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Phylogenetic relationships and comparative larval morphology of epigean and stygobitic species of *Limbodessus* Guignot, 1939 (Coleoptera: Dytiscidae: Bidessini), with a key of identification

MARIANO C. MICHAT[1], YVES ALARIE[2] & CHRIS H.S. WATTS[3]

[1] *CONICET - Laboratorio de Entomología, DBBE, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. E-mail: marianoide@gmail.com*

[2] *Department of Biology, Laurentian University, Ramsey Lake Road, Sudbury, Ontario, Canada. E-mail: yalarie@laurentian.ca*

[3] *South Australian Museum, North Terrace, Adelaide, SA 5000, Australia. E-mail: Watts.Chris@samuseum.sa.gov.au*

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Abstract

The larvae of five epigean and 25 stygobitic species of the diving beetle genus *Limbodessus* Guignot, 1939 are described and illustrated for the first time, with special emphasis on morphometry and chaetotaxy of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi. Those of the following five epigean species are described: *L. amabilis* (Clark, 1862), *L. compactus* (Clark, 1862), *L. inornatus* (Sharp, 1882), *L. praelargus* (Lea, 1899), *L. shuckardii* (Clark, 1862). The 25 stygobitic larvae described are: *L. barwidgeeensis* Watts & Humphreys, 2006, *L. bigbellensis* (Watts & Humphreys, 2000), *L. challaensis* (Watts & Humphreys, 2001), *L. cooperi* Watts & Humphreys, 2006, *L. eberhardi* (Watts & Humphreys, 1999), *L. exilis* Watts & Humphreys, 2006, *L. fridaywellensis* (Watts & Humphreys, 2001), *L. hillviewensis* (Watts & Humphreys, 2004), *L. hinkleri* (Watts & Humphreys, 2000), *L. leysi* Watts & Humphreys, 2006, *L. macrohinkleri* Watts & Humphreys, 2006, *L. masonensis* (Watts & Humphreys, 2001), *L. millbilliensis* Watts & Humphreys, 2006, *L. mirandaae* Watts & Humphreys, 2006, *L. morgani* (Watts & Humphreys, 2000), *L. nambiensis* Watts & Humphreys, 2006, *L. ordinarius* Watts & Humphreys, 2009, *L. palmulaoides* Watts & Humphreys, 2006, *L. pulpa* (Watts & Humphreys, 1999), *L. raeae* Watts & Humphreys, 2006, *L. raesideensis* (Watts & Humphreys, 2001), *L. windarraensis* (Watts & Humphreys, 1999), *L. yandalensis* Watts & Humphreys, 2006, *L. yarrabubbaensis* Watts & Humphreys, 2009, *L. yuinmeryensis* (Watts & Humphreys, 2003). The morphology and chaetotaxy of epigean vs.

stygobitic species are compared, and a key for the identification of the species is presented. Contrary to their epigean counterparts, larvae of stygobitic *Limbodessus* have turned out to be very divergent morphologically. In addition to the common characteristics associated with an underground living (i.e., absence of stemmata, reduced pigmentation, and thin or soft exoskeleton), larvae of these species have undergone a variable modification of the frontoclypeus and have evolved relatively shorter tarsal claws. Two morphological groups of stygobitic species are evident, one including species less deviated from the ancestral (epigean) condition and another group comprising more modified species that typically have a larger size, a more or less pyriform head with a digitiform nasale, and a strongly reduced occipital foramen. Primary chaetotaxy of the species has remained a very conservative expression of the phenotype. Secondary chaetotaxy shows variation among the species, the most obvious being the variable number of lamellae clypeales and the presence or absence of secondary setae on the urogomphus. The phylogenetic relationships of *Limbodessus* are analyzed cladistically. Larvae of this genus lack the primary pore ABc, which is a synapomorphy of the tribe Bidessini. As presently defined, *Limbodessus* is probably paraphyletic with respect to *Allodessus* Guignot, 1953.

Key words: Coleoptera, Dytiscidae, Bidessini, *Limbodessus*, larva, groundwater, morphometry, chaetotaxy, phylogeny

Introduction

Limbodessus Guignot, 1939 is a genus of 70 known species primarily found in Australia. Indeed, except for *L. compactus* (Clark, 1862) and *L. curviplicatus* (Zimmermann, 1927), which are distributed in the Palaearctic-Oriental-Australian and Pacific regions respectively, all other species are endemic to the Australian region (Nilsson 2001, 2003, 2004; Nilsson & Fery 2006). The most recent revision of the genus recognizes nine epigean species, which are often abundant in still to slightly moving, shallow water (Watts & Leys 2005). Recently, however, many species of *Limbodessus* have been found living underground, in what represents the most extensive radiation of subterranean diving beetles known so far (see Watts & Humphreys 2009 and references therein). Within the last 15 years about 60 species of obligate groundwater (stygobitic) *Limbodessus* (many of them previously included in the genera *Tjirtudessus* Watts & Humphreys, 1999 and *Nirridessus* Watts & Humphreys, 1999) have been described, associated with calcrete (terrestrial limestone) aquifers in the Yilgarn region of Western Australia and the Ngalia basin in the Northern Territory (Watts & Humphreys 2009). The species of stygobitic *Limbodessus* have all been found in calcretes of ancient palaeodrainage channels in arid and semiarid areas of western and central Australia (Watts & Humphreys 2006). The calcretes form by precipitation of carbonates from shallow groundwater flow paths in palaeodrainage channels, and are the only permanent freshwater habitats for macro- and mesofauna through much of the arid zone of inland Australia (Leys *et al*. 2003).

Limbodessus is one of the more than 40 genera of the hydroporine tribe Bidessini (ca. 600 species worldwide), which includes most of the smaller species of diving beetles or Dytiscidae (generally smaller than 5 mm long) (Nilsson 2001). All the species of *Limbodessus* are postulated to share a monophyletic origin (Balke & Ribera 2004). Sequence data for members of this genus and other bidessine relatives were presented by Leys *et al*. (2003), Balke and Ribera (2004), Hendrich and Balke (2009), and Hendrich *et al*. (2009) and have confirmed a close relationship between *Limbodessus* and the genus *Allodessus* Guignot, 1953. A recent phylogenetic analysis based on molecular data suggested that the majority of stygobitic *Limbodessus* species independently evolved from a small number of widespread surface species approximately five million years ago (Leys *et al*. 2003).

Despite the Bidessini representing one of the most significant radiations of diving beetles (Nilsson 2001, 2003, 2004; Nilsson & Fery 2006), larval morphology of members of this tribe remains imperfectly known. So far, the larvae of only 16 genera have been described (Meuche 1937; Watts 1963; Bertrand 1972; Perkins 1980; Richoux 1982; Matta 1983; Nilsson 1985; Alarie & Wewalka 2001; Alarie *et al*. 2007; Michat & Alarie 2006, 2008; Michat & Torres 2006; Michat *et al*. 2010, 2011), some of them very superficially, and the larvae of several genera are unknown. Regarding *Limbodessus*, only brief descriptions of the larvae of the epigean *L. amabilis* (Clark, 1862) and the stygobitic *L. eberhardi* (Watts & Humphreys, 1999) and *L. pulpa* (Watts & Humphreys, 1999) have been published (Watts 1963; Watts & Humphreys 1999).

Larval morphology is important in the study of the phylogenetic relationships among Holometabola. As different expressions of the same genotype, larval characters help to complement adult characters that have been traditionally the primary basis for classification. As demonstrated recently, larval chaetotaxy is a significant source of characters both for diagnosis of the genera and species and for the study of the phylogenetic relationships within the Dytiscidae (e.g., Alarie *et al*. 2009a, 2009b, 2011), in particular within the Bidessini (Alarie *et al*. 2007; Michat

& Alarie 2006, 2008; Michat & Torres 2006; Michat *et al*. 2010, 2011). The development of a system of nomenclature for primary sensilla (setae and pores) in first-instar larvae of the Hydroporinae (Alarie & Harper 1990; Alarie *et al*. 1990; Alarie 1991; Alarie & Michat 2007) has demonstrated the taxonomic and phylogenetic value of this character set. There is an overall pattern of setae and pores, which is widespread among taxa, though it is modified in a variety of groups. This generalized pattern is consistent enough to be used for phylogenetic analysis and yet sufficiently variable to allow for taxonomic distinction.

This paper is meant to be a step towards a better knowledge of the larval morphology of the genus *Limbodessus*, and has the following goals: (1) to describe and illustrate in detail five epigean and 25 stygobitic species of *Limbodessus* with an emphasis on chaetotaxic analysis of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphi; (2) to provide a key for the identification of the larvae of these species; (3) to compare the ground-plan of larval features of *Limbodessus* with those of other bidessine genera for which the larvae have been described in detail; and (4) to test cladistically the hypothesis of a monophyletic origin of this genus using larval morphology. In addition to these goals the comparison of epigean and stygobitic *Limbodessus* larvae is of the utmost interest as it allows us to provide, for the first time, a comparative study of the larval morphology of epigean and stygobitic morphotypes and gives us an opportunity to look at the selectable phenotypic variations that are likely to have evolved within the subterranean species as a result of adaptation to an underground environment.

Material and methods

Sampling information. The epigean species of *Limbodessus* were collected with a hand net in still to slightly moving, shallow water in Southern Australia. All stygobitic species were collected by sampling wells and bores in calcretes in the Australian arid zone, specifically in the Yilgarn craton of Western Australia. The Yilgarn craton covers 750,000 km^2 between latitudes 34° and 25° S. The water table varied between 1.5 and 64 m below the ground surface, and the depth of water sampled varied from 0.1 to 30 m below the groundwater surface. The calcrete aquifers may vary up to 30 m in thickness, but those sampled in the Yilgarn are typically thin and the groundwater is close to the surface (Watts & Humphreys 2006). Samples were collected from a range of types of access into the groundwater calcrete aquifers including: monitoring wells in working water borefields, sometimes within meters of functioning pumps; piezometers; aquifer exploration bores; uncased mineral exploration bores; pastoral bores; and hand dug pastoral wells. Stygofauna were present both in narrow bore-holes drilled for geological purposes, water pumping or aquifer assessment, and in wide hand-dug wells established for pastoral purposes (Watts & Humphreys 2003). Specimens were preserved into 100% ethanol to enable DNA analysis. More details in Watts and Humphreys (2006).

Larvae examined, preparation and description. The descriptions of the larval stages and the taxonomic conclusions reported in this paper are based on the examination of larvae found with adults in situations where they could be unequivocally associated with a particular species. Indeed, most species of stygobitic *Limbodessus* are confined to a single calcrete body. If more than one species is found in a calcrete, the size ranges (see Table 1 in Watts & Humphreys 2009) allow a firm association of larvae and adults. Several larvae were identified to species using this criterion. In other cases, the identity of the larvae was confirmed by sequencing a fragment of the CO1 gene and using it to match larvae and adults. The species and instars described and the number of specimens studied for each instar are listed in Table 1. The exact localities from which the specimens were obtained are provided with the species descriptions.

Specimens were cleared in lactic acid, dissected and mounted on glass slides with polyvinyl-lacto-glycerol. Observation (at magnifications up to 1000x) and drawings were made using an Olympus CX31 compound microscope equipped with a camera lucida. Drawings were scanned and digitally inked using a Genius PenSketch tablet. The material is held in the collections of the South Australian Museum and Western Australian Museum.

Morphometric analysis. We employed, with minimal modifications and additions, the terms used in previous papers dealing with the larval morphology of Hydroporinae (Michat & Alarie 2008; Michat & Torres 2008). The following measurements were taken (with abbreviations shown in parentheses): head length (HL) (total head length including the frontoclypeus, measured medially along the epicranial stem); maximum head width (HW); length of frontoclypeus (FRL) (from apex of nasale to the joint of frontal and coronal sutures); occipital foramen width (OCW) (maximum width measured along dorsal margin of occipital foramen); coronal line length (COL);

length of mandible (MNL) (measured from laterobasal angle to apex); width of mandible (MNW) (maximum width measured at base). Lengths of antenna (A), maxillary (MP) and labial (LP) palpi were obtained by adding the lengths of the individual segments; each segment is denoted by the corresponding letter(s) followed by a number (e.g., A1, first antennomere). A3' is used as an abbreviation for the apical lateroventral process of the third antennomere. Length of leg (L), including the longest claw (CL), was obtained by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g., L1, prothoracic leg). The length of trochanter includes only the proximal portion, the length of distal portion is included in the femoral length. The legs of the larvae studied were considered as being composed of six segments following Lawrence (1991). Dorsal length of last abdominal segment (LAS) (measured along midline from anterior to posterior margin). Length of urogomphus (U) was derived by adding the lengths of the individual segments; each segment is denoted by the letter U followed by a number (e.g., U1, first urogomphomere). These measurements were used to calculate several ratios that characterize body shape.

TABLE 1. Species and instars described in the present study. The numbers under each instar indicate the specimens studied.

Species	Habitat	Instar I	Instar II	Instar III
Limbodessus amabilis (Clark, 1862)	Epigean	–	3	2
Limbodessus compactus (Clark, 1862)	Epigean	–	–	2
Limbodessus inornatus (Sharp, 1882)	Epigean	–	–	3
Limbodessus praelargus (Lea, 1899)	Epigean	–	–	1
Limbodessus shuckardii (Clark, 1862)	Epigean	–	1	3
Limbodessus barwidgeeensis Watts & Humphreys, 2006	Stygobitic	–	1	–
Limbodessus bigbellensis (Watts & Humphreys, 2000)	Stygobitic	2	–	2
Limbodessus challaensis (Watts & Humphreys, 2001)	Stygobitic	1	–	1
Limbodessus cooperi Watts & Humphreys, 2006	Stygobitic	–	–	1
Limbodessus eberhardi (Watts & Humphreys, 1999)	Stygobitic	–	–	1
Limbodessus exilis Watts & Humphreys, 2006	Stygobitic	–	–	2
Limbodessus fridaywellensis (Watts & Humphreys, 2001)	Stygobitic	–	–	1
Limbodessus hillviewensis (Watts & Humphreys, 2004)	Stygobitic	–	–	1
Limbodessus hinkleri (Watts & Humphreys, 2000)	Stygobitic	–	1	1
Limbodessus leysi Watts & Humphreys, 2006	Stygobitic	1	–	3
Limbodessus macrohinkleri Watts & Humphreys, 2006	Stygobitic	–	1	–
Limbodessus masonensis (Watts & Humphreys, 2001)	Stygobitic	–	2	2
Limbodessus millbilliensis Watts & Humphreys, 2006	Stygobitic	1	1	2
Limbodessus mirandaae Watts & Humphreys, 2006	Stygobitic	1	–	–
Limbodessus morgani (Watts & Humphreys, 2000)	Stygobitic	1	1	–
Limbodessus nambiensis Watts & Humphreys, 2006	Stygobitic	1	1	–
Limbodessus ordinarius Watts & Humphreys, 2009	Stygobitic	–	3	3
Limbodessus palmulaoides Watts & Humphreys, 2006	Stygobitic	1	–	–
Limbodessus pulpa (Watts & Humphreys, 1999)	Stygobitic	2	1	–
Limbodessus raeae Watts & Humphreys, 2006	Stygobitic	–	–	1
Limbodessus raesideensis (Watts & Humphreys, 2001)	Stygobitic	–	2	2
Limbodessus windarraensis (Watts & Humphreys, 1999)	Stygobitic	1	1	1
Limbodessus yandalensis Watts & Humphreys, 2006	Stygobitic	–	–	1
Limbodessus yarrabubbaensis Watts & Humphreys, 2009	Stygobitic	1	–	–
Limbodessus yuinmeryensis (Watts & Humphreys, 2003)	Stygobitic	2	2	2

Chaetotaxic analysis. Primary (present in instar I) and secondary (added in instars II–III) setae and pores were distinguished on the cephalic capsule, head appendages, legs, last abdominal segment and urogomphus of the studied larvae. Sensilla were coded by two capital letters, in most cases corresponding to the first two letters of the name of the structure on which they are located, and a number (setae) or a lower case letter (pores). The following abbreviations were used: AB, abdominal segment VIII; AN, antenna; CO, coxa; FE, femur; FR, frontoclypeus; LA, labium; MN, mandible; MX, maxilla; PA, parietal; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter; UR, urogomphus. Setae and pores present in instar I were labeled by comparison with the ground-plan of chaetotaxy of the subfamily Hydroporinae (Alarie & Harper 1990; Alarie *et al*. 1990; Alarie 1991; Alarie & Michat 2007). Homologies were recognized using the criterion of similarity of position (Wiley 1981). Setae located at the apices of the maxillary and labial palpi were extremely difficult to distinguish due to their position and small size. Accordingly, they are not well represented in the drawings.

Phylogenetic analysis. The phylogenetic relationships and putative monophyly of the genus *Limbodessus* were analyzed cladistically using the program TNT (Goloboff *et al*. 2008) and considering the characters provided by the larval morphology, morphometry and chaetotaxy. Although instar I of only 12 species of *Limbodessus* were described, primary chaetotaxy characters were included and coded from instars II and III in the species with unknown instar I. The analysis thus included 27 out of 30 described species, with only *L. mirandaae* Watts & Humphreys, 2006, *L. palmulaoides* Watts & Humphreys, 2006 and *L. yarrabubbaensis* Watts & Humphreys, 2009 (unknown as instars II and III) excluded. Representatives of another six Bidessini genera (*Allodessus bistrigatus* (Clark, 1862), *Amarodytes duponti* (Aubé, 1838), *Anodocheilus maculatus* Babington, 1841, *Hydroglyphus balkei* Hendrich, 1999, *Hypodessus cruciatus* (Régimbart, 1903), *Liodessus flavofasciatus* (Steinheil, 1869)) as well as 23 species belonging to the remaining Hydroporinae tribes (*Antiporus uncifer* Sharp, 1882, *Canthyporus kenyensis* Bilardo & Sanfilippo, 1979, *Deronectes latus* (Stephens, 1829), *Heterosternuta wickhami* (Zaitzev, 1908), *Hydrocolus paugus* (Fall, 1923), *Hydroporus columbianus* Fall, 1923, *Laccornellus lugubris* (Aubé, 1838), *Neoporus undulatus* (Say, 1823), *Oreodytes scitulus* (LeConte, 1855), *Scarodytes halensis* (Fabricius, 1787), *Stictonectes canariensis* Machado, 1987, *Hydrovatus caraibus* Sharp, 1882, *Herophydrus musicus* (Klug, 1834), *Hygrotus sayi* J. Balfour-Browne, 1944, *Andex insignis* Sharp, 1882, *Desmopachria concolor* Sharp, 1882, *Hyphydrus ovatus* (Linnaeus, 1761), *Microdytes uenoi* Satô, 1972, *Pachydrus obesus* Sharp, 1882, *Laccornis latens* (Fall, 1937), *Celina parallela* (Babington, 1841), *Derovatellus lentus* (Wehncke, 1876), *Vatellus haagi* Wehncke, 1876) were included. The genus *Laccophilus* Leach, 1815 (Laccophilinae), suggested to be closely related to Hydroporinae (Miller 2001), was included as the outgroup. All characters were treated as unordered and equally weighted. Multistate discrete characters were treated as nonadditive. A heuristic search was implemented using 'tree bisection reconnection' as the algorithm, with 200 replicates and saving 100 trees per replication (previously setting 'hold 20000'). Bremer support values were calculated using the commands 'hold 20000', 'sub n' and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step, until all Bremer values were obtained (Kitching *et al*. 1998).

Results

Description of the larvae of *Limbodessus* Guignot, 1939

Diagnosis. Head subpentagonal or more or less pyriform; occipital suture absent in instar I, absent or present in instars II–III; nasale moderately elongate, subtriangular or digitiform, with small lateral branches; A3 with a ventroapical spinula; cardo fused to stipes; galea absent; prementum without lateral spinulae; abdominal segment VI membranous ventrally; siphon short; pores PAd, PAe and PAj absent; pore ANf absent; seta TR2 and pore FEa absent; seta TI7 short, spine-like; pores ABa and ABc absent; seta AB10 spine-like; seta UR8 inserted distally; legs without natatory setae; U with or without additional setae; U with or without secondary setae.

Instar I (based on stygobitic species only)

Color. Uniformly pale or yellowish testaceous, unpigmented.

Body. Subcylindrical, narrowing towards abdominal apex. Measurements and ratios that characterize the body shape are shown in Tables 2–4.

TABLE 2. Measurements and ratios for the first-instar larvae of species of *Limbodessus*.

Measure	*L. bigbellensis*	*L. challaensis*	*L. leysi*	*L. millbilliensis*
HL (mm)	0.72–0.73	0.46	0.41	0.43
HW (mm)	0.48–0.49	0.31	0.25	0.31
FRL (mm)	0.52	0.35	0.30	0.33
OCW (mm)	0.21–0.22	0.22	0.16	0.18
HL/HW	1.51	1.46	1.61	1.39
HW/OCW	2.23–2.31	1.43	1.59	1.68
COL/HL	0.28–0.29	0.24	0.27	0.23
FRL/HL	0.71–0.72	0.76	0.73	0.77
A/HW	0.72–0.74	0.75	0.88	0.82
A3/A1	2.45–2.60	2.83	2.83	2.86
A3/A2	1.29–1.37	1.42	1.70	1.67
A4/A3	0.52–0.58	0.71	0.71	0.60
A3’/A4	0.87–0.93	0.92	0.75	0.83
MNL/MNW	4.24–4.50	4.60	4.11	4.30
MNL/HL	0.49	0.50	0.45	0.50
A/MP	1.08–1.18	1.15	1.36	1.28
MP2/MP1	1.36–1.38	1.38	1.60	1.67
MP2/MP3	2.31–2.42	1.80	2.29	2.50
MP/LP	1.48	1.21	1.32	1.38
LP2/LP1	1.44–1.47	1.43	1.78	1.90
L3 (mm)	1.44–1.49	0.81	0.70	0.78
L3/L1	1.12–1.21	1.18	1.16	1.17
L3/L2	1.06–1.07	1.09	1.08	1.11
L3/HW	3.00–3.08	2.60	2.79	2.53
L3 (CO/FE)	0.88–0.89	0.95	0.89	0.90
L3 (TI/FE)	0.63–0.65	0.65	0.63	0.66
L3 (TA/FE)	0.74–0.77	0.72	0.74	0.78
L3 (CL/TA)	0.22–0.23	0.39	0.40	0.35
LAS (mm)	0.25–0.26	0.19	0.17	0.19
LAS/HW	0.53	0.60	0.67	0.63
U (mm)	0.96–1.02	0.79	0.69	0.65
U/LAS	3.80–3.98	4.18	4.09	3.38
U/HW	2.00–2.11	2.52	2.73	2.13
U1/U2	1.88–2.03	0.99	1.17	1.36

Head. Cephalic capsule (Figs 31–32, 49–50, 89–90, 115–116, 134–135, 148–149, 162–163, 180–181, 194–195, 216–217, 238–239, 252–253). Subpentagonal, longer than broad; maximum width at level of stemmata (if present), without neck constriction; occipital suture absent; ecdysial line slightly visible, coronal line short; occipital foramen well developed or reduced, broadly emarginate ventrally; posterior tentorial pits visible ventrally; lateral margins of parietal curved to more or less straight; FR elongate, lateral margins sinuate, with two lateral, spine-like egg bursters at mid-length; nasale moderately elongate, subtriangular to more or less digitiform, sides straight or inflated, rounded apically, with one small branch at each side; ventrodistal surface of nasale with spinulae of different shapes and with or without a hole-like structure (Fig. 130); ventrolateral margin with robust spinulae that range from almost absent (Fig. 116) to extremely abundant and forming a half-circle (Fig. 90); stemmata absent in stygobitic species (not evaluated in epigean species). Antenna (Figs 33–34, 51–52, 91–92, 117–118, 136–137, 150–151, 164–165, 182–183, 196–197, 218–219, 240–341, 254–255). Elongate, composed of four

antennomeres, shorter than HW; A1 the shortest (sometimes subequal to A4), A3 the longest, with a ventroapical spinula; A3' elongate. Mandible (Figs 37, 55, 95, 121, 140, 154, 168, 186, 200, 222, 244, 258). Prominent, broad basally, distal half projected inwards and upwards, apex sharp; mandibular channel present. Maxilla (Figs 35–36, 53–54, 93–94, 119–120, 138–139, 152–153, 166–167, 184–185, 198–199, 220–221, 242–243, 256–257). Cardo fused to stipes; stipes short, broad; galea and lacinia absent; MP elongate, composed of three palpomeres, MP3 the shortest, MP2 the longest. Labium (Figs 38–39, 56–57, 96–97, 122–123, 141–142, 155–156, 169–170, 187–188, 201–202, 223–224, 245–246, 259–260). Prementum small, subtrapezoidal, about as long as broad or somewhat broader than long, without lateral spinulae, anterior margin slightly indented medially; LP elongate, composed of two palpomeres; LP2 longer than LP1.

TABLE 3. Measurements and ratios for the first-instar larvae of species of *Limbodessus*.

Measure	*L. mirandaae*	*L. morgani*	*L. nambiensis*	*L. palmulaoides*
HL (mm)	0.54	0.30	0.50	0.83
HW (mm)	0.41	0.23	0.41	0.61
FRL (mm)	0.42	0.23	0.39	0.61
OCW (mm)	0.23	0.18	0.25	0.22
HL/HW	1.31	1.30	1.24	1.37
HW/OCW	1.80	1.28	1.64	2.80
COL/HL	0.23	0.23	0.24	0.26
FRL/HL	0.77	0.77	0.76	0.74
A/HW	0.73	0.65	0.68	0.69
A3/A1	2.30	3.00	2.00	2.07
A3/A2	1.44	2.00	1.33	1.35
A4/A3	0.52	0.67	0.55	0.52
A3'/A4	0.83	0.75	0.91	0.88
MNL/MNW	3.80	4.00	3.71	4.43
MNL/HL	0.52	0.53	0.51	0.55
A/MP	1.17	1.20	1.17	1.10
MP2/MP1	1.21	2.17	1.17	1.21
MP2/MP3	2.30	2.17	2.33	2.27
MP/LP	1.44	1.19	1.41	1.45
LP2/LP1	1.25	2.50	1.13	1.12
L3 (mm)	1.04	0.52	0.92	1.59
L3/L1	1.13	1.16	1.14	1.11
L3/L2	1.06	1.07	1.07	1.05
L3/HW	2.52	2.30	2.26	2.62
L3 (CO/FE)	0.98	1.00	0.88	0.97
L3 (TI/FE)	0.67	0.69	0.68	0.65
L3 (TA/FE)	0.74	0.77	0.74	0.74
L3 (CL/TA)	0.39	0.48	0.31	0.28
LAS (mm)	0.22	0.13	0.20	0.29
LAS/HW	0.53	0.57	0.50	0.48
U (mm)	–	0.52	0.75	1.18
U/LAS	–	4.08	3.68	4.05
U/HW	–	2.30	1.84	1.94
U1/U2	–	0.96	1.52	1.72

TABLE 4. Measurements and ratios for the first-instar larvae of species of *Limbodessus*.

