbratorum* (Fig. 88). The basal tooth in *Ect. princeae* is various; absent at times (Fig. 147) and *Ect. absitus* has no sign of the tooth and a very smooth heel (Fig. 189).

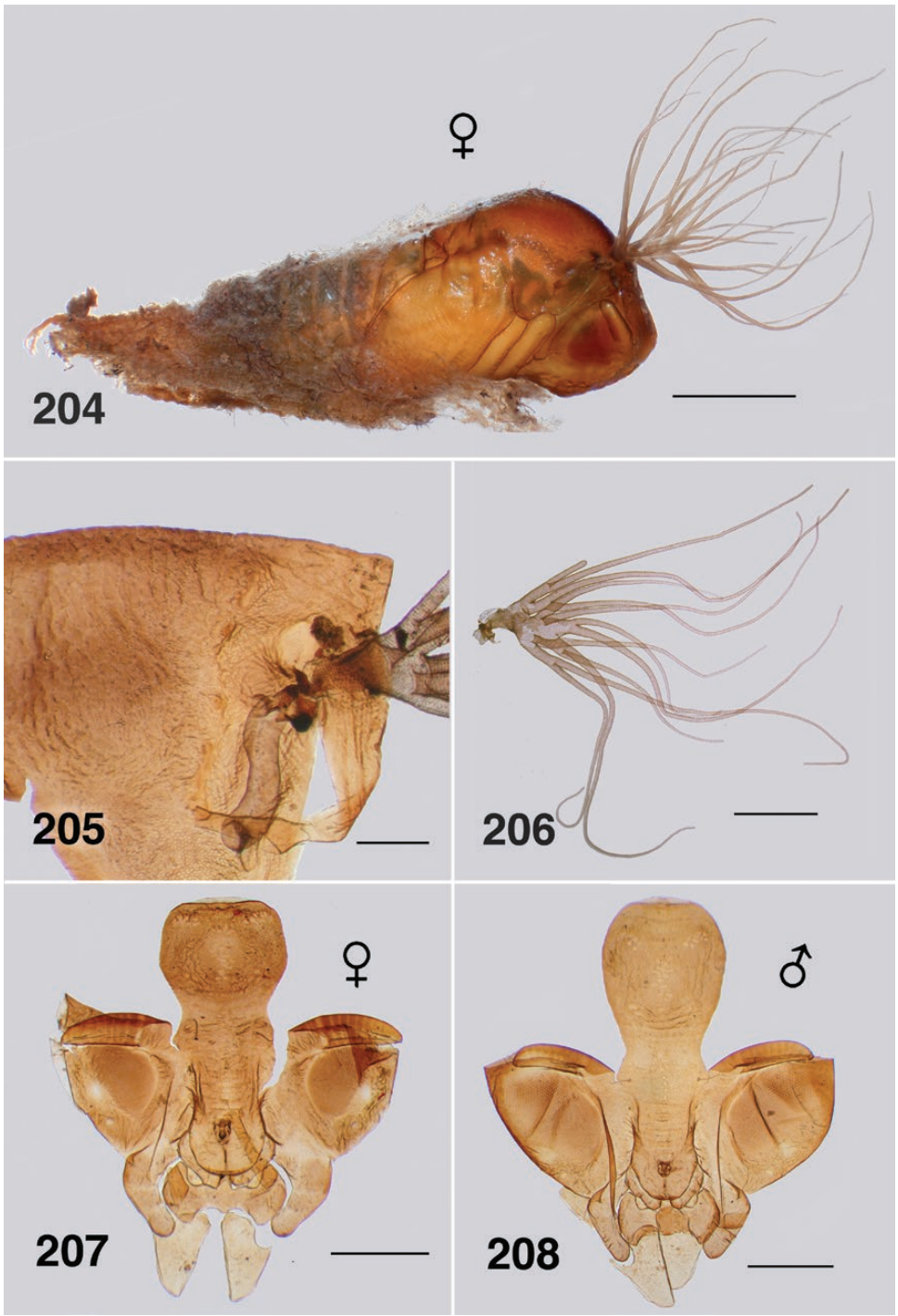
Details of male genitalia of *Ect. umbratorum* are not fully known, but may lack paramere connectors, parameres, and spines (Fig. 21). For *Ect. faecofilus*, while present, these structures are poorly expressed (Fig. 55), but for *Ect. acanthocranius* (Fig. 102), *Ect. princeae* (Fig. 161), and *Ect. absitus* (Fig. 203) these are markedly expressed and together with those of *B. gladiator*, unique within Australian Simuliidae. Such distinct paramere connectors are similar to those seen in some *Prosimulium*, *Greniera*, *Stegopterna*, and *Tlalocomyia* (e.g., Adler et al. 2004). We are of the opinion that when fully known for *Ect. umbratorum* the connectors will be similar to those in *Ect. faecofilus*.

Pupa The pupal gills of *Ect. umbratorum*, *Ect. faecofilus*, *Ect. uvulatus*, and *Ect. acanthocranius*, have a basal fenestral diverticulum (e.g., Figs. 25 and 59) unique in Simuliidae. In *Ect. acanthocranius* the diverticulum is poorly expressed (Fig. 120) and often missing from the deployed pupal gill (Fig. 106). The diverticulum is absent from gills of *Ect. princeae* (Fig. 163), even though the gills are of similar expression to the previous four species; namely long thin trunks with fine filaments, albeit *Ect. princeae* has three trunks in comparison to the others with two. The gill of *Ect. absitus* lacks a fenestral diverticulum and the gill is of more typical expression (Fig. 206). The homology of that diverticulum is not entirely clear, but as we have suggested previously it is highly likely a poorly expressed third gill trunk.

Unique to *Ect. umbratorum* and *Ect. faecofilus* pupae are the double frontal setae on the ovoid frontal plate (Figs. 26, 27, and 60); in *Ect. acanthocranius* they are absent (Figs. 103 and 104) and the frontal plate angulate in the female. For pupae of *Ect. princeae* and *Ect. absitus*, the setae are also absent (Figs. 166, 167, 207, and 208) and again, the frontal plate angulate in the female.