Measure	*L. pulpa*	*L. windarraensis*	*L. yarrabubbaensis*	*L. yuinmeryensis*
HL (mm)	0.39–0.41	0.45	0.80	0.39–0.41
HW (mm)	0.29–0.31	0.32	0.56	0.29
FRL (mm)	0.32	0.33	0.60	0.29–0.30
OCW (mm)	0.20–0.22	0.17	0.23	0.21
HL/HW	1.32	1.41	1.42	1.36–1.39
HW/OCW	1.41–1.48	1.88	2.48	1.38–1.40
COL/HL	0.17–0.22	0.27	0.25	0.25–0.26
FRL/HL	0.78–0.83	0.73	0.75	0.74–0.75
A/HW	0.74–0.81	0.75	0.82	0.78–0.81
A3/A1	2.57	2.25	2.47	2.29–2.67
A3/A2	1.50–1.64	1.38	1.54	1.33–1.42
A4/A3	0.56–0.61	0.50	0.46	0.69–0.71
A3’/A4	0.82–0.90	0.56	0.82	0.73–0.83
MNL/MNW	4.10–4.30	4.00	4.61	3.70–3.90
MNL/HL	0.52–0.53	0.49	0.51	0.47–0.48
A/MP	1.24–1.37	1.23	1.29	1.35–1.38
MP2/MP1	1.64–1.80	1.38	1.21	1.60
MP2/MP3	2.25–2.57	2.25	3.40	2.00
MP/LP	1.23–1.30	1.30	1.47	1.26–1.31
LP2/LP1	1.50–1.70	1.50	1.23	1.60–1.70
L3 (mm)	0.71–0.76	0.77	1.47	0.70–0.74
L3/L1	1.17–1.18	1.18	1.10	1.18
L3/L2	1.10–1.11	1.09	1.03	1.06–1.11
L3/HW	2.41–2.46	2.42	2.61	2.45–2.53
L3 (CO/FE)	0.95–0.97	0.93	1.03	0.97–1.00
L3 (TI/FE)	0.67	0.66	0.67	0.67–0.68
L3 (TA/FE)	0.77–0.81	0.71	0.71	0.74–0.78
L3 (CL/TA)	0.38–0.40	0.41	0.35	0.41–0.42
LAS (mm)	0.18	0.17	0.29	0.18
LAS/HW	0.60–0.63	0.53	0.51	0.62–0.63
U (mm)	0.60	–	1.05	0.73–0.78
U/LAS	3.30	–	3.66	4.11–4.24
U/HW	1.97–2.07	–	1.86	2.55–2.66
U1/U2	1.35	–	1.59	0.90–0.96

Thorax. Terga convex, pronotum about as long as meso- and metanotum combined, meso- and metanotum subequal; protergite subovate, margins rounded, more developed than meso- and metatergite; meso- and metatergite transverse; all sclerites without anterotransverse carina; sagittal line not visible; sterna membranous; spiracles absent. Legs (Figs 40–41, 58–59, 98–99, 124–125, 143–144, 157–158, 171–172, 189–190, 203–204, 225–226, 247–248, 261–262). Long, composed of six articles, L1 the shortest, L3 the longest; CO robust, elongate,

TR divided into two parts, FE, TI and TA slender, subcylindrical, PT with two long, slender, slightly curved claws; posterior claw shorter than anterior claw on L1 and L2, posterior claw longer than anterior claw on L3; surface spinulae reduced or absent; ventral surface of proTA with several elongate spinulae on distal half.

TABLE 5. Measurements and ratios for the second-instar larvae of species of *Limbodessus*.

Measure	*L. amabilis*	*L. barwidgeeensis*	*L. hinkleri*	*L. macrohinkleri*	*L. masonensis*
HL (mm)	0.55–0.56	1.33	0.48	1.33	0.52–0.53
HW (mm)	0.44–0.45	0.92	0.35	0.91	0.36–0.37
FRL (mm)	0.45–0.46	0.95	0.36	0.99	0.41–0.42
OCW (mm)	0.31–0.32	0.48	0.19	0.31	0.24
HL/HW	1.25–1.30	1.45	1.37	1.46	1.45–1.46
HW/OCW	1.39–1.42	1.94	1.84	2.97	1.52–1.54
COL/HL	0.19–0.21	0.29	0.25	0.26	0.22
FRL/HL	0.79–0.81	0.71	0.75	0.74	0.78
A/HW	0.65–0.74	0.68	0.66	0.68	0.73–0.74
A3/A1	2.56–2.67	2.04	2.43	2.60	2.33
A3/A2	1.33–1.37	1.18	1.42	1.30	1.50
A4/A3	0.38–0.43	0.34	0.59	0.25	0.48
A3’/A4	0.60–0.70	0.94	0.80	0.77	0.90
MNL/MNW	3.75–4.21	4.23	4.30	3.97	4.31–4.58
MNL/HL	0.50–0.53	0.55	0.45	0.49	0.51–0.53
A/MP	1.16–1.20	0.98	1.21	1.08	1.10
MP2/MP1	1.33–1.41	0.93	1.21	1.13	1.22
MP2/MP3	2.40–2.89	3.38	2.43	3.86	2.44
MP/LP	1.24–1.29	1.78	1.41	1.51	1.44
LP2/LP1	1.47–1.63	0.80	1.25	0.88	1.13–1.27
L3 (mm)	1.19–1.26	2.43	0.72	2.33	0.91–0.93
L3/L1	1.26–1.34	–	1.16	1.12	1.19–1.20
L3/L2	1.13–1.16	1.03	1.09	1.04	1.10–1.11
L3/HW	2.64–2.90	2.64	2.08	2.56	2.52–2.53
L3 (CO/FE)	0.97–1.05	0.83	0.92	0.92	0.92–0.96
L3 (TI/FE)	0.65–0.67	0.69	0.64	0.73	0.67
L3 (TA/FE)	0.70–0.77	0.69	0.74	0.73	0.73–0.76
L3 (CL/TA)	0.49–0.60	0.27	0.33	0.26	0.35
LAS (mm)	0.31–0.32	0.46	0.21	0.43	0.23–0.24
LAS/HW	0.69–0.73	0.50	0.60	0.47	0.63–0.66
U (mm)	1.04–1.05	–	0.64	1.79	0.82–0.84
U/LAS	3.35–3.64	–	3.10	4.20	3.47–3.61
U/HW	2.32–2.65	–	1.86	1.96	2.27–2.30
U1/U2	0.93–1.06	–	1.24	1.98	0.93–0.98

Abdomen. Eight-segmented; segments I–VI sclerotized dorsally, membranous ventrally; segment VII sclerotized both dorsally and ventrally, with ventral sclerite independent from dorsal sclerite; tergites I–VII narrow, transverse, rounded laterally, without sagittal line; all sclerites without anterotransverse carina, covered with

minute spinulae in transverse rows; spiracles absent on segments I–VII; LAS (Figs 42–43, 60–61, 100–101, 126–127, 145–146, 159–160, 171–172, 191–192, 203–204, 227–228, 249–250, 263–264) the longest, completely sclerotized, ring-like, covered with minute spinulae in transverse rows; siphon short, subconical. Urogomphus (Figs 44, 62, 102, 128, 147, 161, 175, 193, 207, 229, 251, 265). Long, composed of two urogomphomeres; U1 much longer than LAS, covered with minute spinulae except on distal portion; U2 narrow, setiform, subequal or shorter than U1.

TABLE 6. Measurements and ratios for the second-instar larvae of species of *Limbodessus*.

Measure	*L. millbilliensis*	*L. morgani*	*L. nambiensis*	*L. ordinarius*	*L. pulpa*
HL (mm)	0.58	0.38	0.81	0.65–0.66	0.51
HW (mm)	0.39	0.29	0.55	0.50	0.38
FRL (mm)	0.45	0.29	0.62	0.51	0.40
OCW (mm)	0.23	0.20	0.27	0.31–0.34	0.26
HL/HW	1.49	1.29	1.46	1.29–1.33	1.36
HW/OCW	1.68	1.48	2.07	1.48–1.61	1.46
COL/HL	0.24	0.24	0.23	0.21–0.22	0.22
FRL/HL	0.76	0.76	0.77	0.78–0.79	0.78
A/HW	0.78	0.66	0.72	0.67–0.70	0.72
A3/A1	2.30	2.17	1.93	2.00–2.27	2.33
A3/A2	1.35	1.30	1.21	1.20–1.25	1.50
A4/A3	0.52	0.77	0.45	0.48–0.52	0.52
A3’/A4	0.83	0.70	0.92	0.83–0.85	0.64
MNL/MNW	5.00	4.10	4.50	3.74–3.94	4.23
MNL/HL	0.51	0.54	0.55	0.53–0.54	0.53
A/MP	1.19	1.08	1.03	1.08–1.13	1.15
MP2/MP1	1.26	1.33	0.97	0.89–1.00	1.35
MP2/MP3	2.67	2.00	2.75	2.18–2.89	2.88
MP/LP	1.33	1.44	1.65	1.40–1.41	1.33
LP2/LP1	1.44	1.78	0.85	1.05–1.10	1.12
L3 (mm)	1.03	0.63	–	1.17–1.19	0.92
L3/L1	1.23	1.14	–	1.18–1.20	1.23
L3/L2	1.11	1.11	–	1.09–1.11	1.16
L3/HW	2.64	2.15	–	2.33–2.41	2.46
L3 (CO/FE)	0.96	0.97	–	0.85–0.95	0.96
L3 (TI/FE)	0.64	0.69	–	0.66–0.68	0.69
L3 (TA/FE)	0.71	0.75	–	0.67–0.71	0.79
L3 (CL/TA)	0.32	0.46	–	0.32–0.33	0.32
LAS (mm)	0.28	0.19	0.33	0.29–0.32	0.29
LAS/HW	0.71	0.64	0.59	0.58–0.64	0.76
U (mm)	0.76	0.60	1.12	1.02–1.05	–
U/LAS	2.75	3.21	3.44	3.28–3.51	–
U/HW	1.95	2.07	2.03	2.03–2.09	–
U1/U2	1.14	0.79	1.39	0.99–1.07	–

TABLE 7. Measurements and ratios for the second-instar larvae of species of *Limbodessus*.

Measure	*L. raesideensis*	*L. shuckardii*	*L. windarraensis*	*L. yuinmeryensis*
HL (mm)	1.10–1.14	0.50	0.62	0.51–0.53
HW (mm)	0.77–0.81	0.33	0.44	0.38
FRL (mm)	0.85–0.87	0.40	0.49	0.40–0.41
OCW (mm)	0.27–0.28	0.27	0.29	0.25–0.26
HL/HW	1.41–1.44	1.55	1.42	1.37–1.40
HW/OCW	2.77–3.04	1.22	1.53	1.46–1.54
COL/HL	0.23–0.24	0.21	0.22	0.23
FRL/HL	0.76–0.77	0.79	0.78	0.77
A/HW	0.73–0.74	0.83	0.73	0.67–0.70
A3/A1	2.00–2.05	2.22	2.00	2.00–2.11
A3/A2	1.19	1.33	1.22	1.38–1.46
A4/A3	0.35–0.39	0.55	0.64	0.61–0.68
A3’/A4	0.80–0.82	0.73	0.79	0.69–0.82
MNL/MNW	4.39–4.45	4.25	4.00	4.00–4.50
MNL/HL	0.55–0.56	0.50	0.51	0.50
A/MP	1.08–1.11	1.20	1.12	1.17–1.21
MP2/MP1	0.96–1.02	1.57	1.09	1.13–1.31
MP2/MP3	3.29–3.62	2.20	2.50	2.25–2.33
MP/LP	1.66–1.68	1.39	1.45	1.35–1.39
LP2/LP1	0.86–0.91	1.54	1.22	1.21–1.36
L3 (mm)	2.04–2.13	1.00	1.05	0.89–0.92
L3/L1	1.10–1.11	1.30	1.17	1.17–1.21
L3/L2	1.05–1.06	1.15	1.10	1.11–1.13
L3/HW	2.62–2.66	3.07	2.38	2.37–2.41
L3 (CO/FE)	0.98	1.00	0.91	0.90–0.94
L3 (TI/FE)	0.72–0.73	0.62	0.64	0.65–0.67
L3 (TA/FE)	0.70–0.72	0.69	0.69	0.71–0.73
L3 (CL/TA)	0.27–0.28	0.56	0.36	0.33–0.37
LAS (mm)	0.44–0.45	0.28	0.24	0.24–0.25
LAS/HW	0.55–0.57	0.85	0.54	0.63–0.66
U (mm)	1.62	0.85	0.84	0.94
U/LAS	3.64–3.73	3.07	3.54	3.71–3.94
U/HW	2.00–2.12	2.61	1.91	2.45–2.49
U1/U2	1.73	0.93	1.24	0.83

Chaetotaxy (Figs 31–44, 49–62, 89–102, 115–128, 134–175, 180–207, 216–229, 238–265). Similar to that of generalized Hydroporinae larva (Alarie & Harper 1990; Alarie *et al.* 1990; Alarie 1991; Alarie & Michat 2007) except for the following features: anteroventral margin of nasale with 12–14 lamellae clypeales of different lengths and shapes, directed downwards; pore FRc submarginal, contiguous to seta FR7; pores PAd, PAe and PAj absent; pore PAg present; pore ANf absent; pore ANh distal; setae MX4, MX8, MX9 and MX10

absent; seta LA7 absent; seta TR2 absent; pore FEa absent; seta TI7 short, spine-like; pores ABa and ABc absent; seta AB10 spine-like; we were unable to find pore ABd and seta AB8; however, we could not establish if they are really absent due to the presence of spinulae on the siphon; setae UR2, UR3 and UR4 inserted far from each other, or UR2 and UR4 contiguous and far from UR3; setae UR5, UR6 and UR7 elongate; seta UR8 inserted distally.

Instar II (based on both epigean and stygobitic species)

As for instar I except for the following features:

Color. Somewhat darker in general, distal half of mandible sometimes light brown.

Body. Measurements and ratios that characterize the body shape are shown in Tables 5–7.

Head (Figs 27, 85, 107). Cephalic capsule subpentagonal or more or less pyriform; occipital suture absent or present; ecdysial line well visible; egg bursters absent; stemmata present (epigean species) or absent (stygobitic species). Antenna (Figs 1–2). A1 somewhat shorter, subequal or somewhat longer than A4. Mandible (Fig. 5). Distal half more or less narrowed. Maxilla (Figs 3–4). MP1 or MP2 the longest. Labium (Figs 6–7). LP2 longer or shorter than LP1.

Thorax. Meso- and metatergite with anterior transverse carina; sagittal line visible or not. Legs (Figs 28–29, 108–109). Ventral spinulae on proTA absent.

Abdomen (Figs 30, 110). Segment VII completely sclerotized, ring-like; sclerites I–VIII with anterior transverse carina. Urogomphus (Figs 30, 110). U2 longer, subequal or shorter than U1.

Chaetotaxy. Head capsule with numerous secondary setae; anteroventral margin of nasale with 22–228 lamellae clypeales distributed in 1–4 rows; parietal with a variable number of spine-like secondary setae on each lateroventral margin; MN with one hair-like secondary seta on basoexternal margin; thoracic tergites with numerous secondary setae; secondary leg setation detailed in Tables 13–15; abdominal sclerites I–VIII with several secondary setae on posterior half; U1 with (Figs 30, 110) or without secondary setae.

Instar III (based on both epigean and stygobitic species)

As for instar II except for the following features:

Body. Measurements and ratios that characterize the body shape are shown in Tables 8–12.

Head (Figs 8, 12, 14, 18, 22–23, 45, 63, 67, 69, 73, 77, 81, 103, 111, 129, 176, 208, 212, 230, 234, 266).

Antenna. A3 somewhat shorter, subequal or somewhat longer than A2.

Thorax. Spiracles present on mesothorax.

Abdomen. Spiracles present on segments I–VII.

Chaetotaxy. Secondary setation on cephalic capsule, thoracic and abdominal sclerites more abundant; secondary leg setation detailed in Tables 16–20 and Figs 9–10, 15–16, 19–20, 24–25, 46–47, 64–65, 70–71, 74–75, 78–79, 82–83, 86–87, 104–105, 112–113, 131–132, 177–178, 209–210, 213–214, 231–232, 235–236, 267–268; secondary setation on LAS and U detailed in Figs 11, 13, 17, 21, 26, 48, 66, 68, 72, 76, 80, 84, 88, 106, 114, 133, 179, 211, 215, 233, 237, 269.

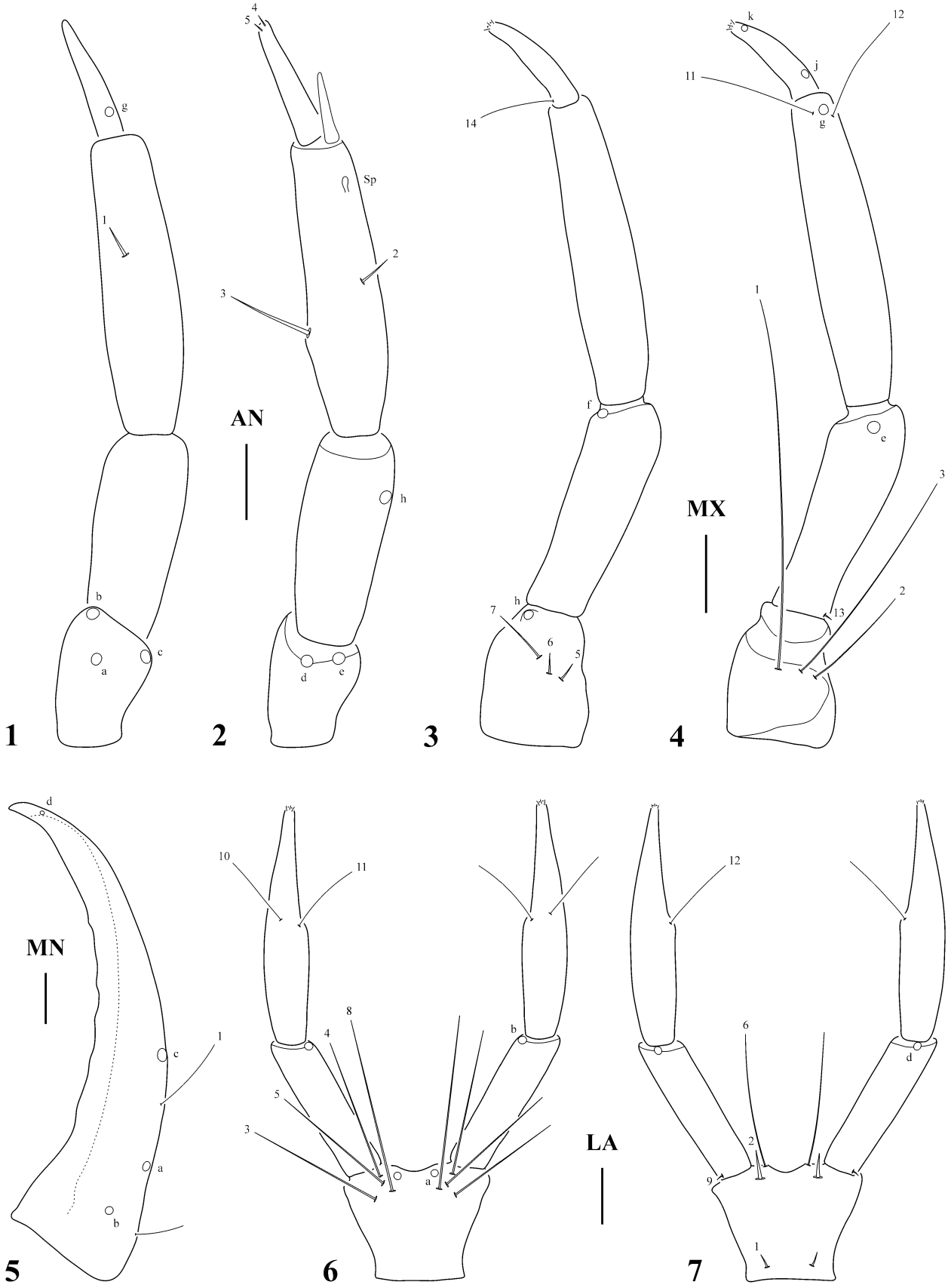
Description of epigean species

Diagnosis. The epigean species of *Limbodessus* can be distinguished from the stygobitic species by the following characters: stemmata present (instars II–III); two rows of secondary hair-like setae present on ventral surface of PA (instars II–III) (Fig. 23); anterior secondary setae on metaCO present (instar III); mesoCO with more than 11 secondary setae (instar III); CL(L3) more than 0.45 times as long as TA (instar III).

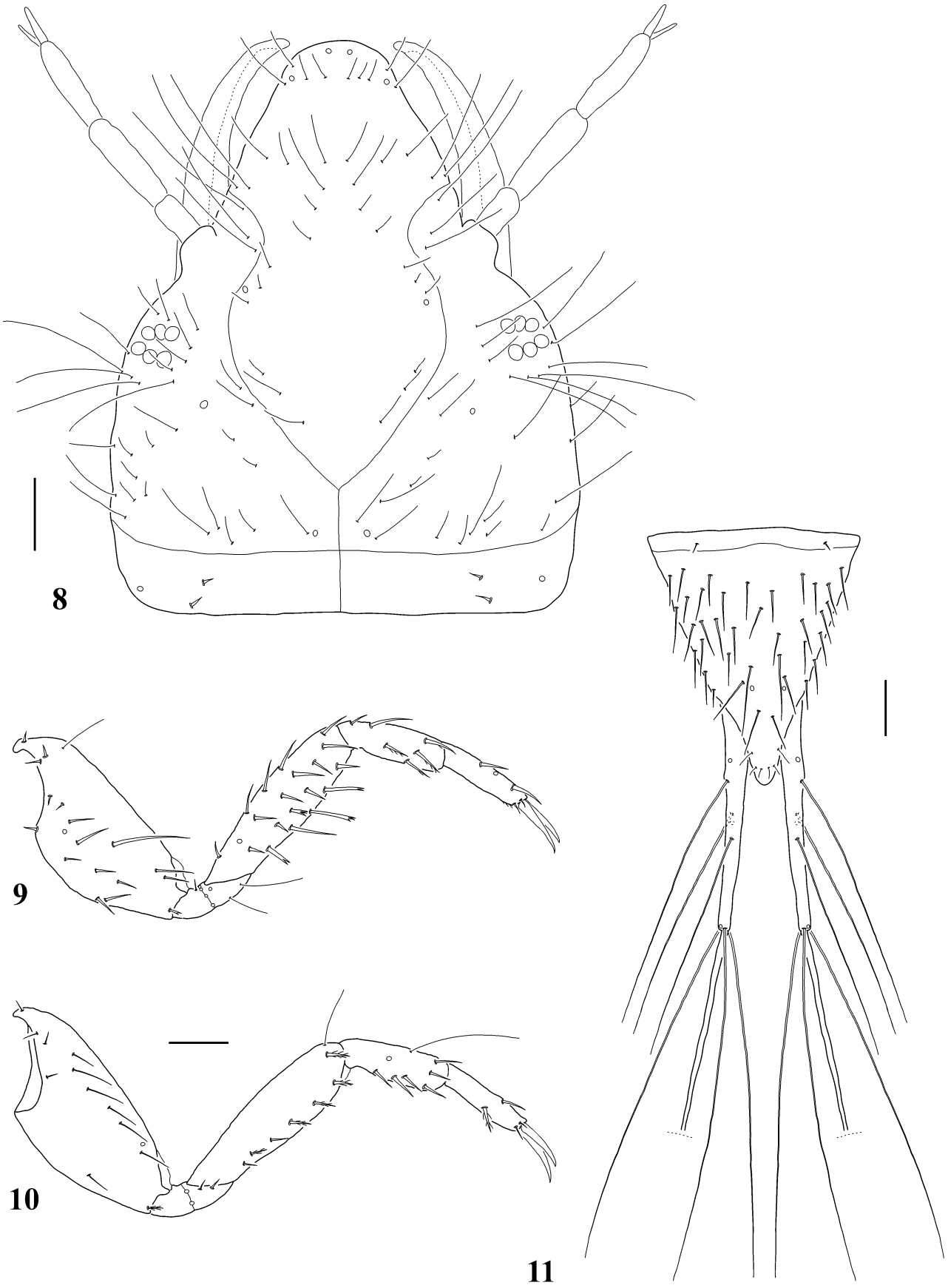
Limbodessus amabilis (Clark, 1862)

(Figs 1–11)

Source of material. Three specimens of instar II and two of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **South Australia**, 1 km S Nangwarry, 5–X–2000 and 22–IX–2007, coll. C. H. S. Watts; 10 km N Forrestown, 1–IX–2002, coll. C. H. S. Watts.



FIGURES 1–7. *Limbodessus amabilis*, second-instar larva. 1, right antenna, dorsal aspect; 2, left antenna, ventral aspect; 3, right maxilla, dorsal aspect; 4, left maxilla, ventral aspect; 5, right mandible, dorsal aspect; 6, labium, dorsal aspect; 7, labium, ventral aspect. Sp, spinula. Scale bars = 0.03 mm.



FIGURES 8–11. *Limbodessus amabilis*, third-instar larva. 8, head, dorsal aspect; 9, left prothoracic leg, anterior aspect; 10, right prothoracic leg, posterior aspect; 11, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 8) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present (Fig. 2); distal half of MN broad (Fig. 5); setae LA3, LA4, LA5 and LA8 hair-like (Fig. 6); secondary setae on U absent (Fig. 11).

Instar I. Not available.

Instar II (Figs 1–7). Head. A3 more than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) more than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U more than 2.25 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 25 lamellae clypeales distributed in a single row; anterior secondary setae on proCO present; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with more than 11 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTI present; anteroventral and posterodorsal secondary setae on proTI absent; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on pro- meso- and metaTI present; metaTI with more than 5 secondary setae; anterodorsal secondary setae on proTA present; anteroventral secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA absent; posteroventral secondary setae on pro-, meso- and metaTA present; metaTA with more than 5 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 5. Secondary leg setation detailed in Table 13.

Instar III (Figs 8–11). Head (Fig. 8). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 9–10). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 11). Chaetotaxy. Anteroventral margin of nasale with 50 lamellae clypeales distributed in 2 rows; proCO with 1–4 anterior secondary setae; mesoCO with 1–5 anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with 12–15 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal and anteroventral secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI absent; metaTI with less than 16 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTA present; anteroventral secondary setae on pro- and mesoTA absent; anteroventral secondary setae on metaTA present; posterodorsal secondary setae on pro-, meso- and metaTA absent; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 8. Secondary leg setation detailed in Table 16.

Remarks. All the instar III specimens of *L. amabilis* examined had the second urogomphomere broken, which prevented the evaluation of urogomphal morphometry. This species belongs to the epigean *Limbodessus* characterized by the absence of secondary setae on the urogomphus (*L. compactus*, *L. shuckardii*) (Fig. 11). Within this group, *L. amabilis* can be distinguished by its larger size, the presence of anterodorsal secondary setae on the tarsus (Fig. 9), and the absence of posterodorsal secondary setae on the meso- and metatarsus. The larva of *L. amabilis* was previously described by Watts (1963) (as *Liodessus amabilis*).

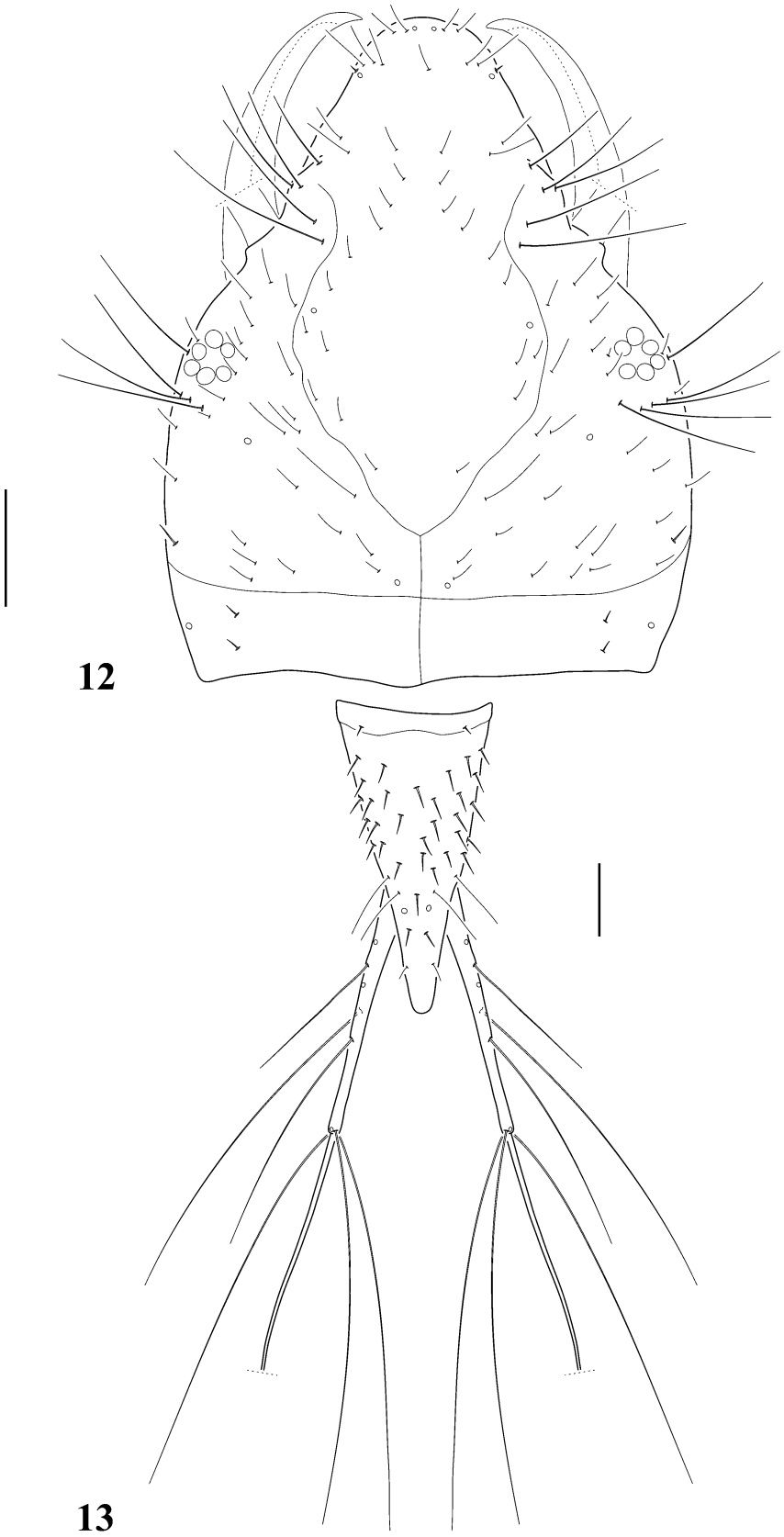
Limbodessus compactus (Clark, 1862)

(Figs 12–13)

Source of material. Two specimens of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following locality: **Australia, NSW**, 2 km N Batemans Bay, 2–XI–1997, coll. C. H. S. Watts.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 12) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender

spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; distal half of mandible broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 13).



FIGURES 12–13. *Limbodessus compactus*, third-instar larva. 12, head, dorsal aspect; 13, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Instar I. Not available.

Instar II. Not available.

Instar III (Figs 12–13). Head (Fig. 12). MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Abdomen (Fig. 13). Chaetotaxy. Anteroventral margin of nasale with 49 lamellae clypeales distributed in 2 rows; proCO without posterior secondary setae; proCO with less than 11 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 8.

Remarks. The description of *L. compactus* is based on two badly preserved instar III specimens which had the antennae, legs (except the coxae) and second urogomphomeres broken. For this reason, several morphometric and chaetotaxic characters could not be evaluated (the leg chaetotaxic characters would provide some good characters to distinguish this species from the others). *Limbodessus compactus* belongs to the epigean species characterized by the absence of secondary setae on the urogomphus (*L. amabilis*, *L. shuckardii*) (Fig. 13), and within this group it is characterized by its smaller size and by some of the morphometric measures given in the Table 8.

Limbodessus inornatus (Sharp, 1882)

(Figs 14–17)

Source of material. Three specimens of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following locality: **Western Australia**, Midland, Perth, 14–XI–2000, coll. C. H. S. Watts.

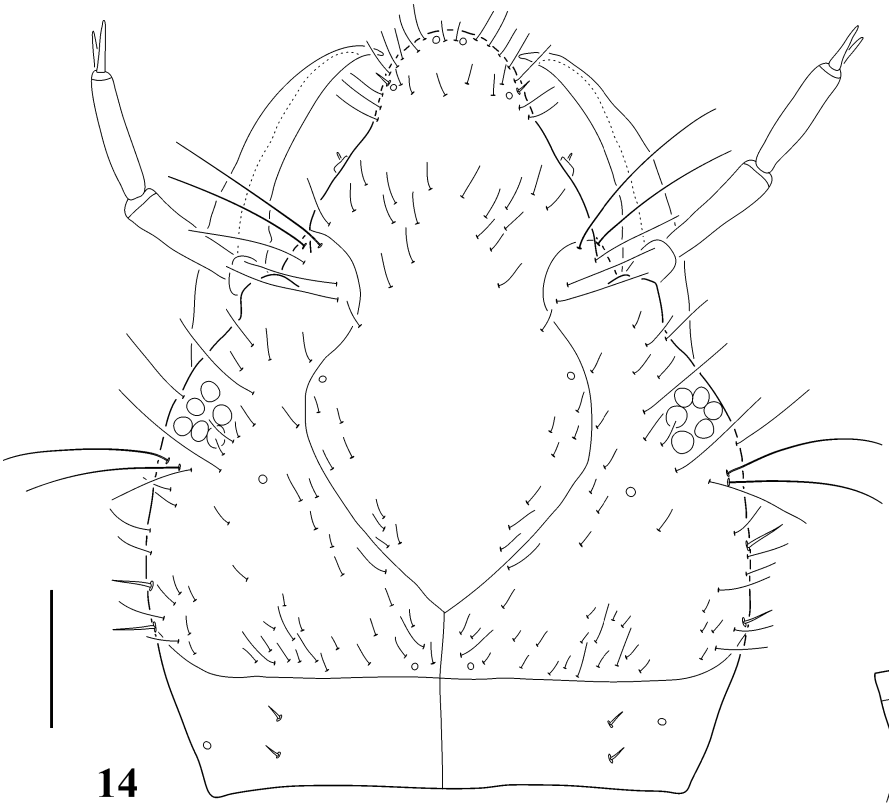
Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 14) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 robust; secondary setae on U present (Fig. 17).

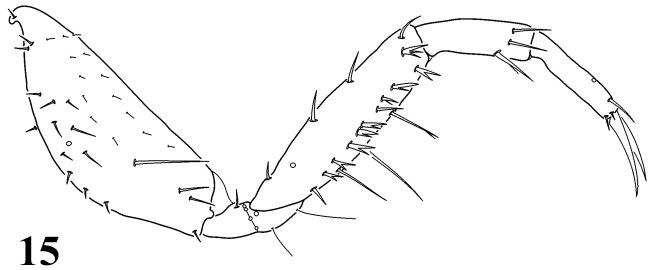
Instar I. Not available.

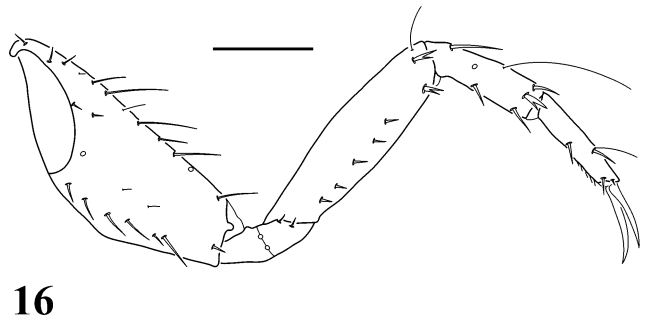
Instar II. Not available.

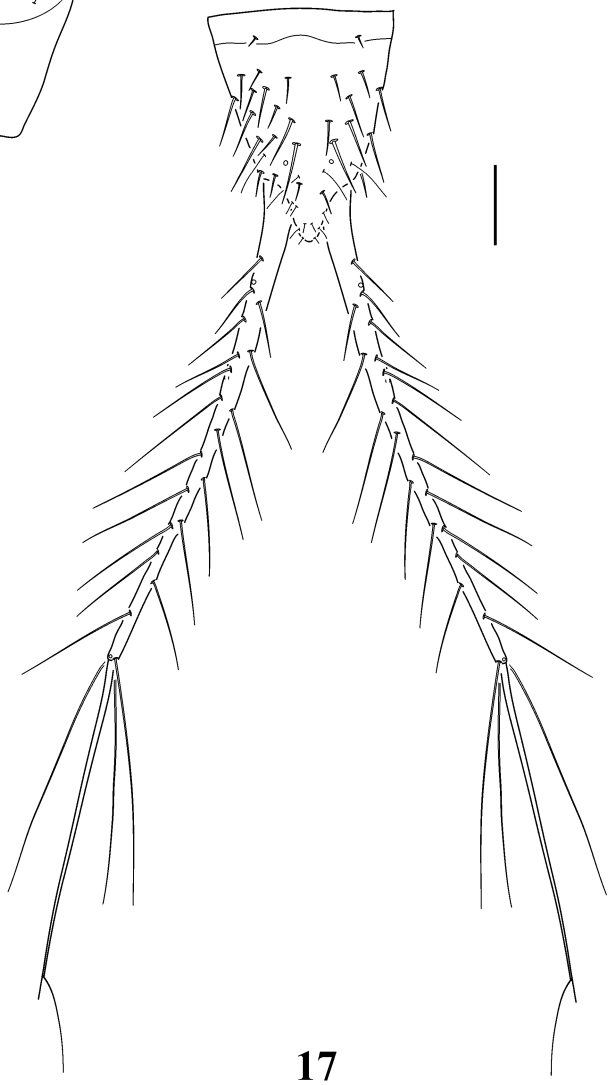
Instar III (Figs 14–17). Head (Fig. 14). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 15–16). L3 more than 2.85 times longer than HW. Abdomen (Fig. 17). U more than 3.10 times longer than LAS; U more than 2.30 times longer than HW; U1 1.80–2.60 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 50 lamellae clypeales distributed in 2 rows; proCO with more than 7 anterior secondary setae; mesoCO with more than 9 anterior secondary setae; proCO with more than 2 posterior secondary setae; mesoCO with more than 13 posterior secondary setae; metaCO with more than 17 posterior secondary setae; proCO with more than 21 secondary setae; metaCO with more than 44 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal and anteroventral secondary setae on proTI absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI present; metaTI with less than 16 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTA absent; anteroventral and posterodorsal secondary setae on proTA absent; anteroventral secondary setae on meso- and metaTA present; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 10. Secondary leg setation detailed in Table 18.

Remarks. Within the group of epigean species, *L. inornatus* is more similar to *L. praelargus*, both taxa sharing the presence of secondary setae on the urogomphus (Fig. 17). *Limbodessus inornatus* differs from *L. praelargus* in its longer legs and urogomphus and in the presence of more than 50 secondary setae on the metacoxa.

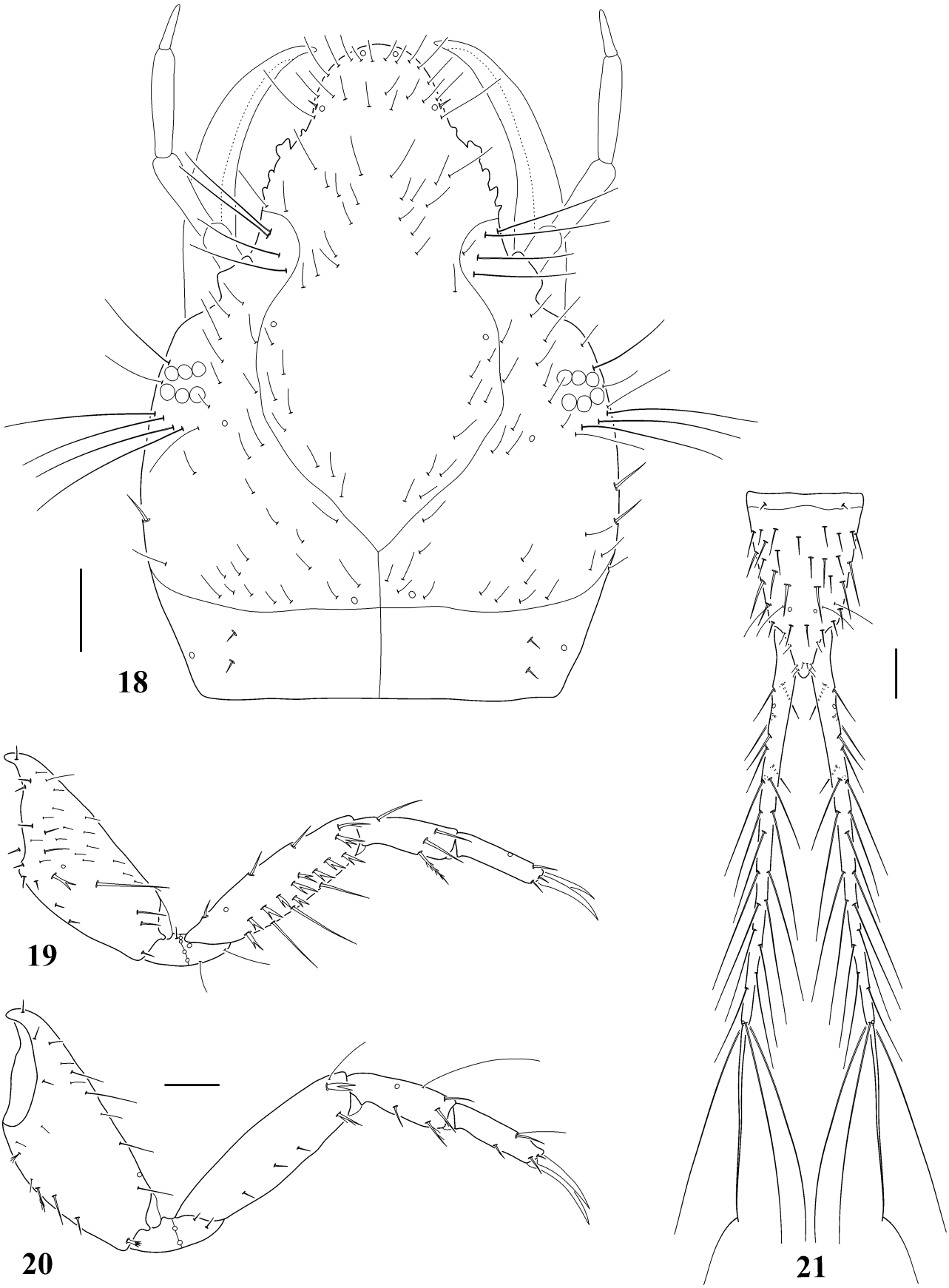








FIGURES 14–17. *Limbodessus inornatus*, third-instar larva. 14, head, dorsal aspect; 15, left prothoracic leg, anterior aspect; 16, right prothoracic leg, posterior aspect; 17, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.15 mm.



FIGURES 18–21. *Limbodessus praelargus*, third-instar larva. 18, head, dorsal aspect; 19, left prothoracic leg, anterior aspect; 20, right prothoracic leg, posterior aspect; 21, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

***Limbodessus praelargus* (Lea, 1899)**
(Figs 18–21)

Source of material. One specimen of instar III was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia**, 18 km W Casterton, Vic, 29–VIII–1999, coll. C. H. S. Watts.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 18) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 robust; secondary setae on U present (Fig. 21).

Instar I. Not available.

Instar II. Not available.

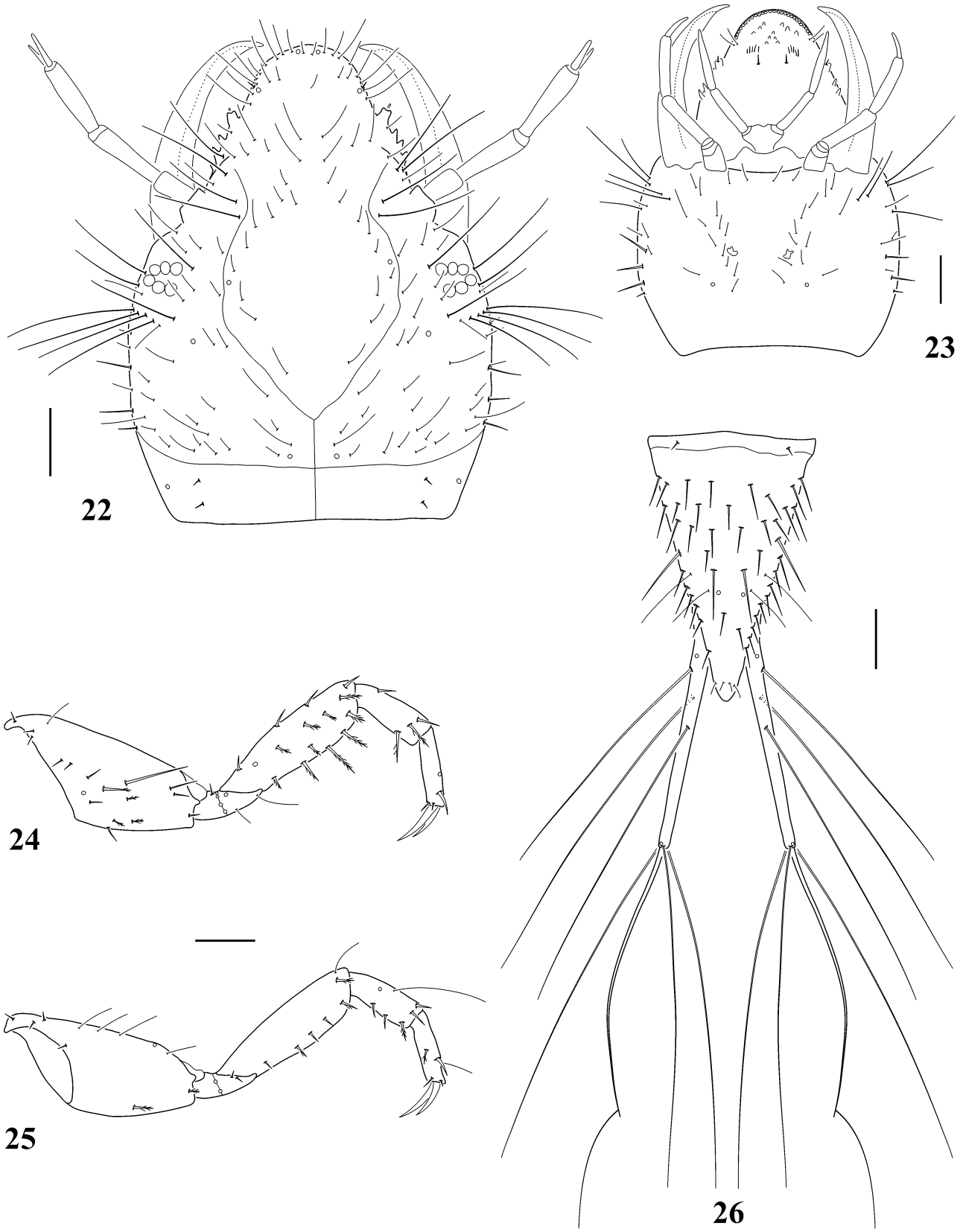
Instar III (Figs 18–21). Head (Fig. 18). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 19–20). L3 more than 2.85 times longer than HW. Abdomen (Fig. 21). U more than 3.10 times longer than LAS; U more than 2.30 times longer than HW; U1 1.80–2.60 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 49 lamellae clypeales distributed in 2 rows; proCO with more than 7 anterior secondary setae; mesoCO with more than 9 anterior secondary setae; proCO with 1 posterior secondary setae; mesoCO with 11 posterior secondary setae; metaCO with 13 posterior secondary setae; proCO with more than 21 secondary setae; metaCO with more than 44 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI present; anteroventral secondary setae on proTI absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI absent; metaTI with less than 16 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTA absent; anteroventral and posterodorsal secondary setae on proTA absent; anteroventral secondary setae on meso- and metaTA present; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 11. Secondary leg setation detailed in Table 19.

Remarks. Within the group of epigean species, *L. praelargus* is more similar to *L. inornatus*, both taxa sharing the presence of secondary setae on the urogomphus (Fig. 21). *Limbodessus praelargus* differs from *L. inornatus* in its shorter legs and urogomphus and in the presence of less than 50 secondary setae on the metacoxa.

***Limbodessus shuckardii* (Clark, 1862)**
(Figs 22–26)

Source of material. One specimen of instar II and three of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Western Australia**, Yallingrup, 22-X-1996, coll. C. H. S. Watts; 4 km SW Bunbury, 3-X-2003, coll. C. H. S. Watts.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Figs 22–23) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 26).



FIGURES 22–26. *Limbodessus shuckardii*, third-instar larva. 22, head, dorsal aspect; 23, head, ventral aspect; 24, left prothoracic leg, anterior aspect; 25, right prothoracic leg, posterior aspect; 26, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Instar I. Not available.

Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 more than 1.50 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 more than 3.00 times longer than HW; CL(L3) more than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U more than 2.25 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 25 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on proCO present; ventral secondary setae on mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on pro-, meso- and metaTI present; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal and posteroventral secondary setae on meso- and metaTA present; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 7. Secondary leg setation detailed in Table 15.

Instar III (Figs 22–26). Head (Figs 22–23). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 24–25). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 26). U less than 2.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 48 lamellae clypeales distributed in 2 rows; proCO with 1–4 anterior secondary setae; mesoCO with 1–5 anterior secondary setae; pro-, meso and metaCO without posterior secondary setae; proCO with 12–15 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal and anteroventral secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI absent; metaTI with less than 16 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTA absent; anteroventral secondary setae on proTA absent; anteroventral secondary setae on meso- and metaTA present; posterodorsal secondary setae on pro-, meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 12. Secondary leg setation detailed in Table 20.

Remarks. This species belongs to the epigean *Limbodessus* characterized by the absence of secondary setae on the urogomphus (*L. amabilis*, *L. compactus*) (Fig. 26). Within this group, *L. shuckardii* can be distinguished by its larger size, the absence of anterodorsal secondary setae on the tarsus (Fig. 24), and the presence of posterodorsal secondary setae on the meso- and metatarsus.

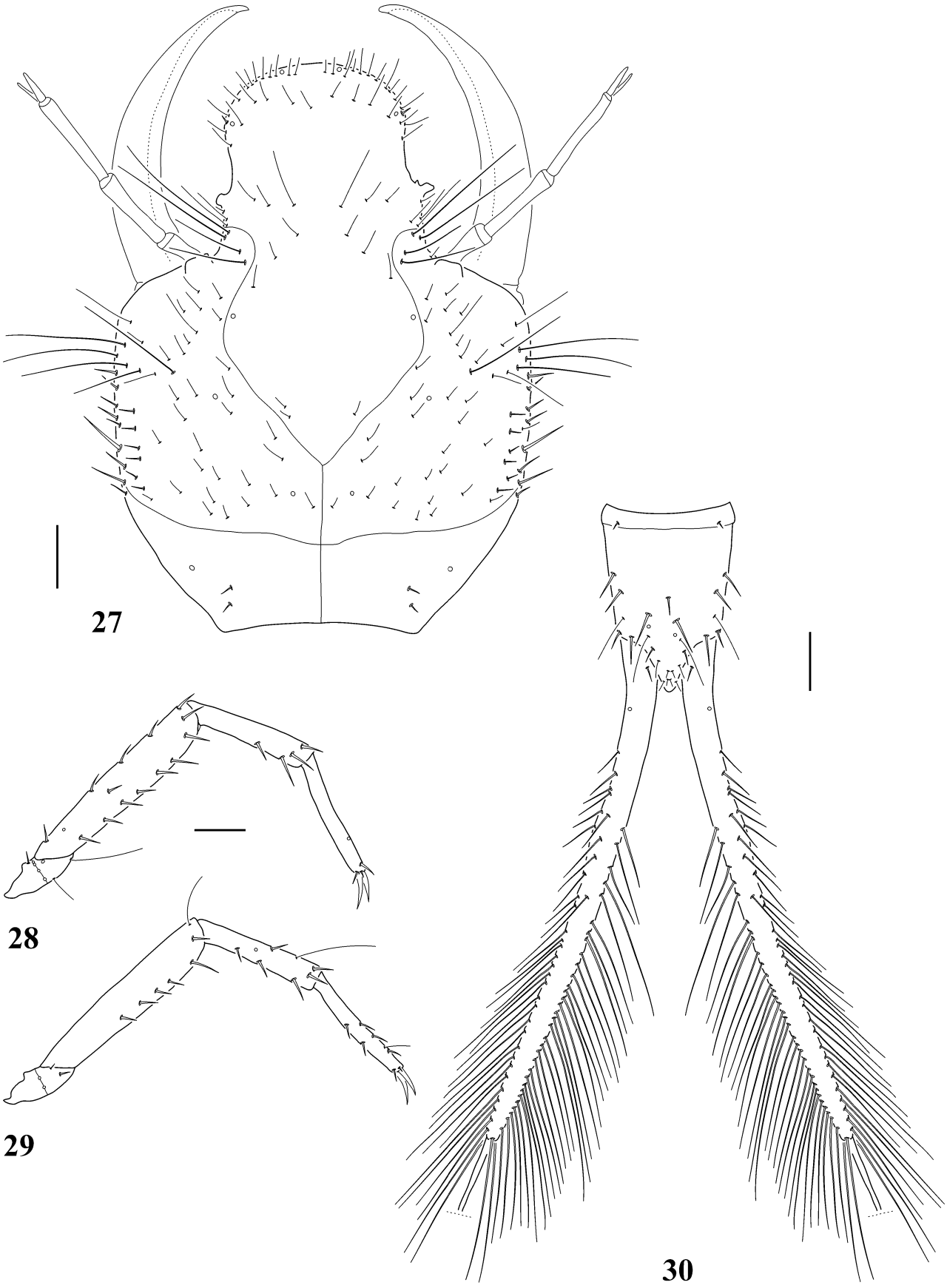
Description of stygobitic species

Diagnosis. The stygobitic species of *Limbodessus* can be distinguished from the epigean species by the following characters: stemmata absent (instars I–III); two rows of secondary hair-like setae on ventral surface of PA absent (instars II–III); anterior secondary setae on metaCO absent (instar III) (present in *L. raesideensis*); mesoCO with less than 11 secondary setae (instar III) (except *L. raesideensis*); CL(L3) less than 0.40 times as long as TA (instar III) (except *L. fridaywellensis*).

Limbodessus barwidgeeensis Watts & Humphreys, 2006

(Figs 27–30)

Source of material. One specimen of instar II was used for the description (Table 1). Larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Barwidgee calcrete, site 144, BES 10367, 27.13760S, 120.94633E, 25–III–2004, coll. W. F. Humphreys and S. J. B. Cooper.



FIGURES 27–30. *Limbodessus barwidgeeensis*, second-instar larva. 27, head, dorsal aspect; 28, left prothoracic leg, anterior aspect; 29, right prothoracic leg, posterior aspect; 30, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.15 mm.