Abdominal chaetotaxy and armature for all species are poorly expressed. The terminal spines (tergite IX) are small, albeit sharp (e.g., Figs. 29 and 62) and the IX sternal setae are not expressed as grapnel hooks; however, sometimes apically curved. All pupae have a spine comb on tergite IX, variously expressed.

Larvae Heads of *Ect. acanthocranius*, *Ect. faecofilus*, *Ect. umbratorum*, and *Ect. uvula* all have short substantial spine-like setae (e.g., Figs. 32 and 37). These are elongated and substantial 'secondary sensilla' (Craig 2005). All too, have the head of

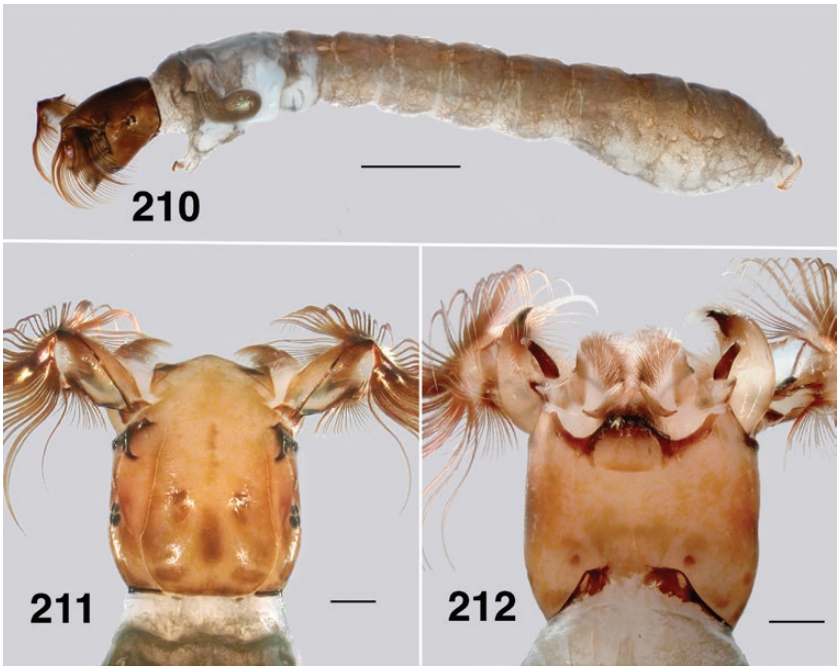


Figs. 204–208. *Ectemnoides absitus* pupa. (204) Habitus, female. Scale bar = 1.0 mm. (205) Thoracic cuticle. Scale bar = 0.2 mm. (206) Gill. Scale bar = 0.5 mm. (207) Female cephalic capsule. Scale bar = 0.5 mm. (208) Male cephalic capsule. Scale bar = 0.5 mm.

similar or larger diameter to the elongated body (Figs. 30, 63, and 109) and labral fans with long stems. The posterior circlet of hooks is markedly directed ventrally—character states unique in Australian Simuliidae. In *Ect. faecofilus* and *Ect. umbratorum* this physiognomy appears to associated with the habit of attaching to the end of a thread (e.g., Fig. 44). This behavior is not yet known for *Ect. acanthocranius* or *Ect. uvulatus*. Other larvae are various; those of *Ect. princeae*, while possessing a ventrally directed circlet of hooks, has a more substantive body (Fig. 169); that for *Ect. absitus* is of more typical body shape for simuliids and has the circlet of hooks directed posteriorly (Fig. 210), that also is more typical.

All larvae have unusual spinous teeth on the mandibles. Rather than being more typically elongated and spine-like, they are saw-toothed in expression (Figs. 36, 70, 114, 174, 215, and 216), markedly so with multiple tips in *Ect. acanthocranius* (Fig. 114). The mandibular serrations and sensillum are unique in *Ect. acanthocranius, Ect. faecofilus*, *Ect. umbratorum*, and *Ect. uvulatus* larvae, being hair-like and proximal to a blade-like region (Figs. 36, 70, 114, and 131), rather than distal, typical in other simuliids. They are

Fig. 209. *Ectemnoides absitus* pupal abdomen showing armature. Scale bar = 0.5 mm.