TABLE 8. Measurements and ratios for the third-instar larvae of species of *Limbodessus*.

Measure	*L. amabilis*	*L. bigbellensis*	*L. challaensis*	*L. compactus*	*L. cooperi*
HL (mm)	0.78–0.80	1.35–1.66	0.80	0.56–0.57	1.41
HW (mm)	0.60–0.63	0.99–1.01	0.57	0.43–0.44	1.14
FRL (mm)	0.61–0.62	0.96–0.97	0.62	0.44–0.45	1.14
OCW (mm)	0.44	0.33–0.35	0.39	0.36–0.37	0.57
HL/HW	1.26–1.29	1.36–1.65	1.41	1.30	1.23
HW/OCW	1.37–1.44	2.91–3.03	1.47	1.19–1.20	1.99
COL/HL	0.22	0.24–0.29	0.23	0.22	0.19
FRL/HL	0.78	0.58–0.71	0.77	0.78	0.81
A/HW	–	0.56–0.62	0.63	–	–
A3/A1	1.93	1.58–1.81	1.57	–	1.90
A3/A2	0.96	0.79–0.86	1.00	–	1.18
A4/A3	–	0.32–0.34	0.64	–	–
A3’/A4	–	0.92	1.00	–	–
MNL/MNW	3.85–4.44	4.28–4.31	5.38	3.86–4.00	4.18
MNL/HL	0.48–0.51	0.46–0.56	0.53	0.47–0.50	0.65
A/MP	–	0.83–0.92	0.96	–	–
MP2/MP1	0.97–1.00	0.72–0.76	0.79	1.00	0.96
MP2/MP3	2.64–3.00	3.31–3.33	1.93	2.00–2.44	3.83
MP/LP	1.23–1.27	1.90–1.91	1.34	1.25–1.26	1.94
LP2/LP1	1.19–1.20	0.55–0.56	0.75	1.21–1.22	0.95
L3 (mm)	1.67–1.69	2.90–2.93	1.43	–	2.45
L3/L1	1.30–1.32	1.17–1.20	1.23	–	–
L3/L2	1.17–1.18	1.08–1.10	1.14	–	–
L3/HW	2.63–2.80	2.90–2.93	2.52	–	2.14
L3 (CO/FE)	0.96	0.76–0.81	0.95	–	0.90
L3 (TI/FE)	0.64	0.69–0.70	0.68	–	0.72
L3 (TA/FE)	0.64–0.66	0.74–0.80	0.67	–	0.64
L3 (CL/TA)	0.48–0.49	0.15–0.16	0.31	–	0.28
LAS (mm)	0.46–0.47	0.44–0.48	0.42	0.41–0.45	0.56
LAS/HW	0.73–0.75	0.43–0.48	0.74	0.94–1.01	0.49
U (mm)	–	1.61–1.67	1.07	–	1.47
U/LAS	–	3.39–3.83	2.54	–	2.60
U/HW	–	1.63–1.65	1.88	–	1.28
U1/U2	–	3.43–4.33	0.86	–	0.92

Diagnosis (instar II). Larger species (HL more than 1.05 mm); head (Fig. 27) pyriform; nasale digitiform; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen moderately reduced (HW/OCW 0.80–2.10); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of

parietal numerous; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 robust; secondary setae on U present (Fig. 30).

Instar I. Not available.

Instar II (Figs 27–30). Head (Fig. 27). A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 less than 1.05 times longer than MP1; MP2 more than 3.20 times longer than MP3; LP2 less than 0.90 times as long as LP1. Legs (Figs 28–29). L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen (Fig. 30). Chaetotaxy. Anteroventral margin of nasale with 132 lamellae clypeales distributed in 2–3 rows; anterior secondary setae on proCO absent; meso- and metaCO with more than 5 posterodorsal secondary setae; ventral secondary setae on mesoCO present; proFE with more than 3 posteroventral secondary setae; metaFE with more than 11 secondary setae; anterodorsal secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; anteroventral and posterodorsal secondary setae on proTI present; mesoTI with less than 2 posterodorsal secondary setae; metaTI with more than 2 posterodorsal secondary setae; posteroventral secondary setae on pro-, meso- and metaTI present; metaTI with more than 5 secondary setae; anterodorsal and anteroventral secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on pro-, meso- and metaTA present; metaTA with more than 5 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 5. Secondary leg setation detailed in Table 13.

Instar III. Not available.

Remarks. The description of *L. barwidgeeensis* is based on a single instar II specimen which has the procoxa and the second urogomphomere broken. For this reason, some morphometric and chaetotaxic characters could not be evaluated. The absence of instar III specimens of this species hampers the comparison with the other species described here, particularly regarding some chaetotaxic characters. *Limbodessus barwidgeeensis* belongs to the group of stygobitic species characterized by the presence of secondary setae on the urogomphus (*L. bigbellensis*, *L. cooperi*, *L. eberhardi*, *L. macrohinkleri*, *L. nambiensis*, *L. raesideensis*, *L. yandalensis*) (Fig. 30), and within this group it can be separated by the following combination of characters: head pyriform (Fig. 27), occipital suture present (Fig. 27), occipital foramen moderately reduced (Fig. 27), and labial setae LA3, LA4, LA5 and LA8 more robust.

Limbodessus bigbellensis (Watts & Humphreys, 2000)

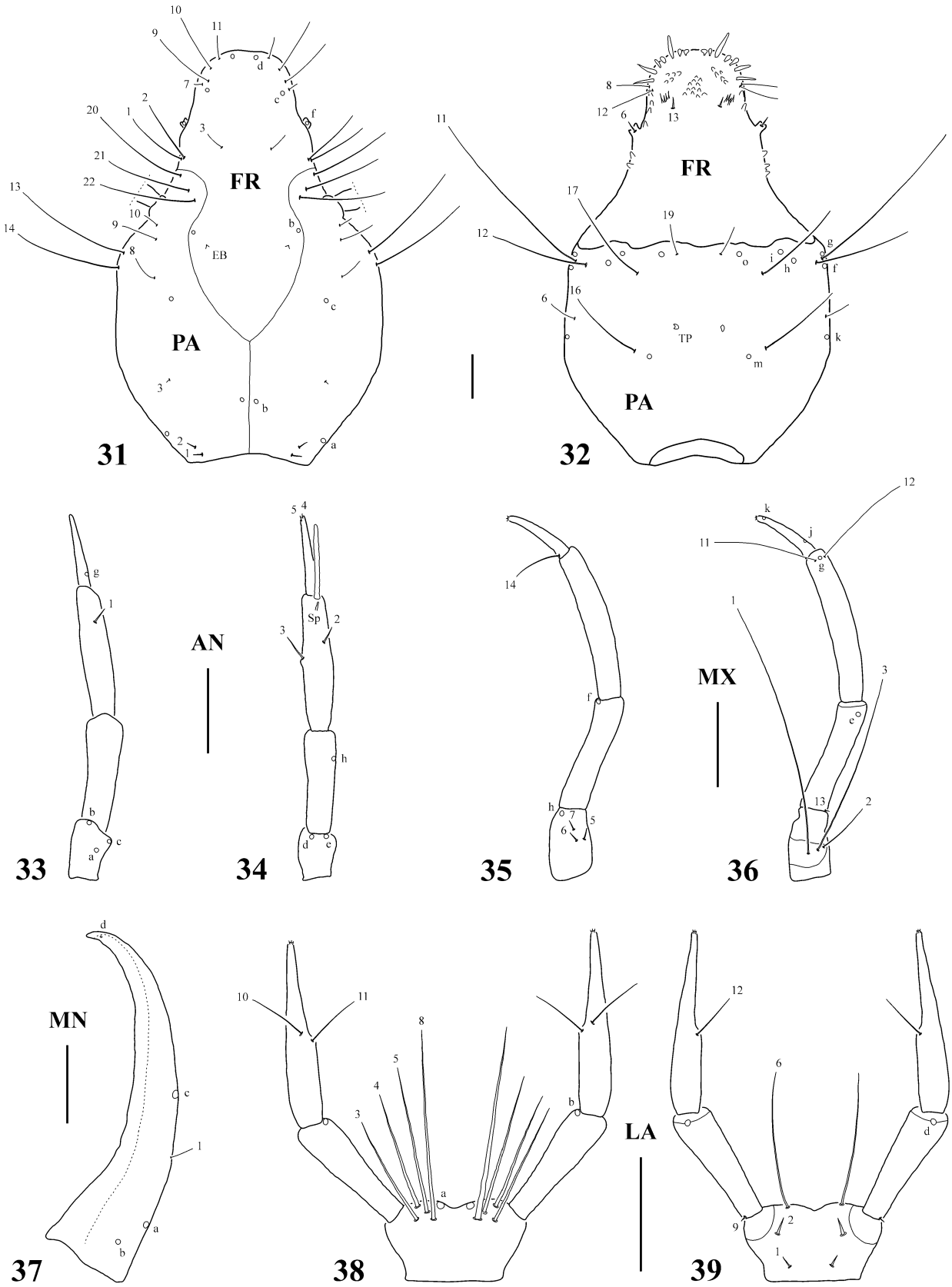
(Figs 31–48)

Source of material. Two specimens of instar I and two of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Murchison palaeovalley**, Austin Downs calcrete, PAT 7, BES 5559, 27.41333S, 117.04444E, 4–V–2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper; Austin Downs calcrete, bore PAT 7, BES 9407, 27.41337S, 117.71122E, 14–VI–2002, coll. W. F. Humphreys and R. Leys.

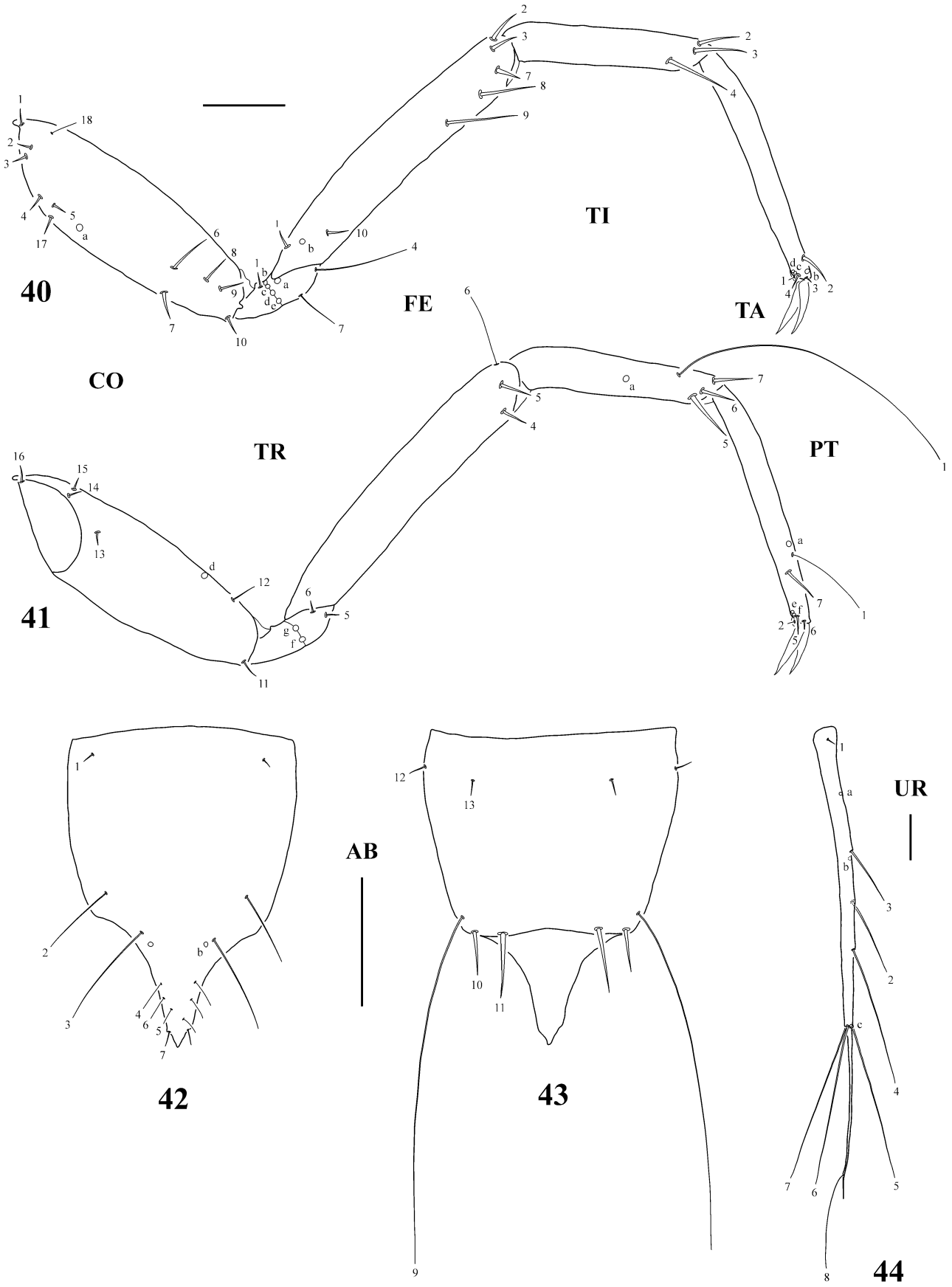
Diagnosis (instar III). Larger species (HL more than 1.25 mm); head (Fig. 45) pyriform; nasale digitiform; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen strongly reduced (HW/OCW more than 2.85); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 robust; secondary setae on U present (Fig. 48).

Instar I (Figs 31–44). Head (Figs 31–39). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 2.20–2.75 times longer than A1; A3 more than 2.25 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 40–41). L3 more than 2.95 times longer than HW. Abdomen (Figs 42–44). U more than 3.75 times longer than LAS; U less than 2.35 times longer than HW; U1 more than 1.45 times longer than U2. Chaetotaxy. Frontoclypeus with 14 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 2.

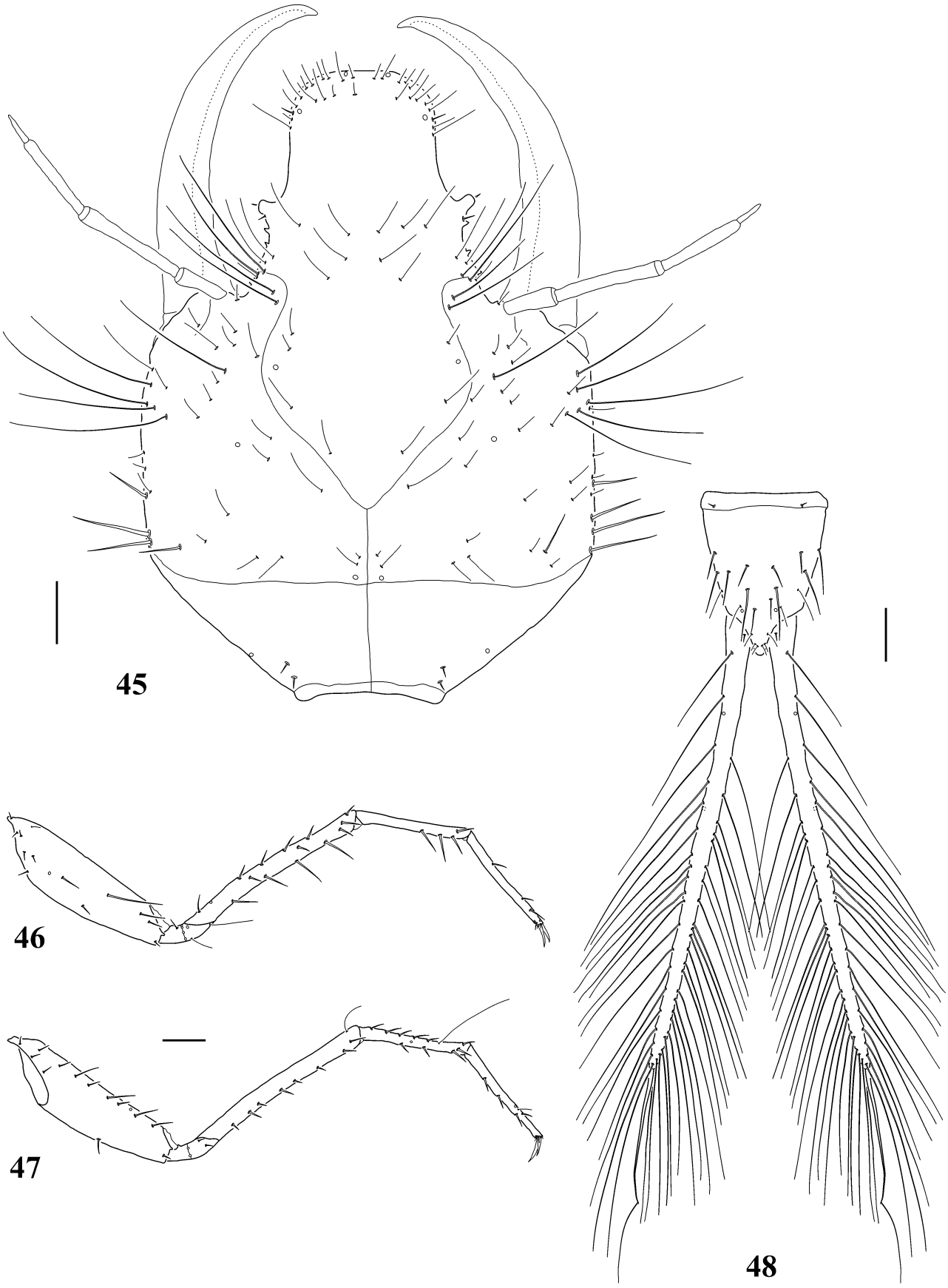
Instar II. Not available.



FIGURES 31–39. *Limbodessus bigbellensis*, first-instar larva. 31, cephalic capsule, dorsal aspect; 32, cephalic capsule, ventral aspect; 33, right antenna, dorsal aspect; 34, left antenna, ventral aspect; 35, right maxilla, dorsal aspect; 36, left maxilla, ventral aspect; 37, right mandible, dorsal aspect; 38, labium, dorsal aspect; 39, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.08 mm.



FIGURES 40–44. *Limbodessus bigbellensis*, first-instar larva. 40, left metathoracic leg, anterior aspect; 41, right metathoracic leg, posterior aspect; 42, abdominal segment VIII, dorsal aspect; 43, abdominal segment VIII, ventral aspect; 44, right urogomphus, dorsal aspect. Scale bars = 0.10 mm.



FIGURES 45–48. *Limbodessus bigbellensis*, third-instar larva. 45, head, dorsal aspect; 46, left prothoracic leg, anterior aspect; 47, right prothoracic leg, posterior aspect; 48, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.15 mm.

Instar III (Figs 45–48). Head (Fig. 45). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP more than 1.75 times longer than labial palpus; MP2 3.20–4.00 times longer than MP3; LP2 less than 0.60 times as long as LP1. Legs (Figs 46–47). L3 more than 2.85 times longer than HW. Abdomen (Fig. 48). U more than 3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 more than 3.35 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 61 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; anterodorsal secondary setae on proTA present; anterodorsal secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on proTA absent; anteroventral secondary setae on meso- and metaTA present; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with more than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 8. Secondary leg setation detailed in Table 16.

Remarks. *Limbodessus bigbellensis* belongs to the group of stygobitic species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis*, *L. cooperi*, *L. eberhardi*, *L. macrohinkleri*, *L. nambiensis*, *L. raesideensis*, *L. yandalensis*) (Fig. 48). Within this group, it can be distinguished by the following combination of characters: head pyriform (Fig. 45), occipital suture present (Fig. 45), occipital foramen strongly reduced (Fig. 45), absence of anterior secondary setae on the procoxa (Fig. 46), absence of posterodorsal secondary setae on the meso- and metafemur, and presence of anterodorsal secondary setae on the protarsus (Fig. 46).

Limbodessus challaensis (Watts & Humphreys, 2001)

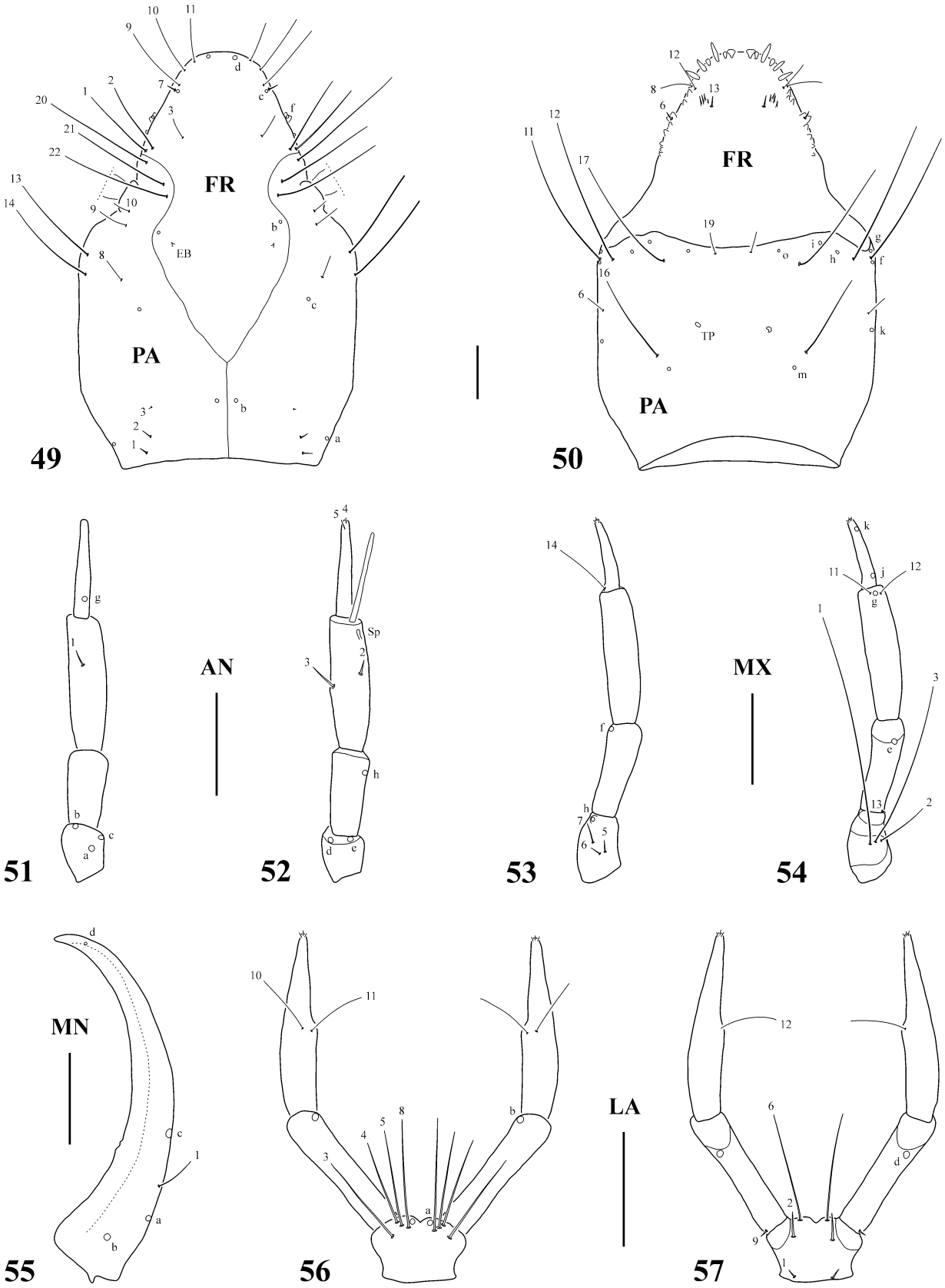
(Figs 49–66)

Source of material. One specimen of instar I and one of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Murchison palaeovalley**, Challa North calcrete, Nyung Well, BES 7251, 27.98833S, 118.5175E, 3–V–2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper; Challa North calcrete, Nyung Well, BES 10386, 27.98842S, 118.51750E, 25–III–2004, coll. W. F. Humphreys and S. J. B. Cooper.

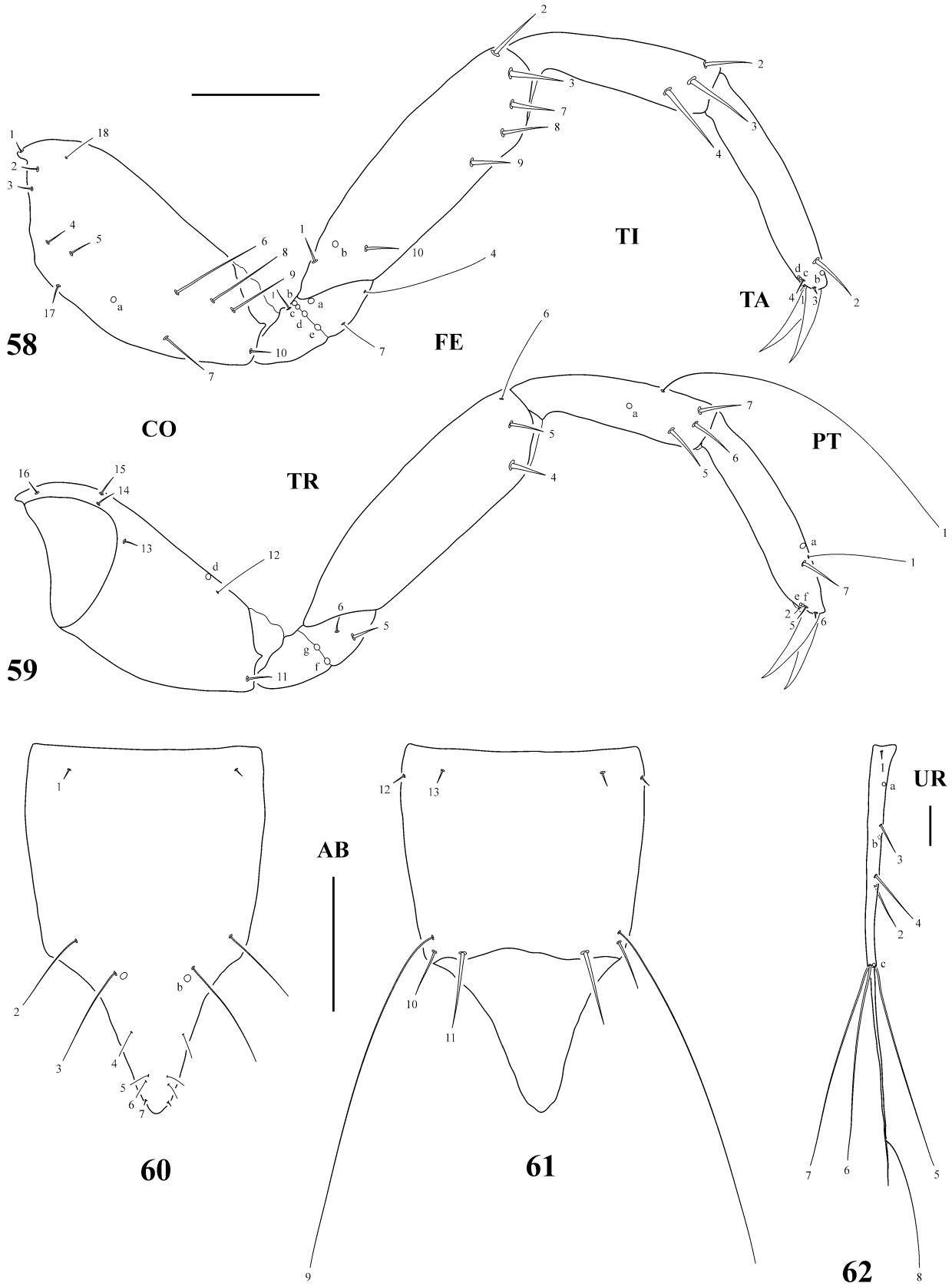
Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 63) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 66).

Instar I (Figs 49–62). Head (Figs 49–57). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted contiguous to setae PA1 and PA2; A3 more than 2.80 times longer than A1; A3 more than 2.25 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 less than 1.85 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 58–59). L3 less than 2.85 times longer than HW. Abdomen (Figs 60–62). U more than 3.75 times longer than LAS; U more than 2.45 times longer than HW; U1 less than 1.05 times longer than U2. Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 2.

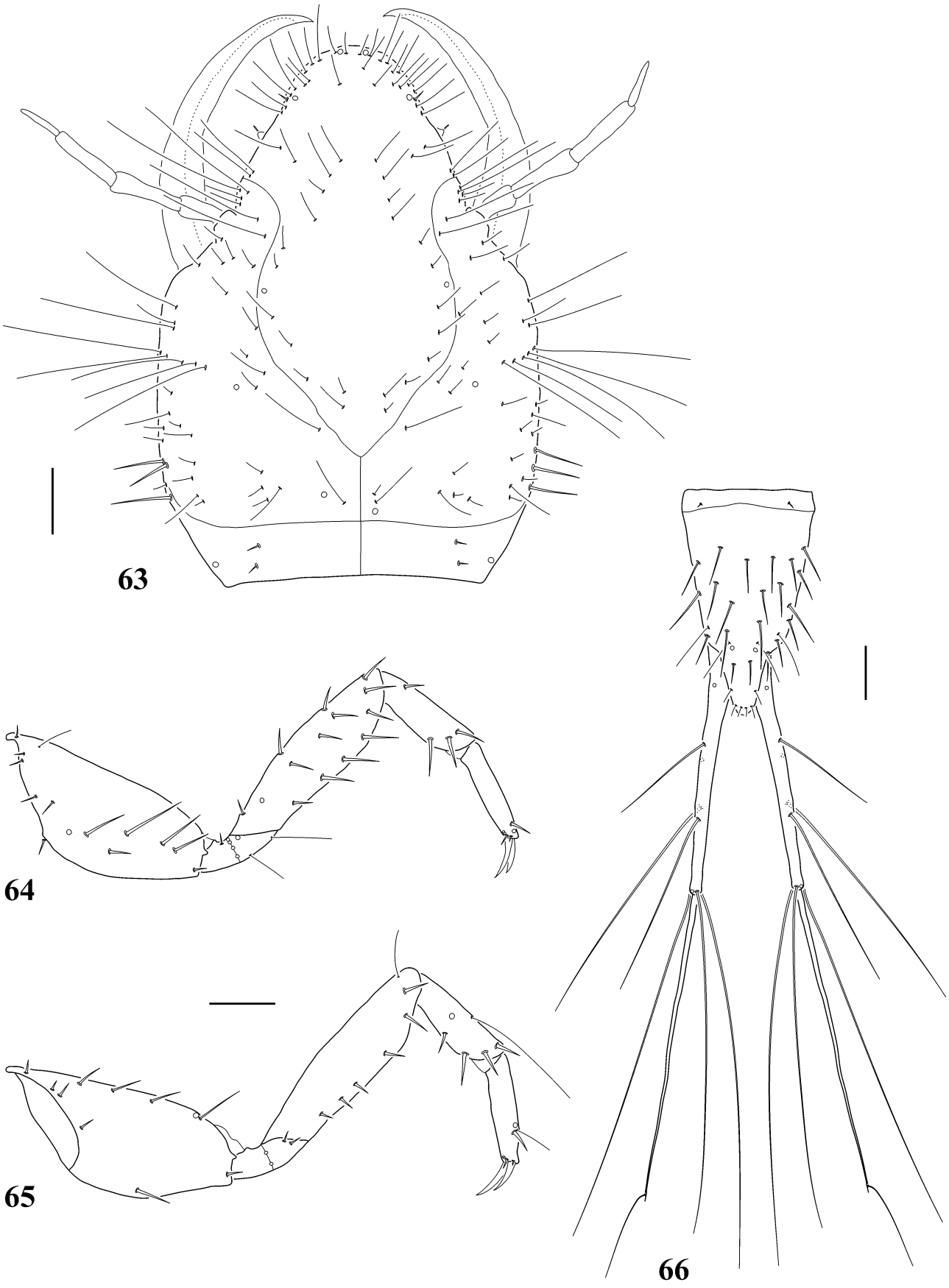
Instar II. Not available.



FIGURES 49–57. *Limbodessus challaensis*, first-instar larva. 49, cephalic capsule, dorsal aspect; 50, cephalic capsule, ventral aspect; 51, right antenna, dorsal aspect; 52, left antenna, ventral aspect; 53, right maxilla, dorsal aspect; 54, left maxilla, ventral aspect; 55, right mandible, dorsal aspect; 56, labium, dorsal aspect; 57, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.06 mm.



FIGURES 58–62. *Limbodessus challaensis*, first-instar larva. 58, left metathoracic leg, anterior aspect; 59, right metathoracic leg, posterior aspect; 60, abdominal segment VIII, dorsal aspect; 61, abdominal segment VIII, ventral aspect; 62, right urogomphus, dorsal aspect. Scale bars = 0.07 mm.



FIGURES 63–66. *Limbodessus challaensis*, third-instar larva. 63, head, dorsal aspect; 64, left prothoracic leg, anterior aspect; 65, right prothoracic leg, posterior aspect; 66, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Instar III (Figs 63–66). Head (Fig. 63). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN more than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 less than 2.00 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 64–65). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 66). U 2.40–3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 51 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI present; anteroventral and posterodorsal secondary setae on proTI absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal and posteroventral secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 8. Secondary leg setation detailed in Table 16.

Remarks. *Limbodessus challaensis* belongs to the group of stygobitic species characterized by the absence of secondary setae on the urogomphus (*L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 66). Larvae of *L. challaensis* can be distinguished from any other species of that group by the following combination of characters: lateral margins of the nasale not inflated in dorsal view (Fig. 63), mandible more than five times longer than broad, metacoxa with 1 secondary seta, presence of anterodorsal secondary setae on the protibia (Fig. 64), absence of anteroventral secondary setae on the protibia (Fig. 64), absence of secondary setae on the protarsus (Figs 64–65), presence of anteroventral secondary setae on the mesotarsus, and absence of posteroventral secondary setae on the tarsus (Fig. 65).

Limbodessus cooperi Watts & Humphreys, 2006

(Figs 67–68)

Source of material. One specimen of instar III was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Mt Morgan calcrete, Mt Weld Station, PB5, BES 10584, 28.73174S, 122.15704E, 30–IX–2004, coll. W. F. Humphreys and S. J. B. Cooper.

Diagnosis (instar III). Larger species (HL more than 1.25 mm); head (Fig. 67) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen moderately reduced (HW/OCW 1.95–2.50); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal numerous; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U present (Fig. 68).

Instar I. Not available.

Instar II. Not available.

Instar III (Figs 67–68). Head (Fig. 67). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP more than 1.75 times longer than labial palpus; MP2 3.20–4.00 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs. L3 less than 2.20 times longer than HW. Abdomen (Fig. 68). U 2.40–3.10 times longer than LAS; U less than 1.35 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 95 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with more than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with more than 30 secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with more than 18 secondary setae; anterodorsal and posterodorsal secondary setae on meso- and metaTA present; anteroventral secondary setae on metaTA present; metaTA with 1–5 posteroventral secondary setae; metaTA with less than 16 secondary setae; secondary setae on U

present. Measurements and ratios that characterize the body shape are shown in Table 8. Secondary leg setation detailed in Table 16.

Remarks. The description of *L. cooperi* provided in this paper is based on a single specimen, which has the fourth antennomere broken and both the pro- and mesothoracic legs broken at the level of femur. For this reason, some morphometric and chaetotaxic characters could not be evaluated. This species is included in the group of stygobitic species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis*, *L. bigbellensis*, *L. eberhardi*, *L. macrohinkleri*, *L. nambiensis*, *L. raesideensis*, *L. yandalensis*) (Fig. 68). Within the group, *L. cooperi* is distinguished by the following combination of characters: head subpentagonal (Fig. 67), occipital suture present (Fig. 67), occipital foramen moderately reduced (Fig. 67), absence of anterior secondary setae on the procoxa, absence of posterodorsal secondary setae on the meso- and metafemur, and presence of anterodorsal secondary setae on the metatarsus. The nasale in *L. cooperi* is more triangular than in other presumably closely related species.

Limbodessus eberhardi (Watts & Humphreys, 1999)

(Figs 69–72)

Source of material. One specimen of instar III was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Paroo calcrete, GSWA6 (north), BES 12916, 26.43389S, 119.77722E, 8–IV–2005, coll. W. F. Humphreys and R. Leys.

Diagnosis (instar III). Larger species (HL more than 1.25 mm); head (Fig. 69) pyriform; nasale digitiform; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 numerous (25 or more); occipital foramen moderately reduced (HW/OCW 1.95–2.50); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U present (Watts & Humphreys 1999).

Instar I. Not available.

Instar II. Not available.

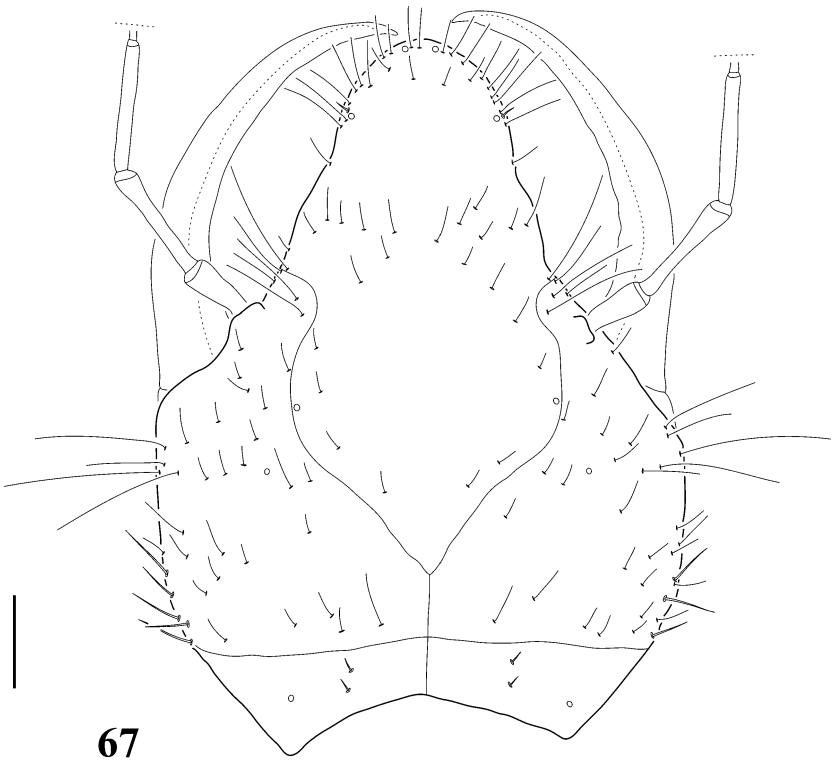
Instar III (Figs 69–72). Head (Fig. 69). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN more than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 more than 4.30 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 70–71). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 72). Chaetotaxy. Anteroventral margin of nasale with about 130 lamellae clypeales distributed in 3 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI present; mesoTI with more than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; anterodorsal secondary setae on proTA absent; anterodorsal secondary setae on meso- and metaTA present; anteroventral secondary setae on pro-, meso- and metaTA present; posterodorsal secondary setae on pro-, meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with more than 7 secondary setae; metaTA with more than 18 secondary setae; secondary setae on U present (Watts & Humphreys 1999). Measurements and ratios that characterize the body shape are shown in Table 9. Secondary leg setation detailed in Table 16.

Remarks. The description of this species was based on a single specimen (with the urogomphi broken at base) from Paroo calcrete, the same locality as the specimen described by Watts and Humphreys (1999) as “Larva form 1”. Based on similarity between the drawings in Watts and Humphreys (1999) and those in the present paper, it is likely that the specimen described as “Larva form 1” is in fact *L. eberhardi*. This species is included in the group of stygobitic species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis*, *L. bigbellensis*, *L. cooperi*, *L. macrohinkleri*, *L. nambiensis*, *L. raesideensis*, *L. yandalensis*), from which it can be distinguished by the following combination of characters: head pyriform (Fig. 69), occipital suture present (Fig. 69), occipital foramen strongly reduced (Fig. 69), absence of anterior secondary setae on the procoxa (Fig. 70),

absence of posterodorsal secondary setae on the meso- and metafemur, femur with less than 20 secondary setae, presence of anterodorsal secondary setae on the protibia (Fig. 70), and absence of anterodorsal secondary setae on the protarsus (Fig. 70). A drawing of the habitus of *L. eberhardi* was presented by Watts & Humphreys (1999).

TABLE 9. Measurements and ratios for the third-instar larvae of species of *Limbodessus*.

Measure	*L. eberhardi*	*L. exilis*	*L. fridaywellensis*	*L. hillviewensis*	*L. hinkleri*
HL (mm)	1.41	1.05–1.06	0.45	0.70	–
HW (mm)	0.88	0.73–0.74	0.31	0.50	–
FRL (mm)	1.06	0.79–0.80	0.34	0.55	–
OCW (mm)	0.37	0.41–0.42	0.24	0.36	–
HL/HW	1.61	1.42–1.45	1.44	1.39	–
HW/OCW	2.39	1.77–1.78	1.31	1.42	–
COL/HL	0.25	0.25	0.24	0.22	–
FRL/HL	0.75	0.75	0.76	0.78	–
A/HW	0.69	0.66–0.68	0.67	0.68	–
A3/A1	2.05	1.60–1.63	1.88	2.17	–
A3/A2	1.15	0.91–0.94	1.50	1.30	–
A4/A3	0.38	0.44–0.45	0.60	0.42	–
A3’/A4	0.94	1.71–1.79	0.89	0.91	–
MNL/MNW	5.23	4.50–4.73	4.60	4.31	4.07
MNL/HL	0.55	0.55–0.58	0.51	0.49	–
A/MP	0.89	0.88–0.93	1.00	1.05	–
MP2/MP1	0.84	0.71–0.73	1.13	0.90	1.00
MP2/MP3	4.38	2.50–2.79	2.25	2.36	2.50
MP/LP	1.70	1.61–1.63	1.40	1.38	1.55
LP2/LP1	0.69	0.74–0.76	1.00	1.00	1.07
L3 (mm)	2.41	1.87	0.75	1.23	–
L3/L1	1.25	1.25–1.27	1.18	1.24	–
L3/L2	1.13	1.12–1.13	1.10	1.12	–
L3/HW	2.75	2.53–2.55	2.40	2.43	–
L3 (CO/FE)	0.88	0.81	1.08	0.98	–
L3 (TI/FE)	0.68	0.66–0.67	0.70	0.71	–
L3 (TA/FE)	0.75	0.66–0.67	0.73	0.69	–
L3 (CL/TA)	0.20	0.28–0.29	0.47	0.39	–
LAS (mm)	0.44	0.43–0.45	0.23	0.34	0.27
LAS/HW	0.50	0.58–0.61	0.75	0.67	–
U (mm)	–	–	0.73	–	–
U/LAS	–	–	3.15	–	–
U/HW	–	–	2.35	–	–
U1/U2	–	–	0.54	–	–



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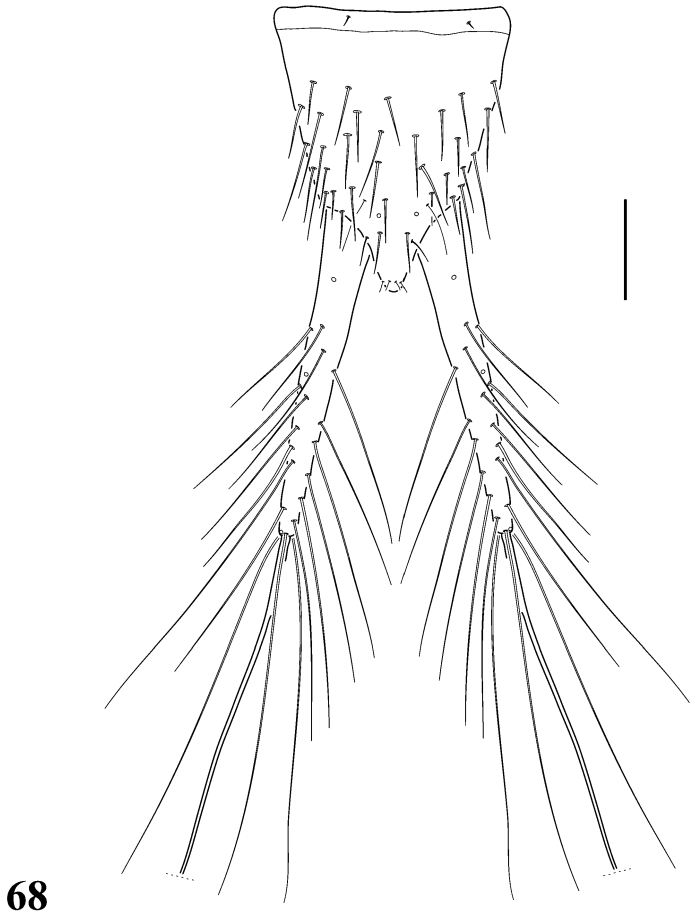
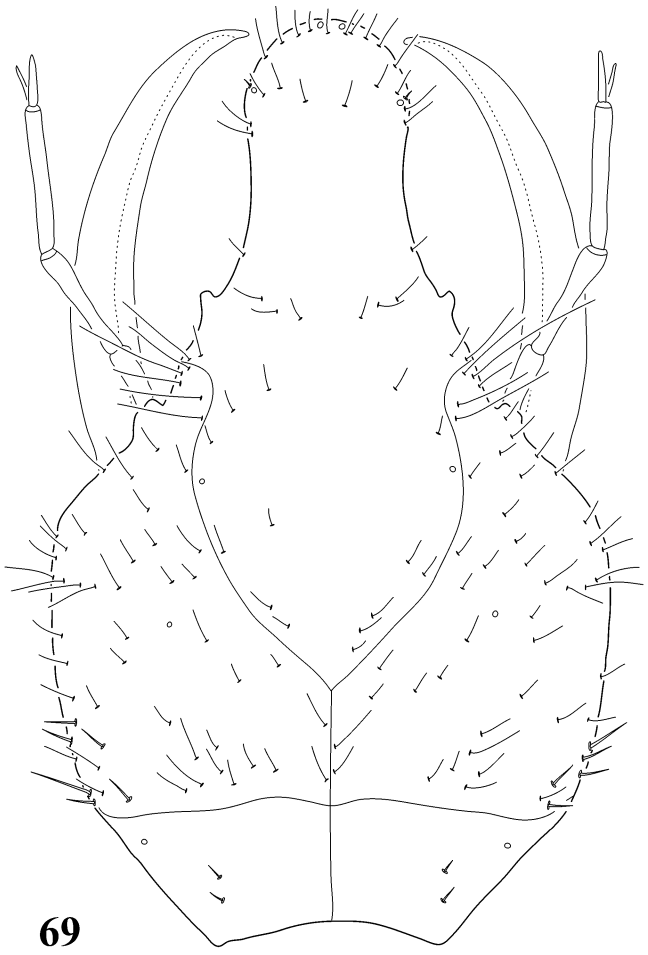


68

FIGURES 67–68. *Limbodessus cooperi*, third-instar larva. 67, head, dorsal aspect; 68, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.20 mm.



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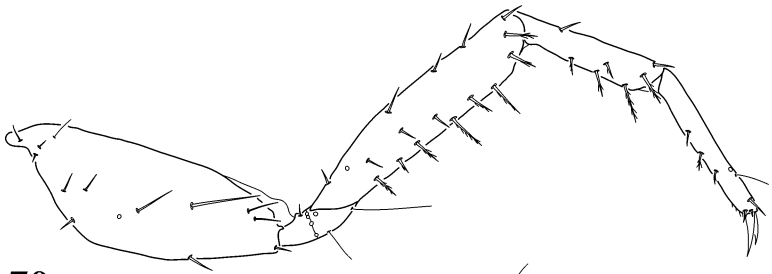

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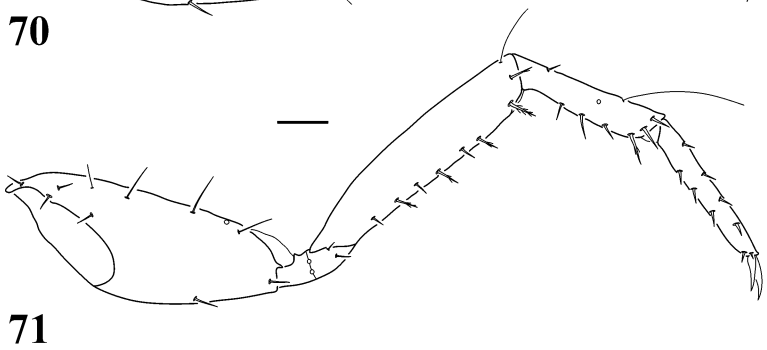

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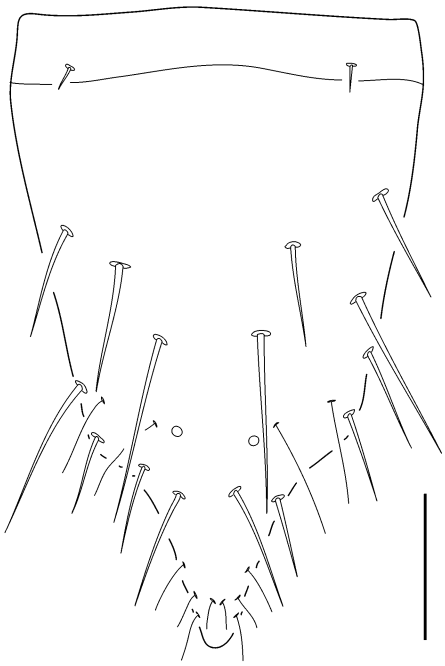
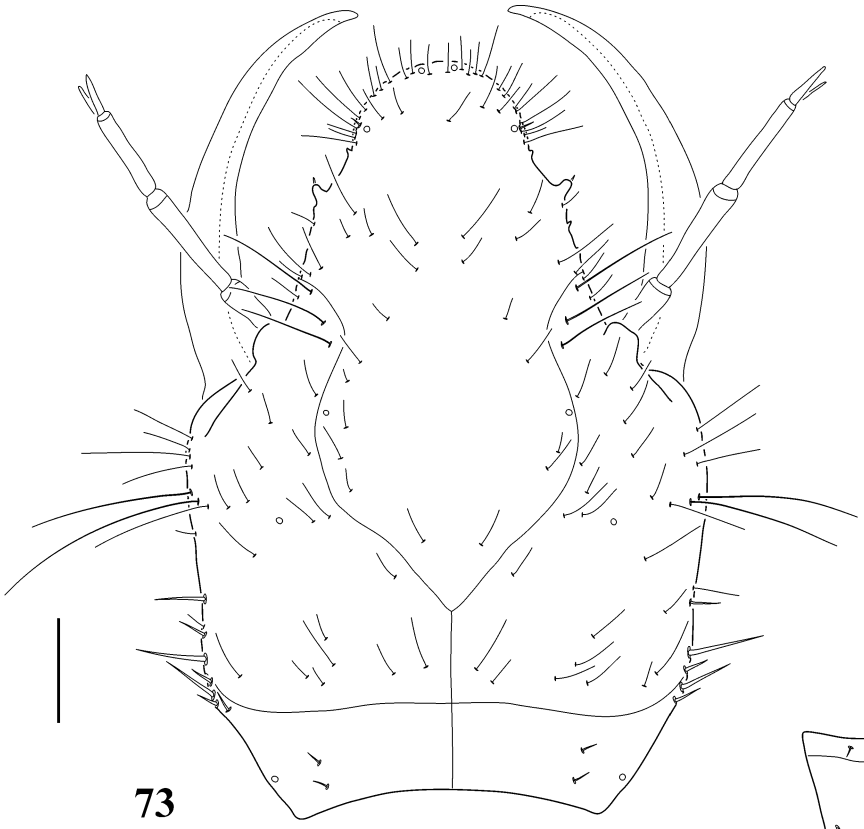
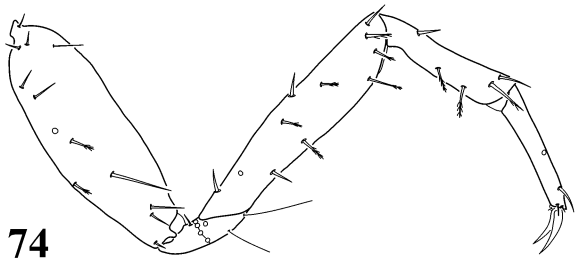
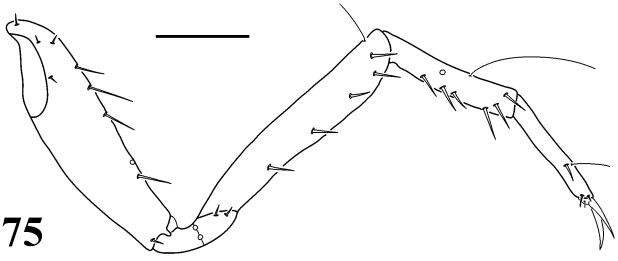


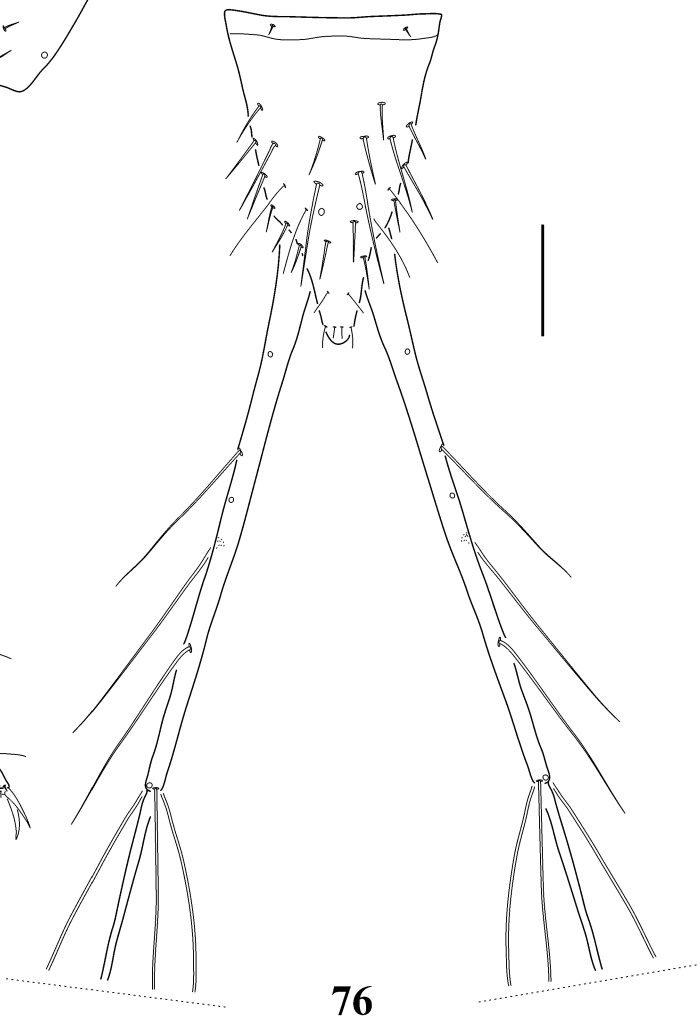
72

FIGURES 69–72. *Limbodessus eberhardi*, third-instar larva. 69, head, dorsal aspect; 70, left prothoracic leg, anterior aspect; 71, right prothoracic leg, posterior aspect; 72, abdominal segment VIII, dorsal aspect. Scale bars = 0.10 mm.