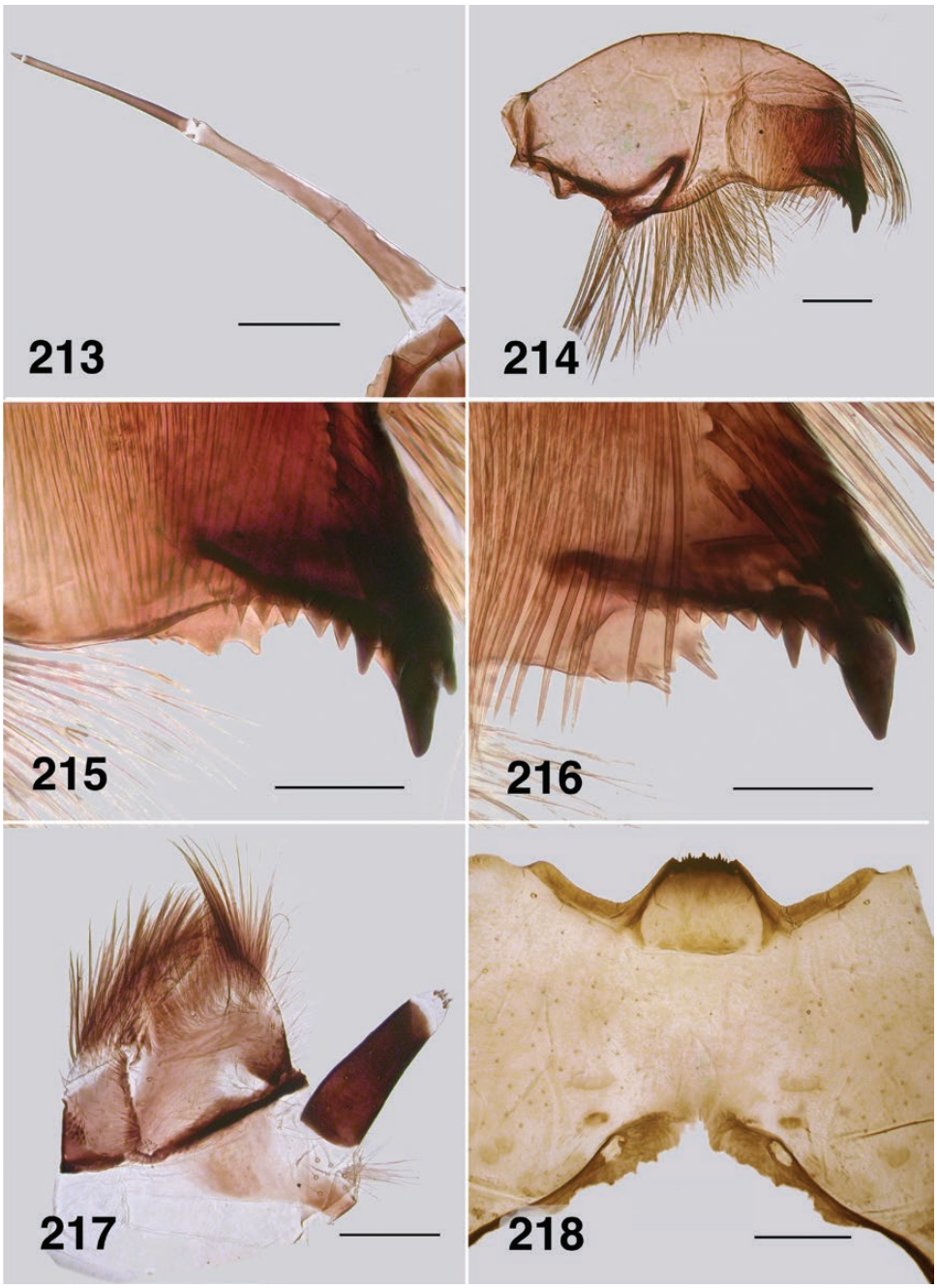


Figs. 210–212. *Ectemnoides absitus* last instar larva. (210) Habitus. Scale bar =1.0 mm. (211) Dorsal view of the head. (Hotham). Scale bar = 0.5 mm. (212) Ventral view of the head. (Hotham). Scale bar = 0.2 mm.

markedly elongated in *Ect. faecofilus* (Fig. 70). In larvae of *Ect. absitus* and *Ect. princeae* they are of more typical expression as cuticular projections, and substantial (Figs. 174, 215, and 216).

Although there is considerable variation in expression of hypostomal teeth in Simuliidae larvae (Adler et al. 2004), what we refer to here as tooth 4 (the lateral tooth) typically forms a protrusive structure laterally on the hypostoma, flanked laterally by teeth 5–7 or 8 (paralateral teeth). Exact function of hypostomal teeth is not fully known, but the apical mandibular teeth and those of the hypostoma are known to cut the salivary silk filament and are certainly co-adapted (Craig 1977, his Figs. 35 and 36). In *Ect. faecofilus*, *Ect. uvula*, and *Ect. umbratorum* larvae, the more typical arrangement for simuliid teeth can still be observed with tooth 4 plus the higher numbers being massively expressed and still forming the lateral 'edge' of the hypostomal teeth. (Figs. 38 and 73). On the other hand, in *Ect. acanthocranius* (Fig. 117), *Ect. princeae*, and *Ect. absitus* (Figs. 219 and 220) the position of the more lateral hypostomal teeth is supplanted by an extension of the hypostoma. That homology is clearly shown by the position of the first hypostomal seta—high on that lateral structure, with the original hypostomal teeth still expressed medially, but variously; in particular that of *Ect. acanthocranius* (Fig. 117), where the overall transformation is extreme.