FIGURES 73–76. *Limbodessus exilis*, third-instar larva. 73, head, dorsal aspect; 74, left prothoracic leg, anterior aspect; 75, right prothoracic leg, posterior aspect; 76, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.15 mm.

***Limbodessus exilis* Watts & Humphreys, 2006**
(Figs 73–76)

Source of material. Two specimens of instar III were used for the description (Table 1). The larvae were collected at the following locality: **Australia, Moore palaeovalley**, Maranalgo calcrete, BES 10424/27, 25–V–2004, coll. W. F. Humphreys and C. H. S. Watts. The larvae studied were identified by comparing the sequence of a fragment of the CO1 gene with that from a known adult.

TABLE 10. Measurements and ratios for the third-instar larvae of species of *Limbodessus*.

Measure	*L. inornatus*	*L. leysi*	*L. masonensis*	*L. millbilliensis*
HL (mm)	0.82–0.84	0.67–0.72	0.66–0.67	0.74
HW (mm)	0.64–0.67	0.41–0.46	0.44–0.48	0.49–0.50
FRL (mm)	0.63–0.67	0.52–0.53	0.51–0.53	0.57
OCW (mm)	0.50–0.55	0.23–0.28	0.30	0.27
HL/HW	1.26–1.29	1.59–1.66	1.42–1.49	1.49–1.52
HW/OCW	1.21–1.29	1.64–1.78	1.48–1.60	1.81–1.84
COL/HL	0.20–0.23	0.23–0.26	0.21–0.22	0.23
FRL/HL	0.77–0.80	0.74–0.77	0.78–0.79	0.77
A/HW	0.61–0.68	0.74–0.76	0.70–0.75	0.73–0.77
A3/A1	1.80–2.00	2.00–2.20	1.85–1.92	2.55–2.64
A3/A2	0.90–1.00	1.22–1.26	1.20–1.39	1.22–1.32
A4/A3	0.37–0.39	0.54–0.55	0.42–0.44	0.43–0.45
A3’/A4	0.67–0.90	0.75–0.85	0.91–1.00	0.92
MNL/MNW	3.73–4.14	4.29–4.64	4.31–4.38	4.88–5.07
MNL/HL	0.49–0.51	0.44–0.45	0.51–0.52	0.51–0.52
A/MP	1.12–1.22	1.13–1.17	1.06	1.10
MP2/MP1	0.76–0.82	0.92–1.00	0.96–1.00	0.97–1.00
MP2/MP3	2.33–2.55	2.40–2.44	2.36–2.60	2.80–2.90
MP/LP	1.31–1.37	1.51–1.54	1.62–1.70	1.42–1.46
LP2/LP1	1.08–1.15	1.06–1.17	0.86–0.95	1.09
L3 (mm)	1.94–2.01	1.13–1.22	1.17–1.18	1.30–1.31
L3/L1	1.41–1.46	1.17–1.23	1.21	1.23
L3/L2	1.19–1.24	1.10–1.11	1.12–1.13	1.12–1.13
L3/HW	2.90–3.07	2.67–2.79	2.48–2.66	2.61–2.67
L3 (CO/FE)	1.00–1.02	0.86–0.88	0.91–0.94	0.89–0.92
L3 (TI/FE)	0.65–0.66	0.61–0.64	0.67–0.69	0.64–0.67
L3 (TA/FE)	0.69–0.70	0.70–0.72	0.68–0.70	0.74–0.75
L3 (CL/TA)	0.53–0.54	0.27–0.30	0.29–0.30	0.25–0.26
LAS (mm)	0.44–0.45	0.27–0.32	0.31–0.32	0.37
LAS/HW	0.66–0.68	0.67–0.70	0.65–0.72	0.73–0.76
U (mm)	1.62–1.66	0.83–0.92	0.91–0.95	0.91–0.94
U/LAS	3.67–3.81	2.91–3.05	2.97–2.98	2.49–2.57
U/HW	2.42–2.58	2.02–2.05	1.92–2.15	1.82–1.94
U1/U2	1.89–1.96	1.09–1.33	0.79–0.82	0.90–0.94

TABLE 11. Measurements and ratios for the third-instar larvae of species of *Limbodessus*.

Measure	*L. ordinarius*	*L. praelargus*	*L. raeae*	*L. raesideensis*
HL (mm)	0.99–1.02	0.79	0.80	1.56–1.61
HW (mm)	0.70–0.73	0.57	0.58	1.12–1.15
FRL (mm)	0.78–0.80	0.62	0.61	1.21–1.25
OCW (mm)	0.41–0.44	0.43	0.36	0.35–0.36
HL/HW	1.36–1.41	1.38	1.36	1.39–1.40
HW/OCW	1.68–1.76	1.35	1.64	3.18–3.23
COL/HL	0.21–0.22	0.22	0.24	0.22
FRL/HL	0.78–0.79	0.78	0.76	0.78
A/HW	0.62–0.66	0.65	0.69	0.72–0.75
A3/A1	1.63–1.72	2.17	1.71	1.82–1.88
A3/A2	1.00–1.03	1.04	1.21	1.11–1.13
A4/A3	0.45–0.48	0.46	0.41	0.29
A3’/A4	0.79–0.86	0.67	0.92	0.94–1.00
MNL/MNW	4.27–4.54	4.16	4.04	4.54–4.79
MNL/HL	0.54–0.55	0.49	0.58	0.57–0.59
A/MP	0.91–0.93	1.07	0.99	1.14–1.20
MP2/MP1	0.76–0.77	0.87	0.87	0.87–0.89
MP2/MP3	2.53–2.71	2.25	2.75	3.88–3.93
MP/LP	1.62–1.66	1.43	1.51	1.78–1.85
LP2/LP1	0.75–0.82	1.23	0.83	0.67
L3 (mm)	1.69–1.72	1.73	1.34	2.81–2.95
L3/L1	1.20–1.21	1.41	1.15	1.09–1.10
L3/L2	1.10–1.12	1.20	–	1.03–1.04
L3/HW	2.31–2.45	3.02	2.29	2.51–2.57
L3 (CO/FE)	0.87–0.88	0.98	0.97	0.90–0.92
L3 (TI/FE)	0.65–0.67	0.67	0.68	0.72–0.73
L3 (TA/FE)	0.62–0.64	0.69	0.72	0.69–0.70
L3 (CL/TA)	0.28–0.29	0.56	0.28	0.22–0.26
LAS (mm)	0.44–0.47	0.42	0.35	0.60
LAS/HW	0.60–0.67	0.72	0.59	0.53–0.54
U (mm)	1.21–1.31	1.35	–	1.90–2.14
U/LAS	2.65–2.88	3.24	–	3.15–3.54
U/HW	1.66–1.79	2.34	–	1.70–1.86
U1/U2	1.08–1.09	2.09	–	1.91–2.48

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 73) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on

lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 76).

Instar I. Not available.

Instar II. Not available.

Instar III (Figs 73–76). Head (Fig. 73). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 74–75). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 76). Chaetotaxy. Anteroventral margin of nasale with 49 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal and anteroventral secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI absent; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on mesoTA absent; metaTA with 1–5 posteroventral secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 9. Secondary leg setation detailed in Table 17.

Remarks. Both specimens of *L. exilis* examined had the second urogomphomere broken, which prevented the evaluation of urogomphal morphometry. Within the stygobitic species studied, *L. exilis* belongs to the group characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 76). Larvae of *L. exilis* can be distinguished from any other species of that group by the following combination of characters: lateral margins of the nasale not inflated in dorsal view (Fig. 73), mandibles less than 4.80 times longer than broad, longer legs, absence of posteroventral secondary setae on the pro- and mesotarsus (Fig. 75), and presence of posteroventral secondary setae on the metatarsus.

Limbodessus fridaywellensis (Watts & Humphreys, 2001)

(Figs 77–80)

Source of material. One specimen of instar III was used for the description (Table 1). Larva was collected in association with adults at the following locality: **Australia, Raeside palaeovalley**, Depot Springs calcrete, site 425, BES 8414, 28.05S, 120.03917E, 28–VI–2000, coll. W. F. Humphreys and S. Hinze.

Diagnosis (instar III). smaller species (HL less than 0.50 mm); head (Fig. 77) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 80).

Instar I. Not available.

Instar II. Not available.

Instar III (Figs 77–80). Head (Fig. 77). A3 less than 2.25 times longer than A1; A3 more than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 78–79). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 80). U more than 3.10 times longer than LAS; U more than 2.30 times longer than HW; U1 less than 0.60 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 31 lamellae clypeales distributed in a single row; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE absent; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with less than 5 secondary setae; anterodorsal secondary setae on proTI present; anteroventral and posterodorsal secondary setae on proTI

absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal, anteroventral and posteroventral secondary setae on meso- and metaTA absent; posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 9. Secondary leg setation detailed in Table 17.

Remarks. *Limbodessus fridaywellensis* belongs to the group of stygobitic species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 77). Larvae of *L. fridaywellensis* are easily distinguished from the other species of this group by the following combination of characters: smaller size, lateral margins of the nasale not inflated in dorsal view (Fig. 77), claws relatively longer as compared to tarsus (ratio CL/TA > 0.40), absence of anteroventral secondary setae on the mesotarsus, and absence of posteroventral secondary setae on the tarsus (Fig. 79).

Limbodessus hillviewensis (Watts & Humphreys, 2004)

(Figs 81–84)

Source of material. One specimen of instar III was used for the description (Table 1). Larva was collected in association with adults at the following locality: **Australia, Murchison palaeovalley**, Hillview calcrete, bore at Camel Well, BES 9399, 26.97222S, 117.4525E, 13–VI–2002, coll. W. F. Humphreys and R. Leys.

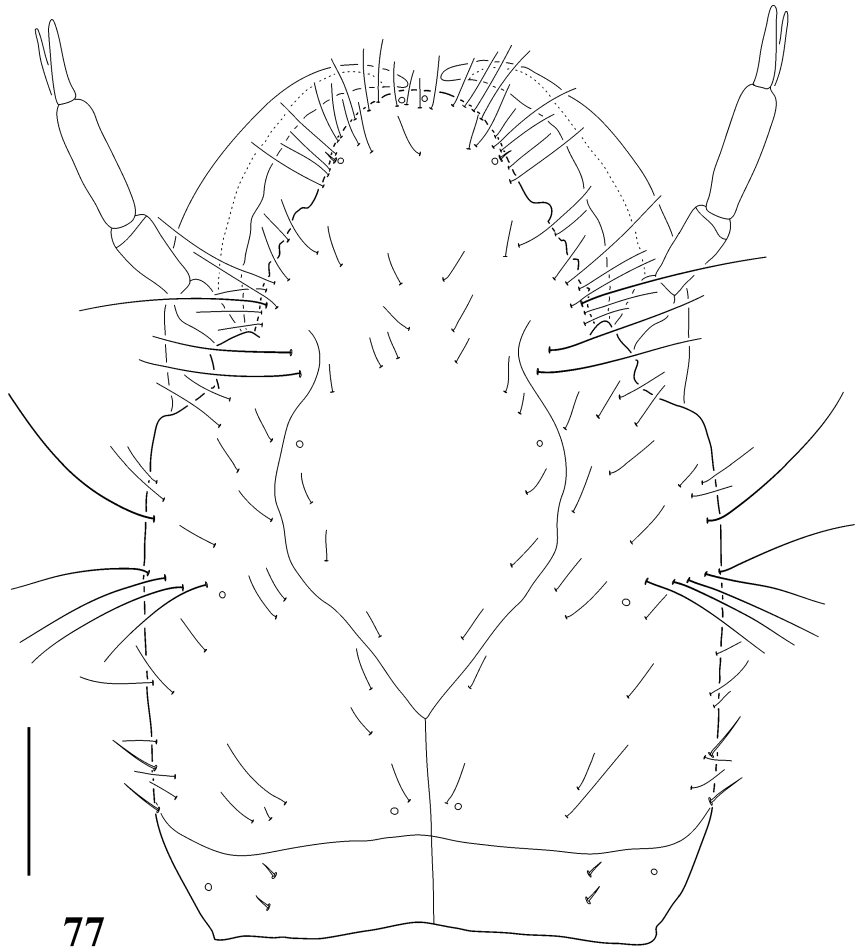
Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 81) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 84).

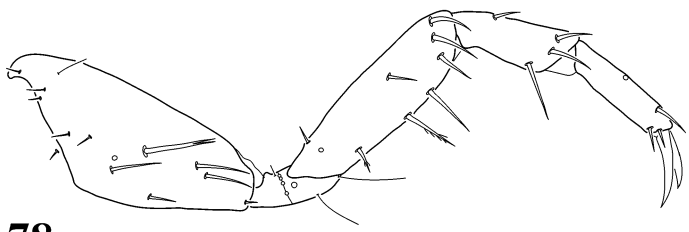
Instar I. Not available.

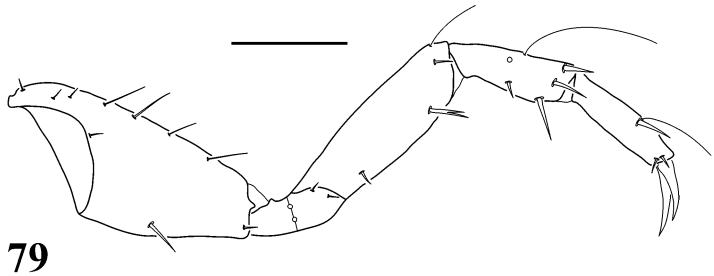
Instar II. Not available.

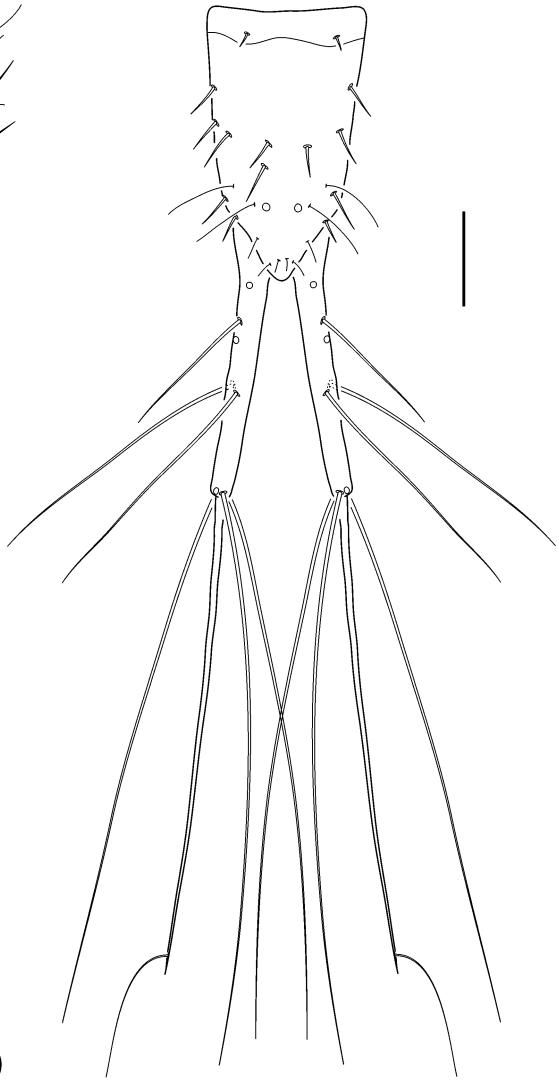
Instar III (Figs 81–84). Head (Fig. 81). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 82–83). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 84). Chaetotaxy. Anteroventral margin of nasale with 50 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI present; anteroventral and posterodorsal secondary setae on proTI absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal and posteroventral secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 9. Secondary leg setation detailed in Table 17.

Remarks. This species was described on the basis of a single instar III which has the second urogomphomere broken. *Limbodessus hillviewensis* belongs to the group of stygobitic species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 84). Compared to other members of this group the larvae of *L. hillviewensis* are distinguished by having the lateral margins of the nasale not inflated in dorsal view (Fig. 81), the claws relatively shorter as compared to tarsus (ratio CL/TA < 0.40), by the presence of anterodorsal secondary setae on the protibia (Fig. 82), the absence of anteroventral secondary setae on the protibia (Fig. 82), and the absence of posteroventral secondary setae on the tarsus (Fig. 83).

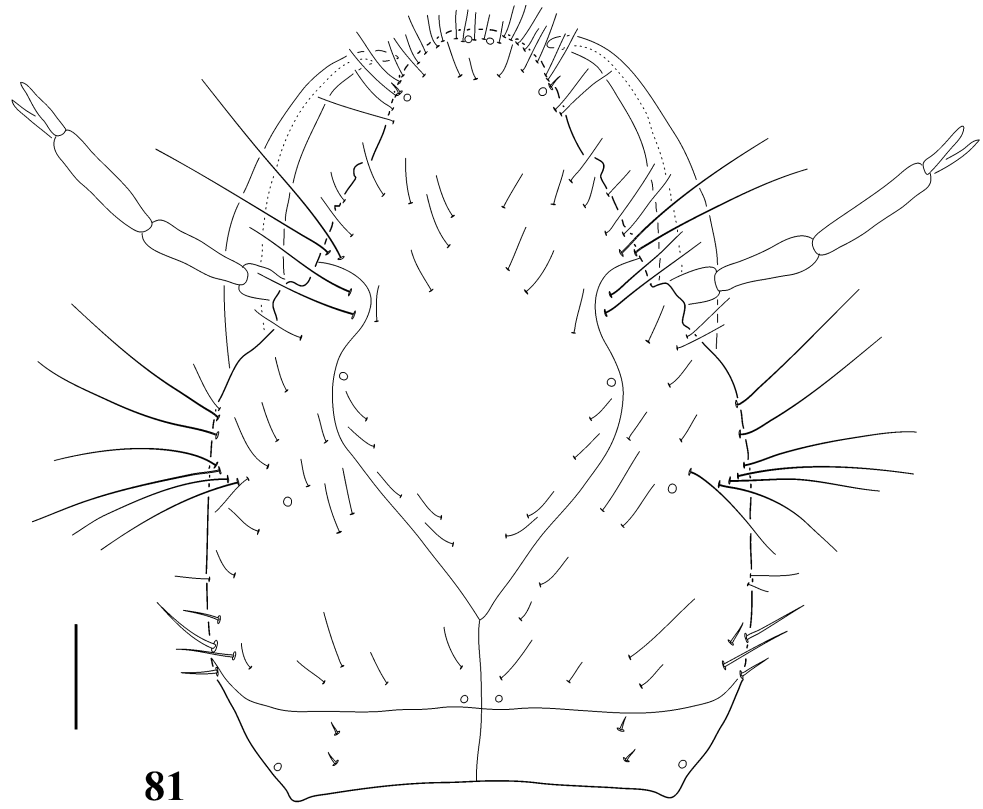


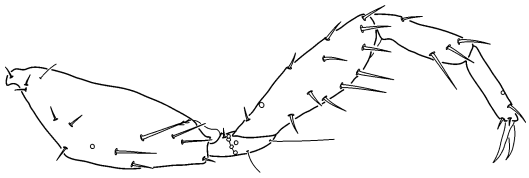


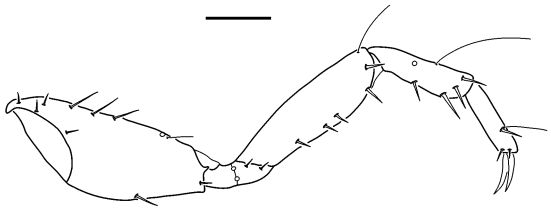


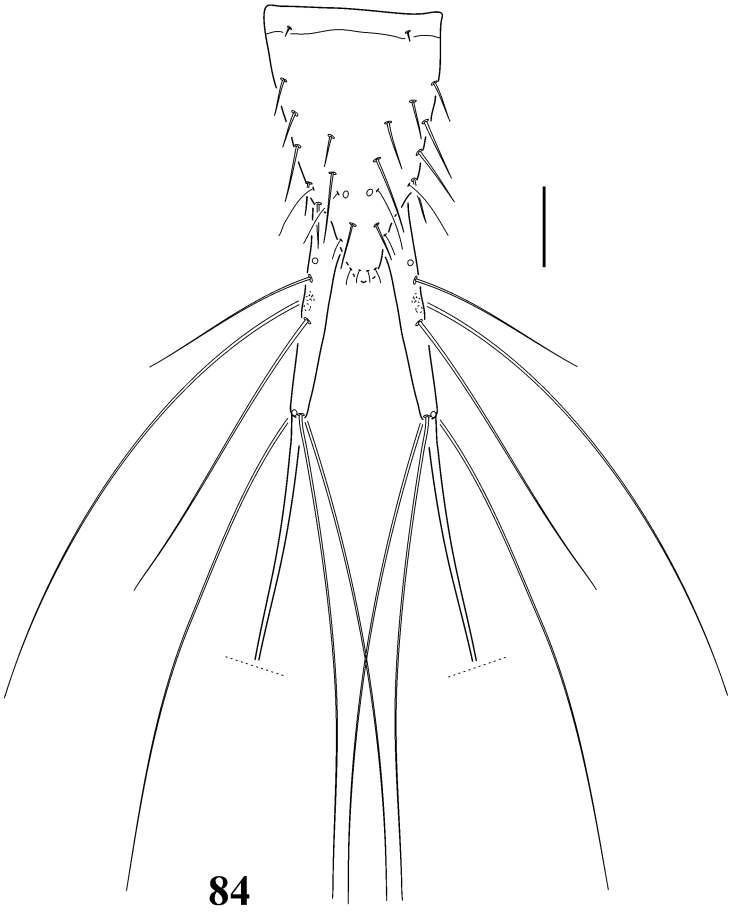


FIGURES 77–80. *Limbodessus fridaywellensis*, third-instar larva. 77, head, dorsal aspect; 78, left prothoracic leg, anterior aspect; 79, right prothoracic leg, posterior aspect; 80, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.08 mm.









FIGURES 81–84. *Limbodessus hillviewensis*, third-instar larva. 81, head, dorsal aspect; 82, left prothoracic leg, anterior aspect; 83, right prothoracic leg, posterior aspect; 84, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

TABLE 12. Measurements and ratios for the third-instar larvae of species of *Limbodessus*.

Measure	*L. shuckardii*	*L. windarraensis*	*L. yandalensis*	*L. yuinmeryensis*
HL (mm)	0.67–0.71	0.86	1.74	0.67
HW (mm)	0.51–0.53	0.58	1.25	0.47
FRL (mm)	0.54–0.56	0.66	1.36	0.51
OCW (mm)	0.38–0.39	0.33	0.39	0.30–0.32
HL/HW	1.28–1.37	1.47	1.40	1.43–1.45
HW/OCW	1.34–1.38	1.79	3.23	1.48–1.57
COL/HL	0.20–0.22	0.23	0.22	0.24
FRL/HL	0.78–0.80	0.77	0.78	0.76
A/HW	0.65–0.68	0.70	0.58	0.70–0.72
A3/A1	1.92–2.08	1.44	1.93	1.57–1.64
A3/A2	1.04–1.09	1.04	1.10	1.21–1.22
A4/A3	0.40–0.44	0.54	0.26	0.52–0.55
A3’/A4	0.80–0.91	0.71	0.86	0.83–0.92
MNL/MNW	4.00–4.25	5.11	4.81	4.19–4.60
MNL/HL	0.48–0.50	0.53	0.57	0.49–0.51
A/MP	1.15–1.18	0.99	0.92	1.08–1.10
MP2/MP1	1.00–1.08	0.80	0.91	0.85–0.96
MP2/MP3	2.18–2.36	2.67	4.53	2.30–2.60
MP/LP	1.23–1.30	1.71	1.58	1.43–1.50
LP2/LP1	1.18–1.29	0.81	0.72	1.10
L3 (mm)	1.38–1.42	1.37	3.05	1.12–1.13
L3/L1	1.28–1.31	1.14	1.16	1.20–1.21
L3/L2	1.15–1.18	1.08	1.06	1.11
L3/HW	2.66–2.71	2.34	2.45	2.40–2.41
L3 (CO/FE)	1.01–1.08	0.95	0.92	0.86–0.92
L3 (TI/FE)	0.63–0.64	0.67	0.74	0.66
L3 (TA/FE)	0.62–0.64	0.66	0.70	0.69
L3 (CL/TA)	0.51–0.52	0.29	0.22	0.31–0.33
LAS (mm)	0.44–0.45	0.34	0.62	0.28–0.31
LAS/HW	0.83–0.88	0.58	0.50	0.60–0.65
U (mm)	0.84–0.91	–	–	1.03
U/LAS	1.86–2.04	–	–	3.35–3.71
U/HW	1.63–1.72	–	–	2.19–2.21
U1/U2	0.78–0.94	–	–	0.86

Limbodessus hinkleri (Watts & Humphreys, 2000)

(Figs 85–88)

Source of material. One specimen of instar II and one of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Carey palaeovalley**, Hinkler Well calcrete, Lake Way Station, Dawson’s Well, BES 10493, 3–VI–2004; Hinkler Well calcrete, Lake Way Station, Dawson’s Well, BES 14305, 26.8866S, 120.1621E, 17–IX–2006, coll. W. F. Humphreys and T. Moulds.