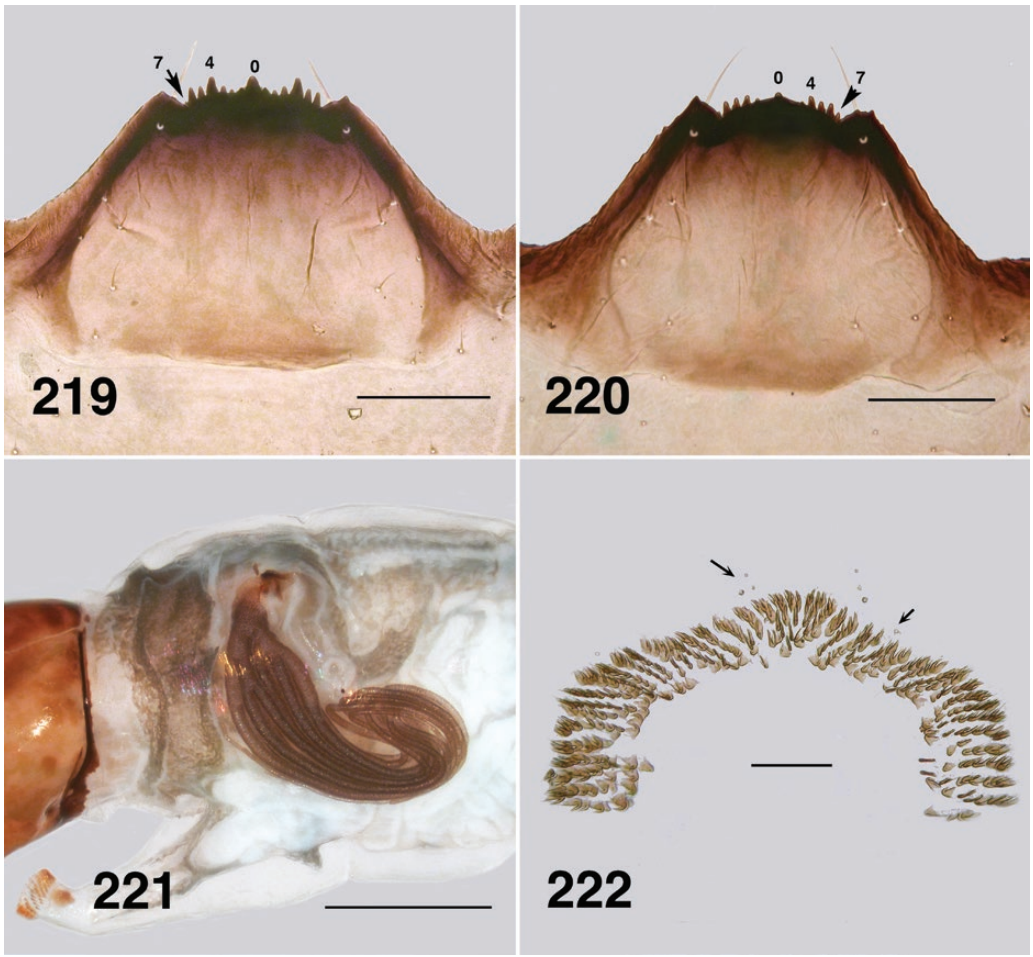
Both *Ect. acanthocranius* and *Ect. faecofilus* larvae have hexagonal patterning on the abdominal cuticle (Figs. 41 and 76), absent in the other *Ect.* species. *Ect. umbratorum*, *Ect. faecofilus* plus *Ect. uvulatus* have reduced anal sclerites, of inverted Y-shape, comprised only of a central portion and posteroventral arms (Figs. 42, 77, and 136), again, unique in Australian simuliids. Also unique is that *Ect. acanthocranius* totally lacks the anal sclerite (Fig. 121) as do larvae of *Ect. princeae*, *Ect. absitus*, and *Ect.* sp. (Figs. 179, 206, and 211). All *Ectemnoides* larvae have markedly low numbers of hooks in the circlet; that for *Ect. acanthocranius* with only ca. 200 is likely a record low number for Simuliidae larvae. The lowest number of hooks reported by Palmer and Craig (2000) was in the range of 600 for some species of *Prosimulium*, *Simulium*, and *Cnephia*; with the species reported usually found in slow to moderate velocity waters. Even *Twinnia nova*



Figs. 213–218. *Ectemnoides absitus* last instar larvae. (21) Antenna. Scale bar = 0.1 mm. (214) Mandible. Scale bar = 0.1 mm. (215) Mandible apex. (Quinine). Scale bar = 0.05 mm. (216) Mandible apex. (Hotham). Scale bar = 0.05 mm. (217) Maxilla. (Hotham). Scale bar = 0.1 mm. (218) Postgenal cleft. (Quinine). Scale bar = 0.2 mm.

with a small inverted Y-shaped anal sclerite has some 580 hooks and *B. gladiator* possess only ca. 440 hooks (Craig et al. 2018a).

Ectemnoides adults, with exceptions, match moderately well the diagnosis of *Paracnephia* by Crosskey (1969), a subgenus of *Prosimulium* at the time. In the recent key by de Moor (2017), *Ectemnoides* adults key out to *Paracnephia*; however, pupae and larvae do not. Wing veins and setae agree well, e.g., shape of CuA is variously sinuous in both *Paracnephia* and *Ectemnoides*. However, the mesepisternal sulcus in *Ectemnoides,* while of similar proportions to a typical Prosimuliini (Crosskey 1969, his Fig. 18), is more directed posteriorly as in Simuliini (Crosskey 1969, his Fig. 19); similarly, the katepisternal sulcus is similar to the latter tribe. The calcipala and tarsal claws of *Ectemnoides* are at certain variance with *Paracnephia*; calcipala are small to well developed in *Paracnephia*, small to essentially absent in *Ectemnoides*; the tooth on females claws is well expressed in *Paracnephia*, poorly developed, various and/or absent in *Ectemnoides*. The female hypogynial valve shape of both genera are markedly dissimilar (Crosskey 1969, his Fig. 34)—in *Procnephia* and *Paracnephia* the lobes are widely separated, divergent and broadly rounded, whereas for *Ectemnoides* they can be closely aligned, or not, but are not so shaped (e.g., Figs. 14 and 90). The male gonstyli of *Paracnephia* and *Ectemnoides* not only differ in shape, but in *Ectemnoides* there are only two terminal spines, with many in the former genus. Presence of parameral plates



Figs. 219–222. *Ectemnoides absitus* last instar larvae. (219) Hypostoma. (Quinine). Scale bar = 0.1 mm. (220) Hypostoma. (Hotham). Scale bar = 0.1 mm. (221) Pharate pupal gill. Scale bar = 0.5 mm. (222) Posterior circlet of hooks. Arrows indicate campaniform sensilla. Scale bar = 0.1 mm.

Figs. 223–225. *Ectemnoides* sp. A, pupa. (223) Frontal plate, female. Scale bar = 0.2 mm. (224) Pupal gill. Scale bar = 0.5 mm. (225) Thoracic cuticle. Scale bar = 0.2 mm.

is not mentioned by Crosskey (1969) and while possibly absent from *Ect. umbratorum*, they are variously expressed, even markedly so (e.g., Fig. 203), in other species of *Ectemnoides*.

Pupae of *Paracnephia* and *Ectemnoides* both lack pleurites; Crosskey (1969) illustrates two hooks only on sternites VI and VII of Ethiopian *Prosimulium* with a substantial hook and base in the pleural region. While *Ectemnoides* pupae are similar in hook number on those two tergites, there are only fine setae on the pleural region (Fig. 29). Grapnel hooks (= biramous anchor-like hooks) are not expressed as such in *Ectemnoides*. The small non-sinuous terminal spines of segment IX in *Ectemnoides* would fit the *Paracnephia brincki*-group (Crosskey 1969, his Fig. 44), but *Ectemnoides* pupae lack the spine comb on tergite V.

The pupal gills are markedly different. While *Ectemnoides* has similar number of terminal filaments, the branching is distinctly different from any *Paracnephia s.s.* species even where some possess long main trunks; plus there appears to be nothing like the fenestral

diverticulum unique to *Ectemnoides umbratorum*, *Ect. faecofilus*, *Ect. acanthocranius*, and *Ect. uvulatus* (e.g., Fig. 25) in *Paracnephia*. The gill branching pattern in *Ectemnoides* is reminiscent of some seen in *Prosimulium* and *Stegopterna* (Adler et al. 2004).

With the marked morphological variance between *Paracnephia* and *Ectemnoides* we have had no hesitation in assigning *P. umbratorum* and allied species to *Ectemnoides*.

While we named *Ectemnoides* because larvae of some species use a thread reminiscent of the stalk produced by *Ectemnia* larvae, there is much to indicate that the structures and associated behaviors are autapomorphic and the two genera not closely related. Formation of the stalk used by *Ectemnia* larvae is well studied (Wolfe and Peterson 1959, Stuart and Hunter 1998). Briefly, the larvae construct the stalk from salivary silk and may include extraneous material. The stalk is maintained and extended, with the larva attached near the apex. Pupation occurs on the stalk. Larval body form is adapted to this way of life; a concave hypostoma is probably used to manipulate the salivary silk, the abdomen has lateral flanges that produce a ventral groove, no doubt to allow close proximity to the stalk. Likewise, lacking the anal sclerite perhaps allows more flexibility of the anal circlet to contact the stalk.

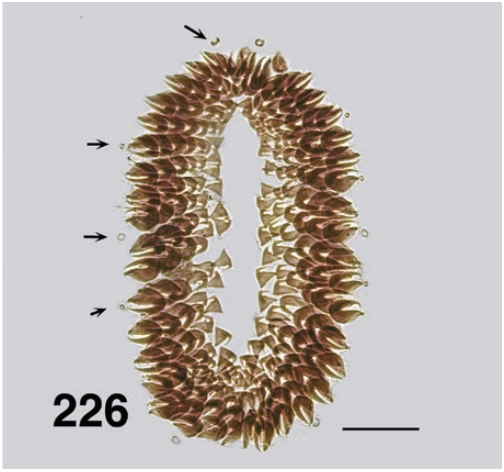
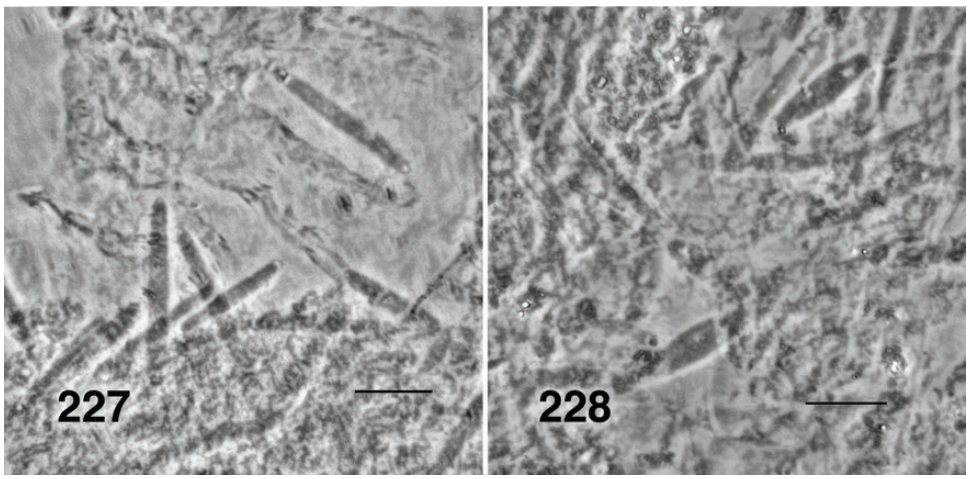


Fig. 226. *Ectemnoides* sp. A, last instar larva, circlet of hooks. Note absence of anal sclerite. Arrows indicate campaniform sensilla. Scale bar = 0.05 mm.

There are no observations on formation of the threads of *Ectemnoides* larvae. However, larvae attach directly to the end of the thread, are fully extended in the direction of flow and do not twist the body (Fig. 44). The thread contains fecal pellets, plus other material and is covered in salivary silk. The diameter of the threads shows distinct changes along the length, suggestive of a larval molt with concomitant increase in size of fecal pellets. Larvae detach to pupate, apparently in the substrate. All of these attributes are of marked difference to *Ectemnia* larvae. *Ectemnoides* larvae that produce a thread have a hypostoma that is overall concave, with the medial teeth depressed in relation to those lateral; the teeth; however, are well expressed, unlike those of *Ectemnia*.

Mackerras and Mackerras (1949) erected a *terebrans* group that consisted then of *C. umbratorum*, *C. terebrans*, *C.* sp. A., *C. fergusoni* and *C. fergusoni* var. They noted that *C. umbratorum* could well be assigned to the *aurantiacum* group and indeed that was done (Mackerras and Mackerras 1950). Female adults of the original *terebrans* group (Mackerras and Mackerras 1949) are superficially similar to those of *Ectemnoides*, namely in dark coloration, and similarly to *N. fergusoni* and *N. occidentalis* (Craig et al. 2018b). So, a question arises as to the taxonomic validity of the two remaining species of the original *terebrans* group *viz*. *P. terebrans* and *Paracnephia* sp. A. We are of the opinion that they do not belong in *Ectemnoides*. Examined in detail by D.A.C. (personal observation, 2014), both of those species, e.g., have distinctly different genital forks from species in *Ectemnoides* and the pedisulcus is markedly more accentuated. Indeed, unpublished molecular data (J.K.M.) indicates that *P. terebrans* (Tonnoir 1925) is related to *P. pilfreyi* (Davies and Györkös 1988) plus a now known sister species from Western Australia. Those latter two species, plus *P. terebrans* and *Paracnephia* sp. A, will be grouped together in a new genus presently under consideration by the current authors.