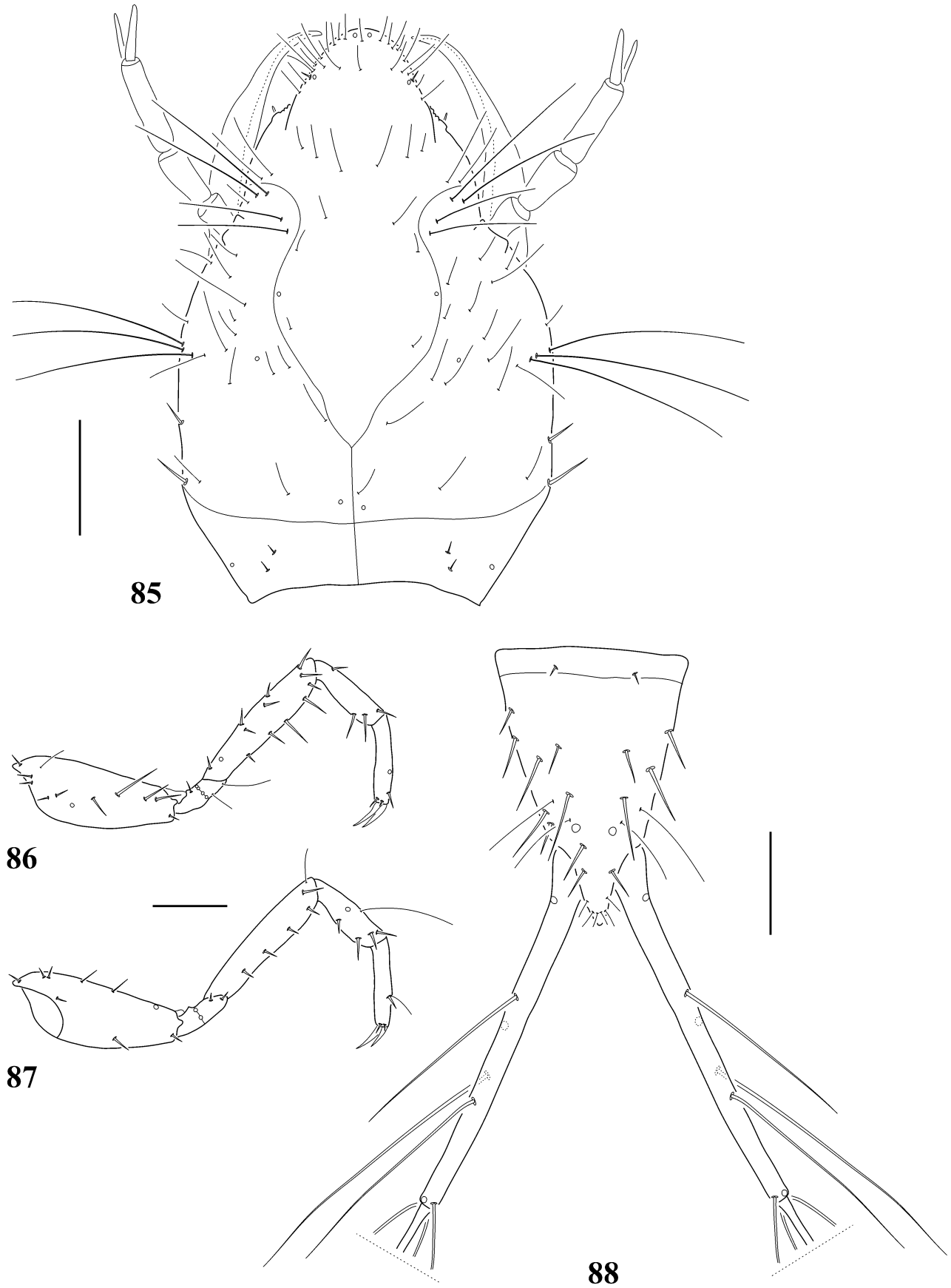
Diagnosis (instar III). Medium-sized species; head (Fig. 85) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale present; hole-like structure on ventrodistal surface of nasale present; lateral margins of nasale inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 absent; occipital foramen moderately reduced (instar II: HW/OCW 0.80–2.10); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 absent; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 88).

Instar I. Not available.

Instar II (Fig. 85). Head (Fig. 85). A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 less than 2.20 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U less than 2.15 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 24 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; secondary setae on proTI absent; anterodorsal secondary setae on mesoTI present; anterodorsal secondary setae on metaTI absent; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on meso- and metaTI absent; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 5. Secondary leg setation detailed in Table 13.

TABLE 13. Number and position of secondary setae on the legs of second-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. amabilis*	*L. barwidgeeensis*	*L. hinkleri*	*L. macrohinkleri*	*L. masonensis*
Coxa	A	0–3 / 0 / 0–1	– / 0 / 0	0 / 0 / 0	1 / 0 / 0	0 / 0 / 0
	PD	2–3 / 3–4 / 3–4	– / 6 / 6	1 / 1 / 1	3 / 3 / 3	2–3 / 2–3 / 2–3
	V	1–3 / 2–4 / 2–4	– / 3 / 2	1 / 1 / 1	3 / 2 / 2	1 / 1 / 0–1
	Total	4–9 / 5–8 / 6–7	– / 9 / 8	2 / 2 / 2	7 / 5 / 5	3–4 / 3–4 / 3
Trochanter	Pr	0 / 1–2 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	Total	0 / 1–2 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
Femur	AD	2–3 / 2–4 / 3–6	3 / 5 / 5	1 / 2 / 3	4 / 4 / 6	2 / 2–3 / 2
	AV	1–3 / 2–3 / 4	4 / 4 / 4	1 / 1 / 1	7 / 6 / 4	2 / 2 / 1–2
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PV	0–2 / 4 / 5–6	4 / 4 / 5	0 / 1 / 1	5 / 5 / 5	2 / 2 / 2
	Total	4–8 / 8–11 / 12–15	11 / 13 / 14	2 / 4 / 5	16 / 15 / 15	6 / 6–7 / 5–6
Tibia	AD	1 / 1 / 1–3	0 / 2 / 1	0 / 1 / 0	0 / 0 / 0	0 / 1 / 1
	AV	0 / 1–2 / 2–3	1 / 2 / 2	0 / 1 / 1	2 / 2 / 3	0 / 1 / 1
	PD	0 / 0–1 / 0–1	1 / 1 / 3	0 / 0 / 1	2 / 4 / 3	0 / 0 / 0
	PV	1 / 1–2 / 2–3	2 / 2 / 3	0 / 0 / 0	2 / 2 / 2	1 / 0 / 0
	Total	2 / 3–6 / 6–9	4 / 7 / 9	0 / 2 / 2	6 / 8 / 8	1 / 2 / 2
Tarsus	AD	1 / 1 / 2	0 / 2 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	AV	0 / 1–2 / 2–3	0 / 3 / 2	0 / 1 / 1	2 / 2 / 4	0 / 1 / 1
	PD	0 / 0 / 0	2 / 1 / 4	0 / 1 / 1	2 / 2 / 3	0 / 1 / 1
	PV	1 / 1–3 / 2–3	2 / 1 / 2	0 / 0 / 0	2 / 4 / 4	0 / 0 / 0
	Total	2 / 3–6 / 6–8	4 / 7 / 8	0 / 2 / 2	6 / 8 / 11	0 / 2 / 2



FIGURES 85–88. *Limbodessus hinkleri*. 85, second-instar larva, head, dorsal aspect; 86–88, third-instar larva; 86, left prothoracic leg, anterior aspect; 87, right prothoracic leg, posterior aspect; 88, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Instar III (Figs 86–88). Head. MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 86–87). Abdomen (Fig. 88). Chaetotaxy. Anteroventral margin of nasale with 33 lamellae clypeales distributed in 1–2 rows; proCO without anterior and posterior secondary setae; proCO with less than 11 secondary setae; anterodorsal secondary setae on proFE present; anterodorsal secondary setae on proTI present; anteroventral and posterodorsal secondary setae on proTI absent; secondary setae on proTA absent; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 9. Secondary leg setation detailed in Table 17.

Remarks. This species was described on the basis of one instar II and one badly preserved instar III, of which only the mouth parts and the last abdominal segment could be measured, and only the prothoracic leg was available for chaetotaxic analysis. *Limbodessus hinkleri* belongs to the group of species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 88). Larvae of *L. hinkleri* are very distinctive and can easily be recognized by the following combinations of characters: lateral margins of the nasale inflated in dorsal view (Fig. 85), presence of a hole-like structure on the ventrodistal surface of the nasale (more evident in instar III), absence of slender spinulae on the ventral surface of the nasale (anterior to seta FR13), and primary seta AN2 absent. The occipital foramen is somewhat reduced.

Limbodessus leysi Watts & Humphreys, 2006

(Figs 89–106)

Source of material. One specimen of instar I and three of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Carey palaeovalley**, Mt Morgan calcrete, Mt Weld Station, PB1, BES 11816, 28.73439S, 122.14942E, 30–IX–2004, coll. W. F. Humphreys and S. J. B. Cooper; Mt Morgan calcrete, Mt Weld Station, PB4, BES 10581, 28.72177S, 122.1569E, 30–IX–2004, coll. W. F. Humphreys and S. J. B. Cooper.

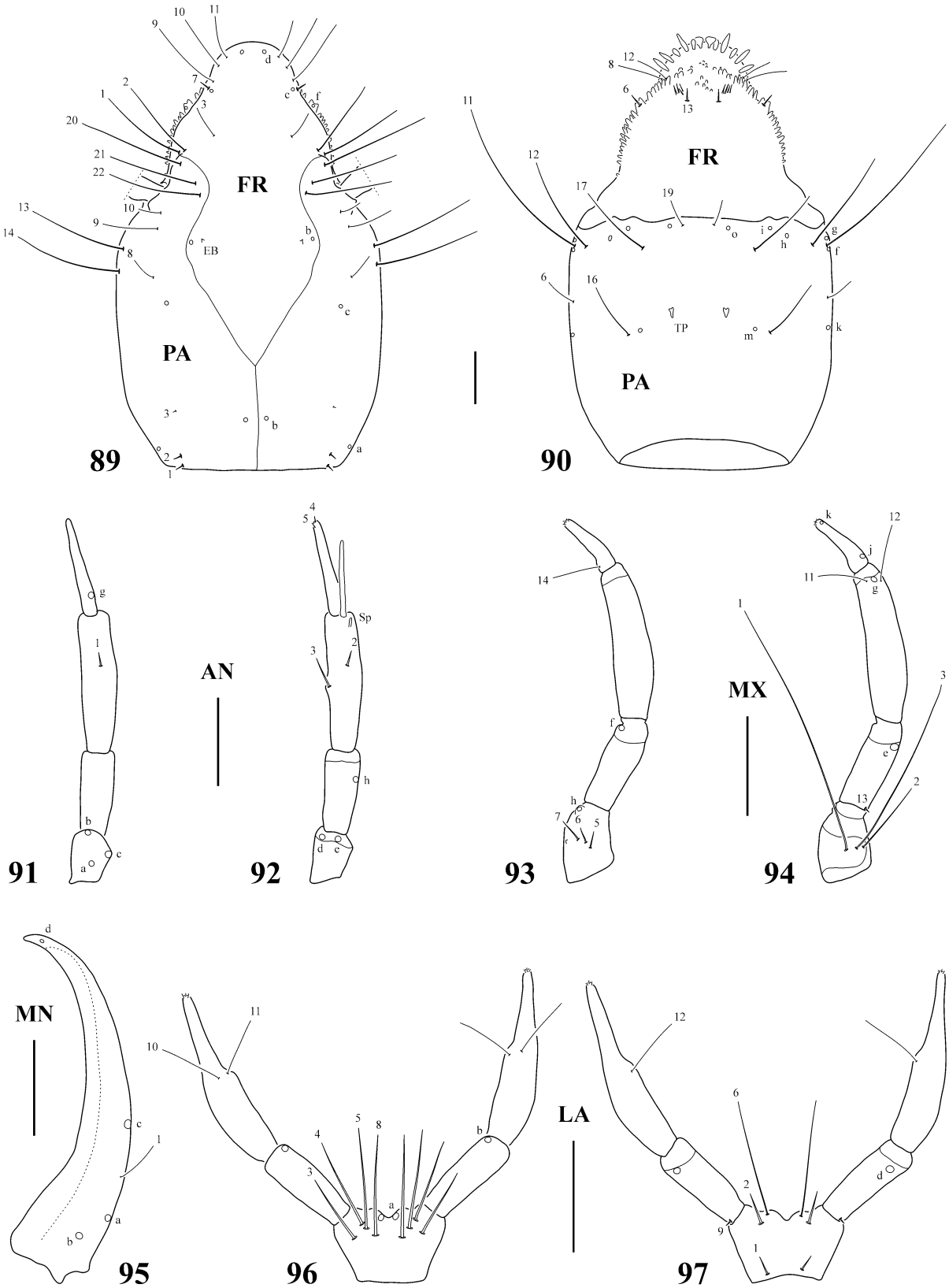
Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 103) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale present; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 106).

Instar I (Figs 89–102). Head (Figs 89–97). Cephalic capsule strongly elongate (HL/HW more than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 more than 2.80 times longer than A1; A3 more than 2.25 times longer than A2; MP2 1.55–1.85 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 98–99). L3 less than 2.85 times longer than HW. Abdomen (Figs 100–102). U more than 3.75 times longer than LAS; U more than 2.45 times longer than HW; U1 1.10–1.40 times longer than U2. Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 2.

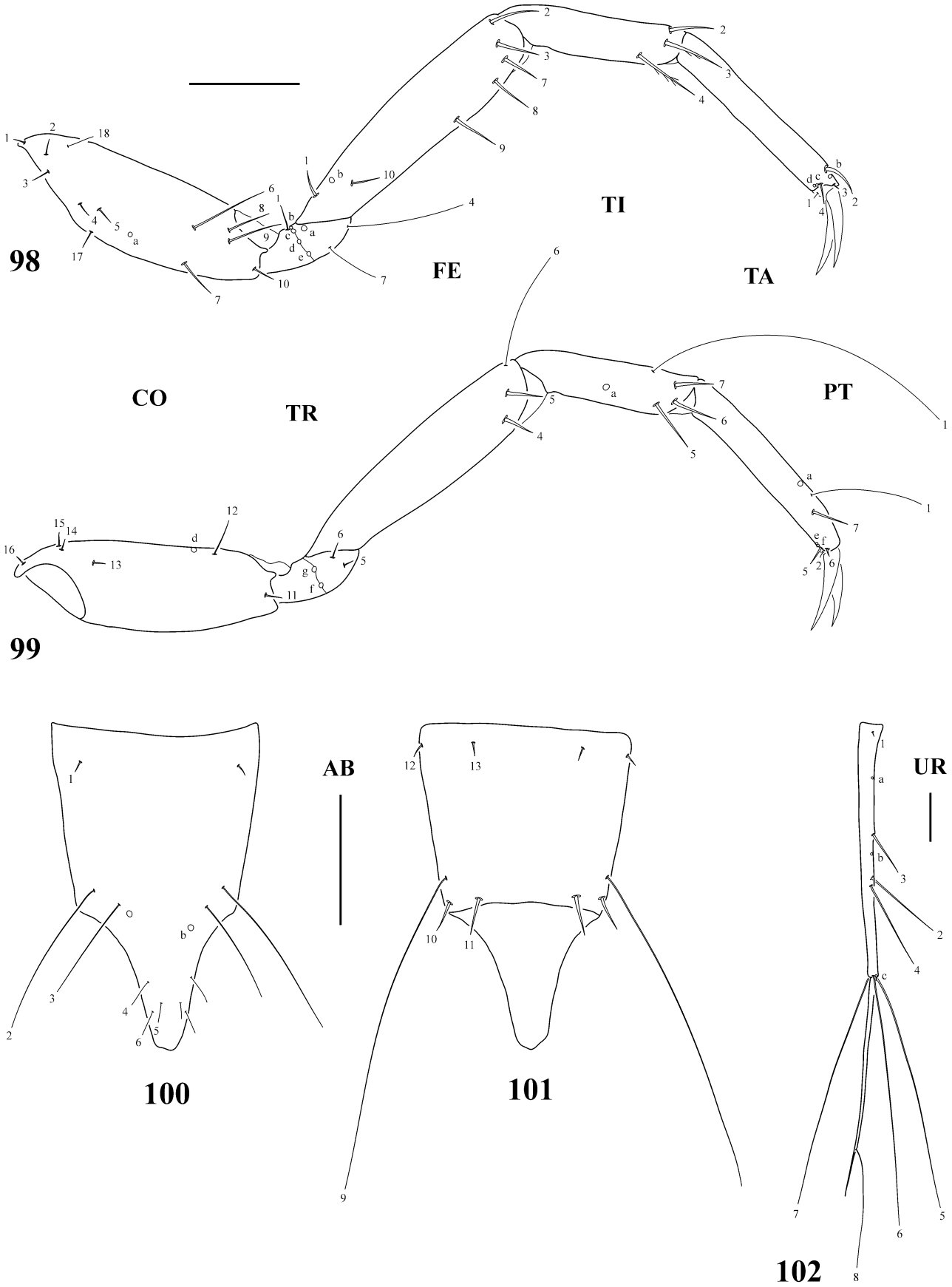
Instar II. Not available.

Instar III (Figs 103–106). Head (Fig. 103). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 104–105). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 106). U 2.40–3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 48 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI absent; anteroventral and posterodorsal secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; anterodorsal and posteroventral secondary setae on pro-, meso- and metaTA absent; anteroventral secondary setae on pro-, meso- and metaTA present; posterodorsal secondary setae on proTA absent;

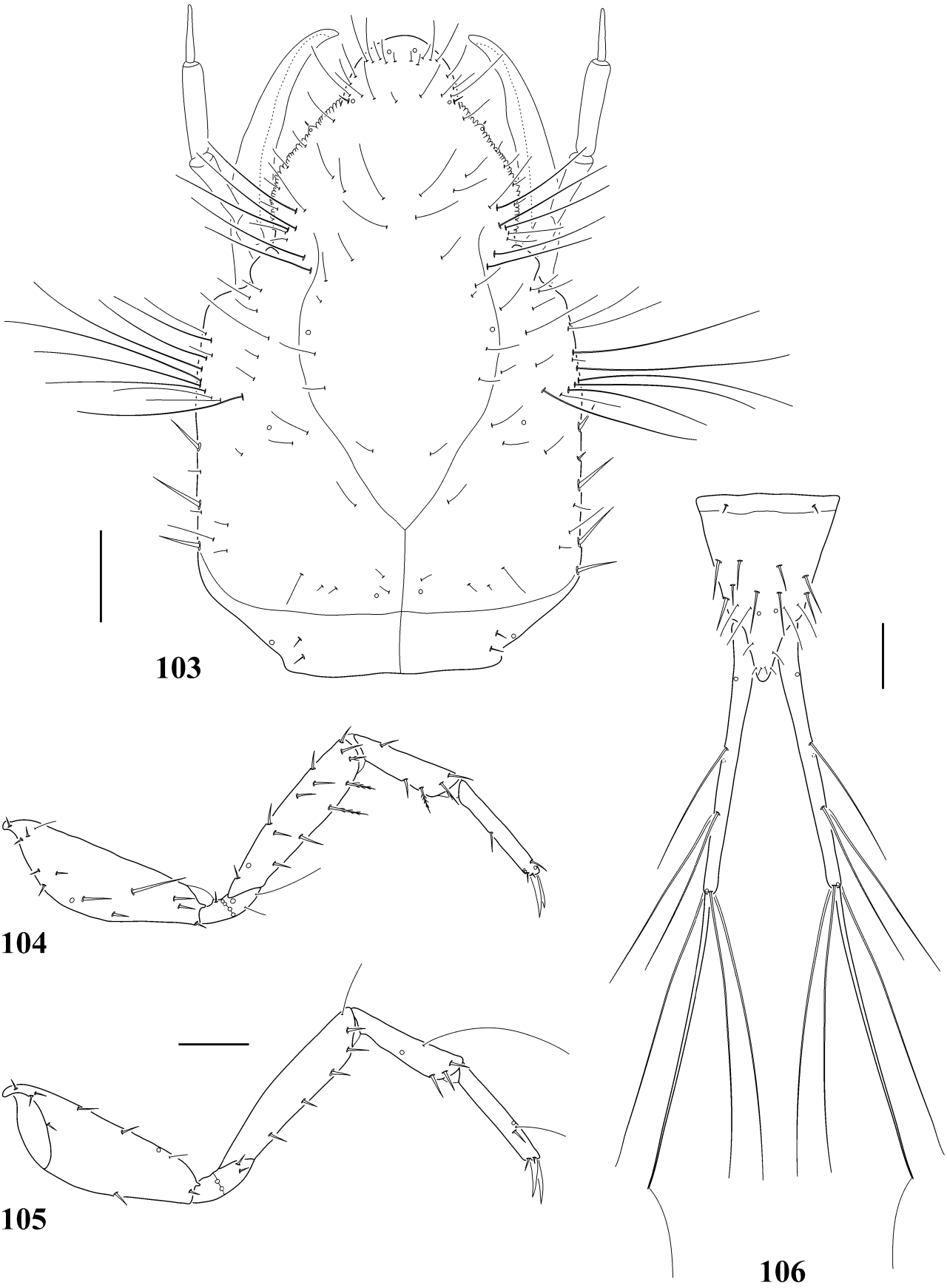
posterodorsal secondary setae on meso- and metaTA present; proTA with 1–7 secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 10. Secondary leg setation detailed in Table 18.



FIGURES 89–97. *Limbodessus leysi*, first-instar larva. 89, cephalic capsule, dorsal aspect; 90, cephalic capsule, ventral aspect; 91, right antenna, dorsal aspect; 92, left antenna, ventral aspect; 93, right maxilla, dorsal aspect; 94, left maxilla, ventral aspect; 95, right mandible, dorsal aspect; 96, labium, dorsal aspect; 97, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.05 mm.



FIGURES 98–102. *Limbodessus leysi*, first-instar larva. 98, left metathoracic leg, anterior aspect; 99, right metathoracic leg, posterior aspect; 100, abdominal segment VIII, dorsal aspect; 101, abdominal segment VIII, ventral aspect; 102, right urogomphus, dorsal aspect. Scale bars = 0.07 mm.



FIGURES 103–106. *Limbodessus leysi*, third-instar larva. 103, head, dorsal aspect; 104, left prothoracic leg, anterior aspect; 105, right prothoracic leg, posterior aspect; 106, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Remarks. *Limbodessus leysi* belongs to the group of species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 106). Compared to other members of this group, the larvae of *L. leysi* can readily be distinguished by the following combinations of characters: lateral margins of the nasale inflated in dorsal view, bearing a half-circle of dense spinulae (Figs 90, 103), and primary seta AN2 present.

Limbodessus macrohinkleri Watts & Humphreys, 2006

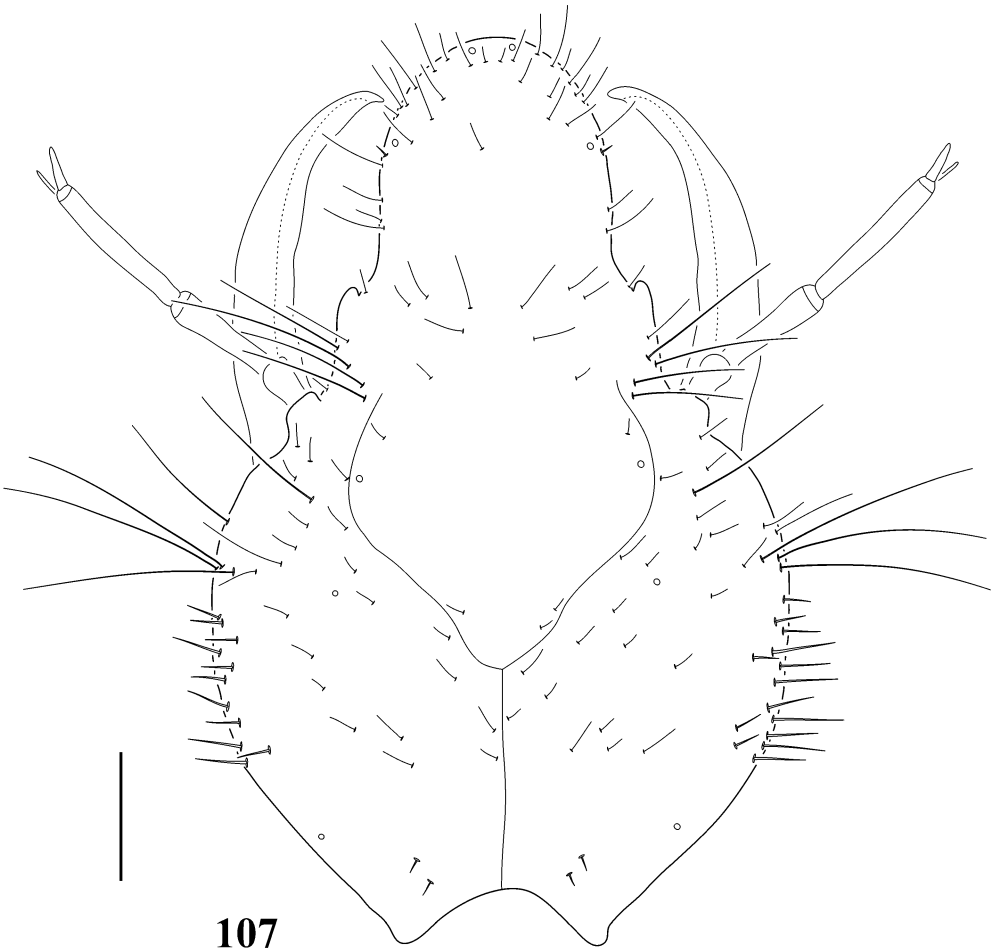
(Figs 107–110)

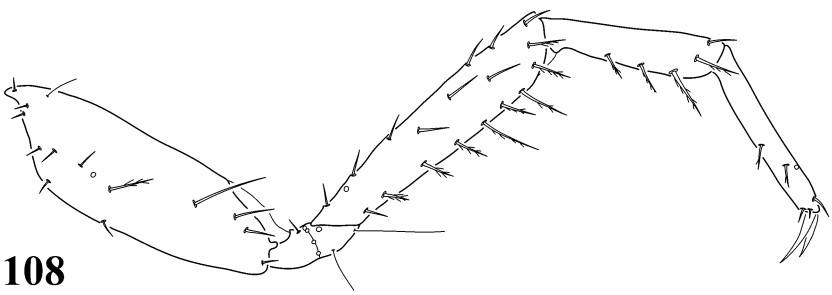
Source of material. One specimen of instar II was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Hinkler Well calcrete, Lake Way Station, Dawson's Well, BES 10493, 26.88651S, 120.16203E, 3–VI–2004, coll. W. F. Humphreys, C. H. S. Watts and C. Clay.

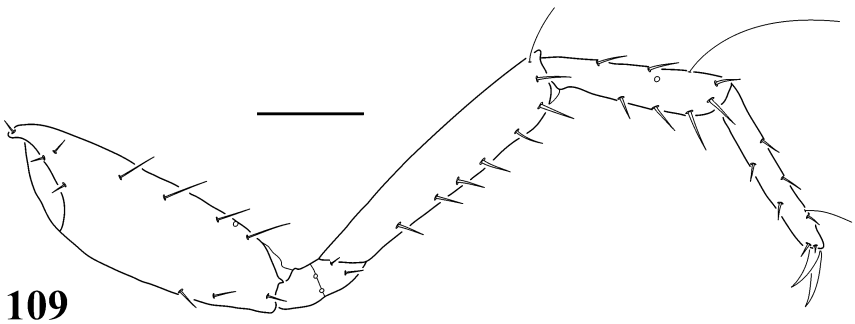
Diagnosis (instar II). Larger species (HL more than 1.05 mm); head (Fig. 107) pyriform; nasale digitiform; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen strongly reduced (HW/OCW more than 2.70); occipital suture absent; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal numerous; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U present (Fig. 110).