Given that many simuliid species have been shown to be complexes of cryptic species (e.g., Adler et al. 2004, plus many others) and that those in other Australian simuliid genera show morphological variation, as do *Ectemnoides* species, it is expected that some of the entities dealt with in this work will also be complexes. Indeed, this is one aspect of the Australian Gondwana simuliids that needs investigation; such, however, will require extensive collecting over considerable periods of time. To mitigate this issue, specimens examined from localities other than the type locality have not been included in the primary type series.



Figs. 227 and 228. *Ectemnoides* sp. A, larval hindgut trichomycetes. (227) *Furculomyces westraliensis*. Phase contrast. Scale bar = 0.01 mm. (228) *Zancudomyces culisetae*. Phase contrast. Scale bar = 0.01 mm.

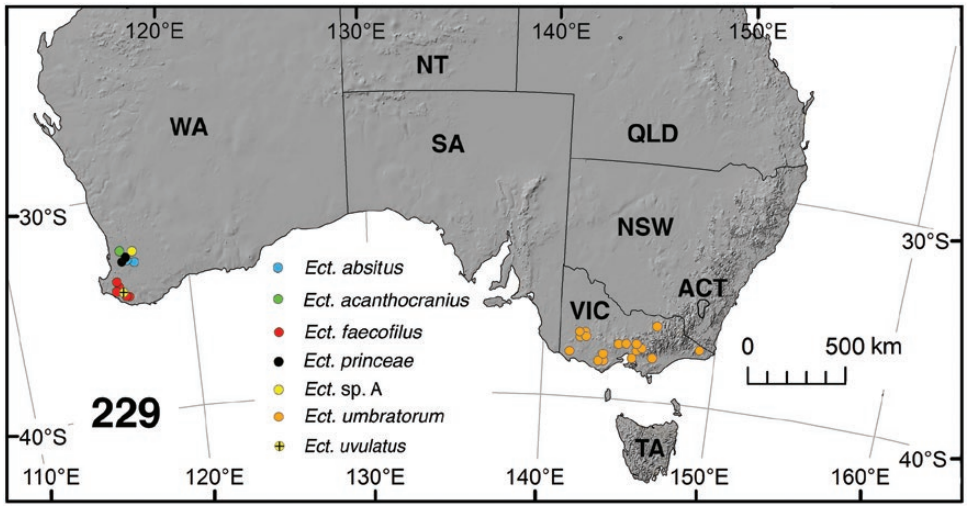


Fig. 229. Map of South Australia showing the distribution of *Ectemnoides* spp.

Historical biogeography has been discussed for *Paraustrosimulium* (Craig et al. 2017), *Bunyipellum* (Craig et al. 2018a), and *Nothogreniera* (Craig et al. 2018b)—Australian simuliid genera of Gondwana provenance and, in short, the same reasoning applies for distribution of *Ectemnoides* species. We again suggest here that the divergence event for, at minimum, eastern Australian *Ect. umbratorum* and the Western Australia *Ect. faecofilus*—two species with unique adaption to using threads as attachment sites for their larvae, was intrusion of the Eromanga Sea in the Cretaceous (*ca*. 110 million years ago [mya]) and eventual formation of the arid Nullarbor Plain; a vicariant event that split much of the southern continental biota into western or eastern Australia. It has, however, been noted (e.g., Toussaint et al. 2016 and others) that prior to the Late Miocene (7–5 mya) the region was mesic, so a vicariant event might have been more recent than Cretaceous.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

Acknowledgments

A great deal of thanks must go to Peter and Heide Zwick. They provided unique material of a male pupa of *Ect. umbratorum*, plus that of females. Heide graciously allowed use of her unpublished images based on that material—highly appreciated! Ros StClair kindly provided data on collections of *Ect. umbratorum* in the Environmental Protection Agency, Victoria and searched the samples for pupae. Charles 'Eddie' Beard was most helpful with the trichomycetes. Peter Adler suggested the term 'fenestral diverticulum' and Robert Hoare provided sage advice. Our collections were made under the aegis of the Victoria Department of Sustainability and Environment, Permit No: 10005893, File No: FF383203 and Department of Environment and Primary Industries, Permit 10007128, File No: FF383356. Western Australia material was collected under License Number SF009908, File No: 175368. Financial support for D.A.C. was from personal funds. J.K.M.'s 1996 expedition was funded by a NSF grant (9520613) awarded to J.K.M., a Flinn Foundation grant awarded to J.K.M., a NSF Research Training Group Grant in the Analysis of Biological Diversification (9113362) awarded to the University of Arizona, and a NSF grant (9420219) awarded to D.R. Maddison. J.K.M.'s 2014 expedition was funded by a NSF (MidgePEET) grant (0933218). Financial assistance for D.C.C. was provided, in part, through the Royal Ontario Museum's DMV Acquisition and Research Fund, plus an NSERC Discovery Grant.

References Cited

Adler, P. H., and R. W. Crosskey. 2008. World Blackfly (Diptera: Simuliidae): a fully revised edition of the taxonomic and geographic inventory. http://blackflies.info/sites/blackflies.info/files/u13/blackflyinventory_2008_Adler___Crosskey_1.pdf. Accessed 17 July, 2018.

Adler, P. H., and R. W. Crosskey. 2018. World Blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory [2018]. http://www.clemson.edu/cafls/biomia/pdfs/blackflyinventory.pdf. Accessed 17 July, 2018.

Adler, P. H., D. C. Currie, and D. M. Wood. 2004. The black flies of (Simuliidae) of North America. Royal Ontario Museum and Comstock University Press, Ithaca, NY.

Barr, W. B. 1984. Prolegs and attachment of *Simulium vittatum* (sibling IS-7) (Diptera: Simuliidae) larvae. Can. J. Zool. 62: 1355–1362.

Bugledich, E.-M. A. 1999. Simuliidae, pp. 325–337. *In* A. Wells and W. W. K. Houston (eds.), Zoological catalogue of Australia, vol. 30.1. CSIRO Publishing, Melbourne, Australia.

Chance, M. M., and D. A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64: 1295–1309.

Craig, D. A. 1974. The labrum and cephalic fans of larval Simuliidae (Diptera: Nematocera). Can. J. Zool. 52: 133–159.

Craig, D. A. 1977. Mouthparts and feeding behaviour of Tahitian larval Simuliidae (Diptera Nematocera). Quaest. Ent. 13: 195–218.

Craig, D. A. 2003. Geomorphology, development of running water habitats, and evolution of black flies on Polynesian islands. Bioscience. 53: 1079–1093.

Craig, D. A. 2005. A chaetotaxy for cephalic sensilla in larval Simuliidae (Diptera). Can. J. Zool. 83: 344–357.

Craig, D. A., D. C. Currie, F. F. Hunter, and M. Spironello. 2006. A taxonomic revision of the southwestern Pacific subgenus *Hebridosimulium* (Diptera: Simuliidae: *Simulium*). Zootaxa. 1380: 1–90.

Craig, D. A., R. E. G. Craig, and T. K. Crosby. 2012. Simuliidae. Fauna of New Zealand. 68: 1–336.

Craig, D. A., J. K. Moulton, and D. C. Currie. 2017. Taxonomic revision of *Paraustrosimulium* Wygodzinsky & Coscarón: reassignment of *Austrosimulium colboi* and description of *P. obcidens* n. sp. from Western Australia. Zootaxa. 4337: 451–492.

Craig, D. A., D. C. Currie, and J. K. Moulton. 2018a. Reassignment of Western Australia *Paracnephia gladiator* Moulton & Adler to a new genus, *Bunyipellum* (Diptera: Simuliidae). Zootaxa. 4375: 341–357.

Craig, D. A., D. C. Currie, and J. K. Moulton. 2018b. *Nothogreniera* new genus, for two species of Australian "*Paracnephia*" (Diptera: Simuliidae). Zootaxa. 4444: 351–380.

Crisp, M. D., H. P. Linder, and P. H. Weston. 1995. Cladistic biogeography of plants in Australia and New Guinea: congruent patterns reveals two endemic tropical tracks. Syst. Bio. 44: 457–473.

Crosskey, R. W. 1965. The identification of African Simuliidae (Diptera) living in phoresis with nymphal Ephemeroptera, with special reference to *Simulium berneri* Freeman. Proc. R. Ent. Soc. Lond. (A). 40: 118–124.

Crosskey, R. W. 1969. A re-classification of the Simuliidae (Diptera) of Africa and its islands. Bull. Brit. Mus. (Nat. Hist.), Ent. Suppl. 14: 1–195.

Crosskey, R. W. 1987. Part VIII. Black fly species of the world. 32 An annotated checklist of the world black flies (Diptera: Simuliidae), pp. 425–520. *In* K. C. Kim and R. W. Merritt (eds.), Black flies. Ecology, population management, and annotated world list. The Pennsylvania State University, University Park, PA.

Crosskey, R. W. 1989. Chapter 24. Simuliidae, pp. 221–225. *In* N. L. Evenhuis (ed.), Catalog of the Diptera of the Australasian and Oceanian Region. Bishop Museum Special Publication 86. Bishop Museum Press and E. J. Brill, Honolulu, Leiden.

Crosskey, R. W. 1990. The natural history of blackflies. John Wiley & Sons, Chichester, United Kingdom.

Crosskey, R. W., and T. M. Howard. 1997. A new taxonomic and geographical inventory of world Blackflies. Department of Entomology, The Natural History Museum, London, United Kingdom.

Crosskey, R. W., and T. M. Howard. 2004. A revised taxonomic and geographical inventory of world Blackflies. Department of Entomology, The Natural History Museum, London, United Kingdom.

Cumming, J. M., and D. M. Wood. 2017. Adult morphology and terminology. Chapter 3, pp. 89–133. *In* A. H. Kirk-Spriggs and B. J. Sinclair (eds.), Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. Suricata 4. South African Biodiversity Institute, Pretoria, South Africa.

Davies, D. M., and H. Györkös. 1988. Two new Australian species of Simuliidae (Diptera). J. Aus. Ent. Soc. 27: 105–115.

Ebach, M. C., Gill, A. C., Kwan, A., Ahyong, S. T., Murphy, D. J., and G. Cassis. 2013. Towards an Australian Bioregionalisation Atlas: a provisional area taxonomy of Australia's biogeographical regions. Zootaxa. 3619: 315–342.

Edwards, F. W. 1931. Simuliidae, pp. 121–154. *In* Diptera of Patagonia and South Chile. Part II. Fascicle 4. Nematocera. British Museum (Natural History), London, United Kingdom.

Eymann, M. 1988. Drag on single larvae of the Black Fly *Simulium vittatum* (Diptera: Simuliidae) in a thin, growing boundary layer. J. North Amer. Ben. Soc. 7: 109–116.

Hart, D. D., and C. M. Finelli. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Ann. Rev. Ecol. Syst. 30: 363–395.

Horne, P. A., and V. Pettigrove. 1989. A new record of *Cnephia umbratorum* (Tonnoir) (Diptera: Simuliidae) and *Apsectrotanypus pallipes* (Freeman) comb. n. (Diptera: Chironomidae) from the Otway Ranges, Victoria. Aust. Ent. Mag. 16: 21–26.

Lacoursière, J. O., and D. A. Craig. 1993. Fluid transmission and filtration efficiency of the labral fans of black fly larvae (Diptera: Simuliidae): hydrodynamic, morphological, and behavioural aspects. Can. J. Zool. 71: 148–162.

Lewis, D. J., R. H. L. Disney, and R. W. Crosskey. 1969. A new phoretic species of *Simulium* (Dipt., Simuliidae) from West Cameroon, with taxonomic notes on allied forms. Bull. Ent. Res. 59: 229–239.

Lichtwardt, R. W., and M. C. Williams. 1990. Trichomycete gut fungi in Australian aquatic insect larvae. Can. J. Bot. 68: 1057–1074.

Lichtwardt, R. W., and M. C. Williams. 1992. *Furculomyces*, a new homothallic genus of Harpallales (Trichomycetes) from Australian midge larvae. Can. J. Bot. 70: 1196–1198.

Mackerras, I. M., and M. J. Mackerras. 1949. Revisional notes on Australasian Simuliidae (Diptera). Proc. Linn. Soc. New South Wales. 73: 372–405.

Mackerras, M. J., and I. M. Mackerras. 1950. Notes on Australasian Simuliidae (Diptera). II. Proc. Linn. Soc. New South Wales. 75: 167–187.

Mackerras, I. M., and M. J. Mackerras. 1952. Notes on Australasian Simuliidae (Diptera). III. Proc. Linn. Soc. New South Wales. 77: 104–113.

Mackerras, M. J., and I. M. Mackerras. 1955. Notes on Australasian Simuliidae (Diptera). IV. Proc. Linn. Soc. New South Wales. 80: 105–112.

McIver, S. 1987. Sensilla of haematophagous insects sensitive to vertebrate host- associated stimuli. Int. J. Trop. Ins. Sci. 8: 627–635.

von Mering, S., and J. W. Kadereit. 2010. Phylogeny, systematics, and recircumscription of Juncaginaceae – A cosmopolitan wetland family, pp. 55–78. *In* O. Seberg, G. Petersen, A. S. Barfod, and J. I. Davis (eds.), Diversity, phylogeny, and evolution in the monocotyledons. Aarhus University Press, Aarhus, Denmark.

Merritt, R. W., D. A. Craig, R. S. Wotton, and E. D. Walker. 1996. Feeding behavior of aquatic insects: case studies on black fly and mosquito larvae. Invert. Biol. 115: 206–217.

de Moor, F. C. 2017. Chapter 32. Simuliidae (Blackflies), pp. 693–728. *In* A. H. Kirk-Sprigs and B. J. Sinclair (eds.), Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. Suricata 5. South African National Biodiversity Institute, Pretoria, South Africa.

Moulton, J. K. 2000. Molecular sequence data resolves basal divergences within Simuliidae (Diptera). Sys. Ent. 25: 95–113.

Moulton, J. K. 2003. Can the current molecular arsenal adequately track rapid divergence events within Simuliidae (Diptera)? Mol. Phylogenetics Evol. 27: 45–57.

Moulton, J. K., and P. H. Adler. 1997. The genus *Ectemnia* (Diptera: Simuliidae): taxonomy, polytene chromosomes, new species and phylogeny. Can. J. Zool. 75: 1896–1915.

Moulton, J. K., P. H. Adler, and J. Prince. 2004. An unusual new species of *Paracnephia* Rubtsov (Diptera: Simuliidae) from Western Australia. Zootaxa. 409: 1–12.

Nowell, A. R. M., and P. A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15: 303–328.

Palmer, R. W., and D. A. Craig. 2000. An ecological classification of primary labral fans of filter-feeding black fly (Diptera: Simuliidae) larvae. Can. J. Zool. 78: 199–218.

Prince, J. 1980. Resource partitioning in a guild of stream insects. M. Sc. thesis. University of Western Australia, Perth, Australia. pp. 123.

Smart, J. 1945. The classification of the Simuliidae (Diptera). Trans. Roy. Ent. Soc. Lond. 95: 463–532.

Stuart, A. E., and F. F. Hunter. 1998. Phylogenetic placement of *Ectemnia*, an autapomorphic black fly (Diptera: Simuliidae), using behavioural characters. Can. J. Zool. 76: 1942–1948.

Tonnoir, A. L. 1925. Australasian Simuliidae. Bull. Ent. Res. 15: 213–255.

Toussaint, E. A., L. Hendrich, H. Escalona, N. Porch, and M. Balk. 2016. Evolutionary history of a secondary terrestrial Australian diving beetle (Coleoptera, Dytiscidae) reveals a lineage of high morphological and ecological plasticity. Sys. Ent. 41: 650–657.

Trayler, K. M., J. A. Davis, P. Horwitz, and D. L. Morgan. 1996. Aquatic fauna of the Warren bioregion, south-west Western Australia: does reservation guarantee preservation? J. Roy. Soc. West. Aust. 79: 281–291.

Wang, Y., E. D. Tretter, R. W. Lichwardt, and M. M. White. 2013. Overview of 75 years of *Smittium* research, establishing a new genus for *Smittium culisetae*, and prospects for future revisions of the 'Smittium' clade. Mycologia. 105: 90–111

Williams, M. C., and R. W. Lichtwardt. 1990. Trichomycete gut fungi in New Zealand aquatic insect larvae. Can. J. Bot. 68: 1045–1056.

Wolfe, L. S., and D. G. Peterson. 1959. Black flies (Diptera: Simuliidae) of the forests of Quebec. Can. J. Zool. 37: 137–159.

Zwick, H. 1997. *Cnephia umbratorum* (Tonnoir)–eine besondere Kreiebelmücke der australischen Fauna. Bericht des IX Deutchprachigen/ I. Mitteleuropäischen Simuliiden-Symposiums, 27–29 September 1996 in Wein. Schriftenreihe des Instituts für Parasitologie und der Zoologie der Veterinärmedizinischen Universität Wien, Band. 1: 49–50.