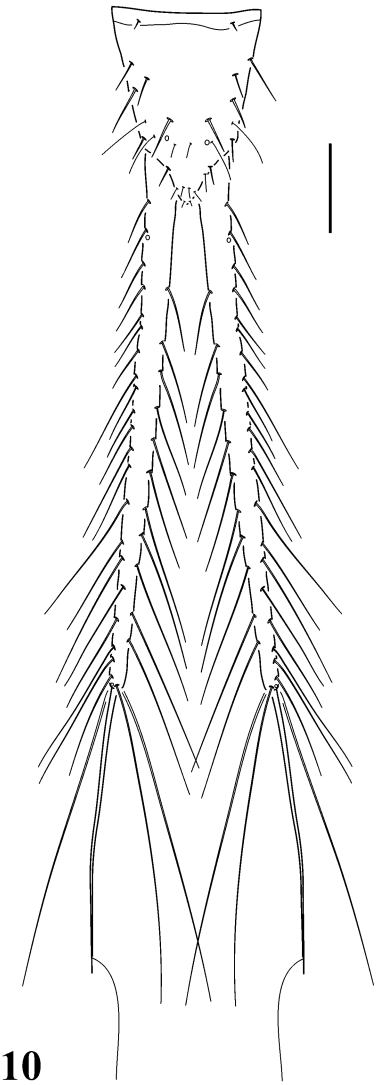
TABLE 14. Number and position of secondary setae on the legs of second-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. millbilliensis*	*L. morgani*	*L. ordinarius*	*L. pulpa*
Coxa	A	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PD	2 / 1 / 1	2 / 1 / 1	1–2 / 1–2 / 1–2	1 / 1 / 1
	V	1 / 0 / 1	0 / 1 / 1	1 / 1 / 1	1 / 1 / 1
	Total	3 / 1 / 2	2 / 2 / 2	2–3 / 2–3 / 2–3	2 / 2 / 2
Trochanter	Pr	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	Total	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
Femur	AD	2 / 2 / 2	1 / 2 / 2	2 / 2 / 2	2 / 2 / 2
	AV	1 / 1 / 0	1 / 1 / 1	1 / 1–2 / 1–2	1 / 2 / 2
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PV	0 / 0 / 1	1 / 1 / 2	1 / 1 / 2	1 / 2 / 2
	Total	3 / 3 / 3	3 / 4 / 5	4 / 4–5 / 5–6	4 / 6 / 6
Tibia	AD	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	AV	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PV	0 / 0 / 0	0 / 0 / 0	1 / 0 / 0	0 / 0 / 0
	Total	0 / 2 / 2	0 / 2 / 2	1 / 2 / 2–4	0 / 2 / 2
Tarsus	AD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	AV	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	PD	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	PV	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	Total	0 / 2 / 2	0 / 2 / 2	0 / 2 / 2	0 / 2 / 2









FIGURES 107–110. *Limbodessus macrohinkleri*, second-instar larva. 107, head, dorsal aspect; 108, left prothoracic leg, anterior aspect; 109, right prothoracic leg, posterior aspect; 110, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.20 mm.

Instar I. Not available.

Instar II (Figs 107–110). Head (Fig. 107). A3 more than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 more than 3.20 times longer than MP3; LP2 less than 0.90 times as long as LP1. Legs (Figs 108–109). L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen (Fig. 110). U more than 4.15 times longer than LAS; U less than 2.15 times longer than HW; U1 more than 1.65 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 228 lamellae clypeales distributed in 3–4 rows; anterior secondary setae on proCO present; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with more than 3 posteroventral secondary setae; metaFE with more than 11 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTI absent; anteroventral and posterodorsal secondary setae on proTI present; mesoTI with more than 3 posterodorsal secondary setae; metaTI with more than 2 posterodorsal secondary setae; posteroventral secondary setae on pro-, meso- and metaTI present; metaTI with more than 5 secondary setae; anterodorsal secondary setae on proTA absent; anteroventral and posteroventral secondary setae on proTA present; posterodorsal and posteroventral secondary setae on meso- and metaTA present; metaTA with more than 5 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 5. Secondary leg setation detailed in Table 13.

Instar III. Not available.

Remarks. The absence of instar III specimens of *L. macrohinkleri* hampers the comparison with the other species described here, particularly regarding some chaetotaxic characters. *Limbodessus macrohinkleri* belongs to the group of stygobitic species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis, L. bigbellensis, L. cooperi, L. eberhardi, L. nambiensis, L. raesideensis, L. yandalensis*) (Fig. 110), and within this group it can be distinguished by the following combination of characters: head pyriform (Fig. 107), occipital suture absent (Fig. 107), occipital foramen strongly reduced (Fig. 107), and absence of anterodorsal secondary setae on the protibia (Fig. 108).

Limbodessus masonensis (Watts & Humphreys, 2001)

(Figs 111–114)

Source of material. Two specimens of instar II and two of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following locality: Australia, **Raeside palaeovalley**, Lake Mason calcrete, Salt Well, BES 14361, 27.586S, 119.5218E, 20–IX–2006, coll. W. F. Humphreys and T. Moulds.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 111) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 114).

Instar I. Not available.

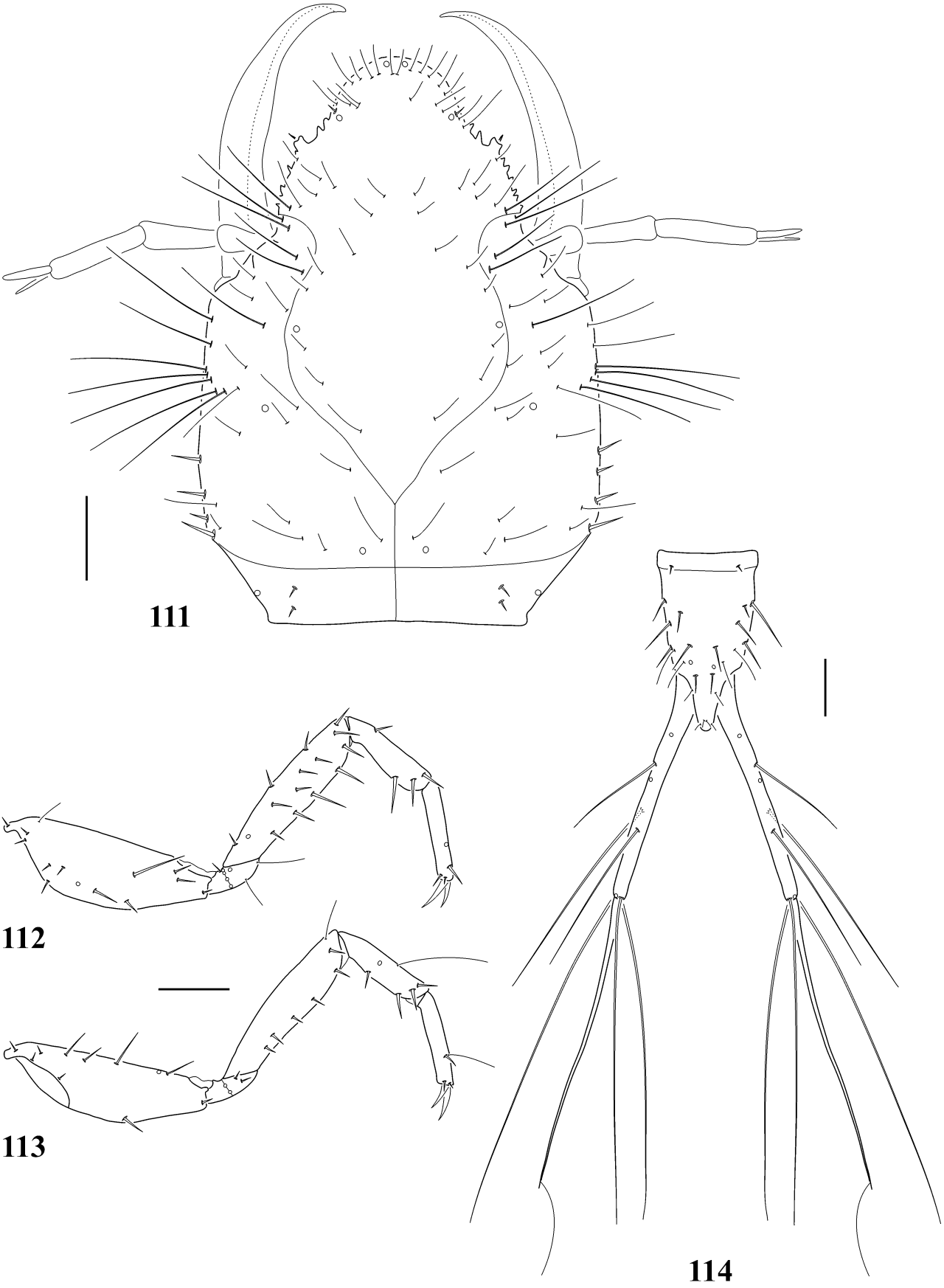
Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U more than 2.25 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 25 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on proTI present; posteroventral secondary setae on meso- and metaTI absent; metaTI with less than 5 secondary setae;

secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 5. Secondary leg setation detailed in Table 13.

Instar III (Figs 111–114). Head (Fig. 111). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 112–113). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 114). U 2.40–3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 50 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI present; anteroventral and posterodorsal secondary setae on proTI absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal and posteroventral secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 10. Secondary leg setation detailed in Table 18.

TABLE 15. Number and position of secondary setae on the legs of second-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. raesideensis*	*L. shuckardii*	*L. windarraensis*	*L. yuinmeryensis*
Coxa	A	0 / 0 / 0	0 / 0 / 0	1 / 0 / 0	0 / 0 / 0
	PD	3 / 2–3 / 2–3	2 / 2 / 2	2 / 2 / 2	1 / 2 / 1
	V	2–3 / 2–3 / 2	1 / 1 / 1	1 / 1 / 1	1 / 1 / 1
	Total	5–6 / 4–6 / 4–5	3 / 3 / 3	4 / 3 / 3	2 / 3 / 2
Trochanter	Pr	1 / 1 / 1	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
	Total	1 / 1 / 1	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
Femur	AD	3 / 3–4 / 4–5	3 / 3 / 3	2 / 2 / 3	2 / 2 / 2
	AV	5–7 / 6–7 / 5–8	2 / 2 / 3	2 / 2 / 4	1 / 1 / 1
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PV	4 / 5 / 5	1 / 2 / 4	2 / 2 / 3	2 / 2–3 / 2–3
	Total	12–14 / 15 / 14–18	6 / 7 / 10	6 / 6 / 10	5 / 5–6 / 5–6
Tibia	AD	0 / 2 / 2	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
	AV	1 / 3 / 2–3	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
	PD	1 / 0–1 / 1	0 / 0 / 0	1 / 0 / 1	0 / 0 / 0
	PV	1–2 / 2–3 / 2	1 / 1 / 1	0 / 0 / 0	1 / 0 / 1
	Total	3–4 / 8 / 7–8	1 / 3 / 3	3 / 2 / 3	1 / 2 / 3
Tarsus	AD	0 / 0–1 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	AV	1–2 / 2–3 / 3	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
	PD	0–1 / 2 / 2	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	PV	1–2 / 2 / 2–3	0 / 1 / 1	0 / 0 / 0	0 / 0 / 0
	Total	2–5 / 7 / 7–8	0 / 3 / 3	1 / 2 / 2	0 / 2 / 2



FIGURES 111–114. *Limbodessus masonensis*, third-instar larva. 111, head, dorsal aspect; 112, left prothoracic leg, anterior aspect; 113, right prothoracic leg, posterior aspect; 114, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Remarks. This species belongs to the group characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 114). Larvae of *L. masonensis* can be distinguished from any other species of that group by the following combination of features: lateral margins of the nasale not inflated in dorsal view (Fig. 111), mandibles less than 4.80 times longer than broad, shorter legs, presence of anterodorsal secondary setae on the protibia (Fig. 112), absence of anteroventral secondary setae on the protibia (Fig. 112), absence of secondary setae on the protarsus (Figs 112–113), presence of anteroventral secondary setae on the mesotarsus, and absence of posteroventral secondary setae on the tarsus (Fig. 113).

Limbodessus millbilliensis Watts & Humphreys, 2006

(Figs 115–133)

Source of material. One specimen of instar I, one of instar II and two of instar III were used for the description (Table 1). The larvae were collected in association with adults at the following localities: **Australia, Carey palaeovalley**, Lake Violet calcrete, Wiluna Gold, Bore Field, observation bore for pump 1, BES 7148, 26.675S, 120.23194E, 18–V–1999, coll. W. F. Humphreys and H. J. Hahn; Lake Violet calcrete, Wiluna Gold, Bore Field, BES 6437, 26.675S, 120.23194E, 9–V–2001; Millbillie Station, MB for pump 3, BES 14317, 26.6801S, 120.2248E, 18–IX–2006, coll. W. F. Humphreys and T. Moulds.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 129) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale present (Fig. 130); lateral margins of nasale inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 absent; occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN narrow; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 133).

Instar I (Figs 115–128). Head (Figs 115–123). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 more than 2.80 times longer than A1; A3 more than 2.25 times longer than A2; MP2 1.55–1.85 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 124–125). L3 less than 2.85 times longer than HW. Abdomen (Figs 126–128). U less than 3.45 times longer than LAS; U less than 2.35 times longer than HW; U1 1.10–1.40 times longer than U2. Chaetotaxy. Frontoclypeus with 14 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 2.

Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN more than 4.90 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U less than 2.80 times longer than LAS; U less than 2.15 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 31 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on proCO present; ventral secondary setae on mesoCO absent; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on meso- and metaTI absent; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 6. Secondary leg setation detailed in Table 14.

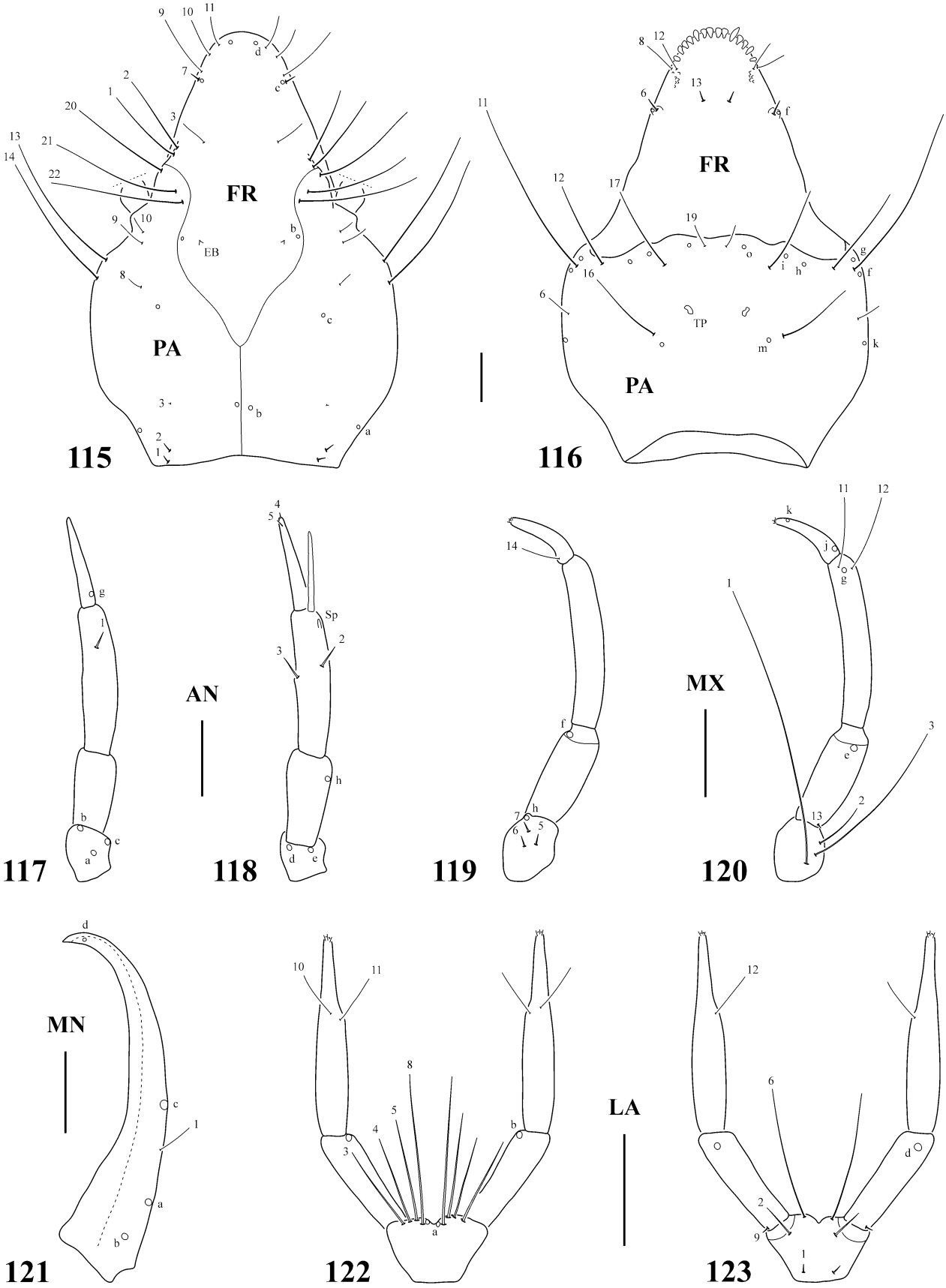
Instar III (Figs 129–133). Head (Fig. 129). A3 more than 2.50 times longer than A1; A3 less than 1.45 times longer than A2; MN more than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 131–132). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 133). U 2.40–3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 56 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary

setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI present; anteroventral and posterodorsal secondary setae on proTI absent; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal and posteroventral secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 10. Secondary leg setation detailed in Table 18.

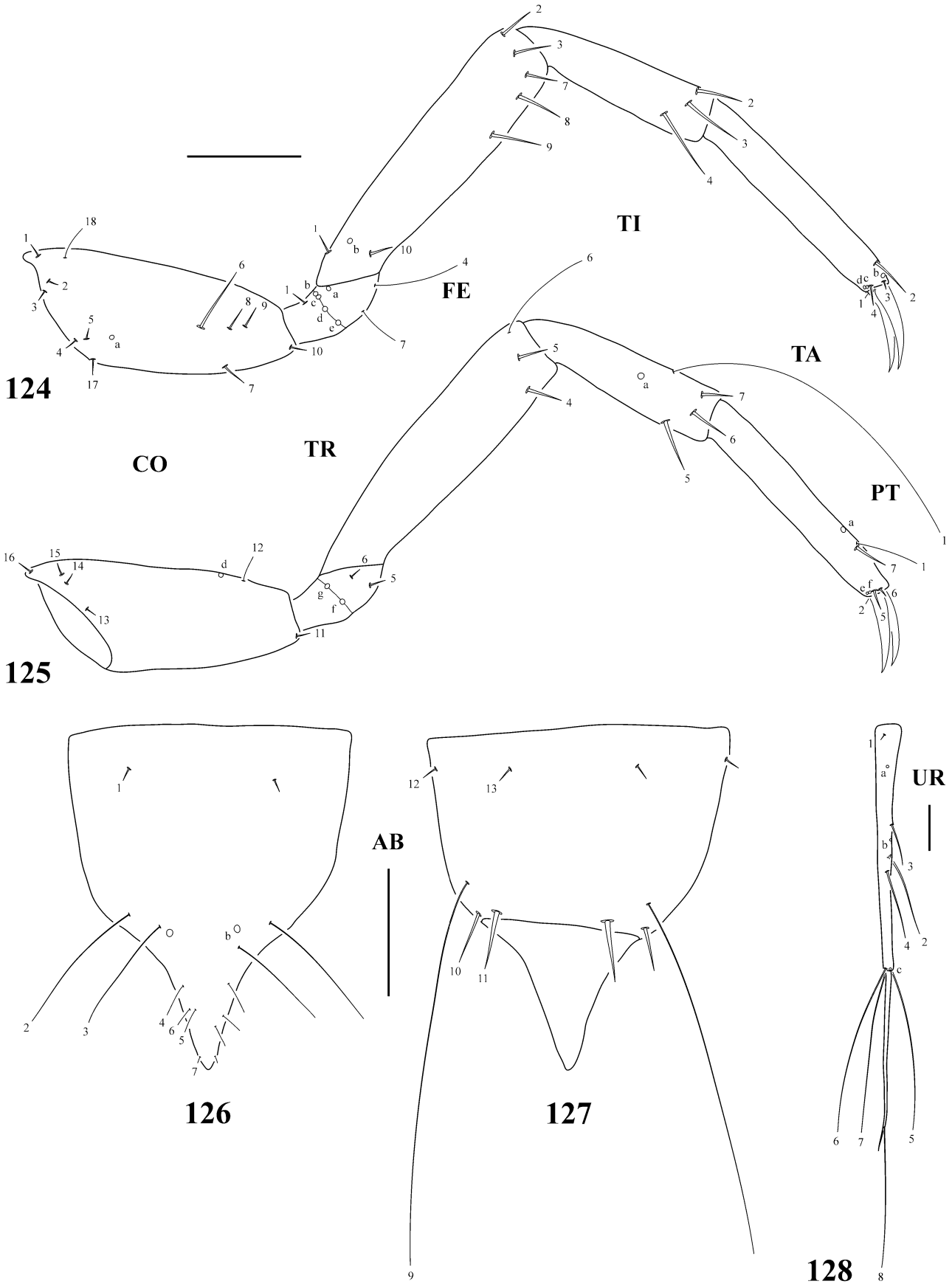
Remarks. *Limbodessus millbilliensis* is a very distinctive stygobitic species. It belongs to the group characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 133). The species is unique in that the distal half of the mandible is narrower than in the other species studied (Figs 121, 129). Also, other characteristic features are the lateral margins of the nasale inflated in dorsal view (shared with *L. hinkleri* and *L. leysi*) (Fig. 129), the presence of a hole-like structure on the ventrodistal surface of the nasale (well visible both in instars II and III) (Fig. 130), and the absence of slender spinulae on the ventral surface of the nasale, anterior to seta FR13 (shared only with *L. hinkleri*).

TABLE 16. Number and position of secondary setae on the legs of third-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

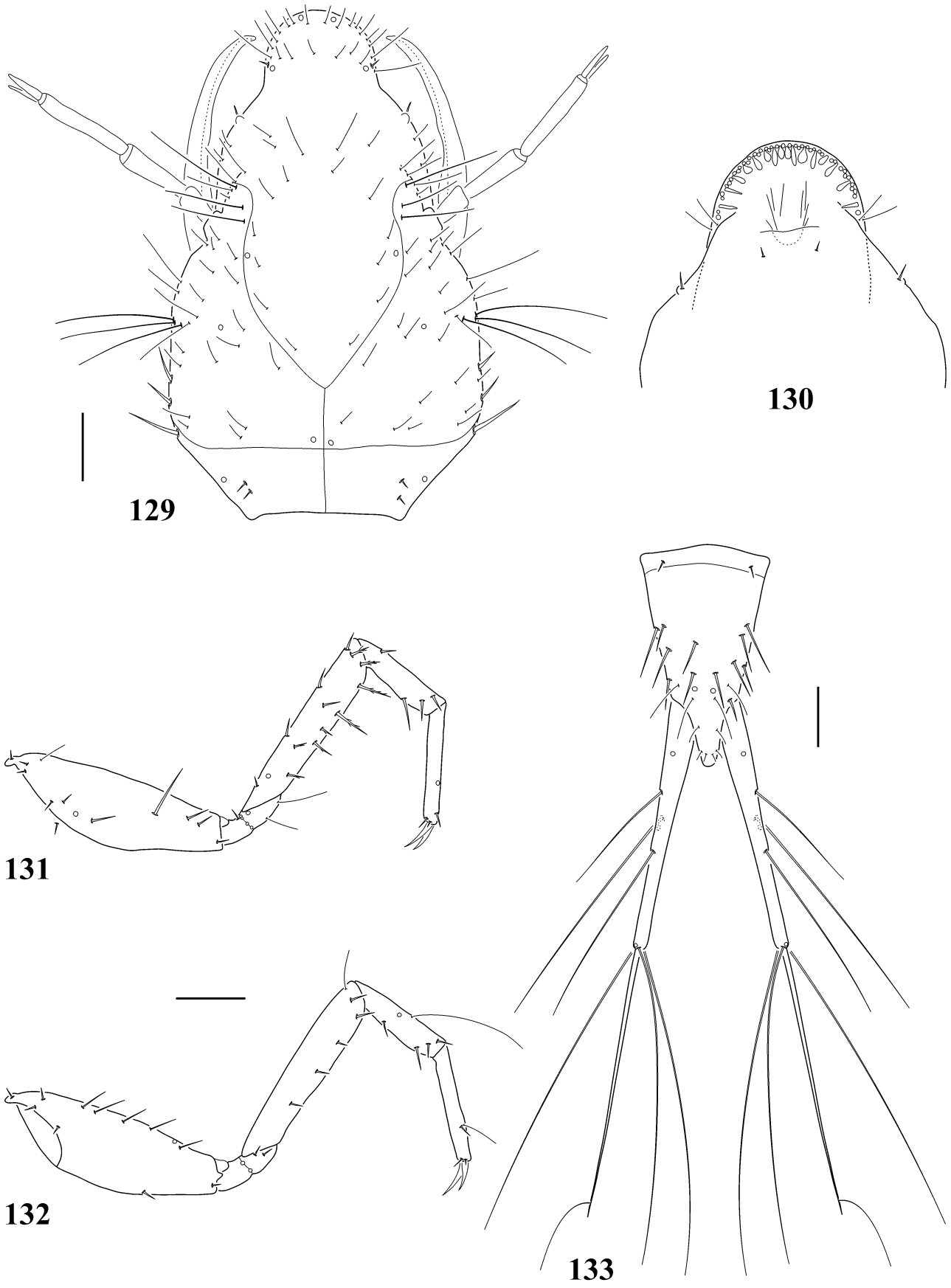
Segment	Position	*L. amabilis*	*L. bigbellensis*	*L. challaensis*	*L. cooperi*	*L. eberhardi*
Coxa	A	3–4 / 3–5 / 3–4	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	P	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PD	5–7 / 7–8 / 5–9	3–6 / 3–4 / 3	2 / 3 / 1	4 / 4 / 3	3 / 5 / 5
	V	5 / 4–6 / 7–8	2 / 1–2 / 1	2 / 1 / 0	5 / 4 / 2	1 / 1 / 2
	Total	14–15 / 16–17 / 17–19	5–8 / 5 / 4	4 / 4 / 1	9 / 8 / 5	4 / 6 / 7
Trochanter	Pr	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	Total	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
Femur	AD	2–4 / 2–4 / 5–9	3–6 / 4–5 / 5–7	2 / 2 / 2	– / – / 9	2 / 2 / 4
	AV	6–7 / 6–10 / 6–7	4–5 / 3 / 3–6	4 / 4 / 6	– / – / 13	8 / 5 / 7
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	– / – / 0	0 / 0 / 0
	PV	5–8 / 7–8 / 8–10	4–5 / 7 / 8	4 / 3 / 5	– / – / 9	6 / 5 / 8
	Total	14–18 / 17–20 / 20–25	11–16 / 14–15 / 16–21	10 / 9 / 13	– / – / 31	16 / 12 / 19
Tibia	AD	2 / 1 / 2	0–1 / 0–1 / 1	1 / 1 / 1	– / – / 2	1 / 1 / 1
	AV	1 / 3 / 4–5	1 / 2–3 / 3–4	0 / 2 / 3	– / – / 7	3 / 5 / 8
	PD	0 / 1 / 1	5 / 5–7 / 5	0 / 1 / 1	– / – / 4	1 / 3 / 3
	PV	3 / 5 / 5–6	1–2 / 2–3 / 5	1 / 1 / 2	– / – / 6	3 / 4 / 3
	Total	6 / 10 / 13	8 / 9–14 / 14–15	2 / 5 / 7	– / – / 19	8 / 13 / 15
Tarsus	AD	1 / 1 / 1–2	1–2 / 0 / 0	0 / 0 / 0	– / – / 1	0 / 1 / 3
	AV	0 / 0 / 2–3	0 / 3–6 / 4–5	0 / 2 / 2	– / – / 4	1 / 6 / 8
	PD	0 / 0 / 0	0 / 3–4 / 5	0 / 1 / 1	– / – / 3	3 / 4 / 3
	PV	1 / 3 / 3–4	3 / 2–4 / 2	0 / 0 / 0	– / – / 3	3 / 4 / 5
	Total	2 / 4 / 7–8	4–5 / 8–14 / 11–12	0 / 3 / 3	– / – / 11	7 / 15 / 19



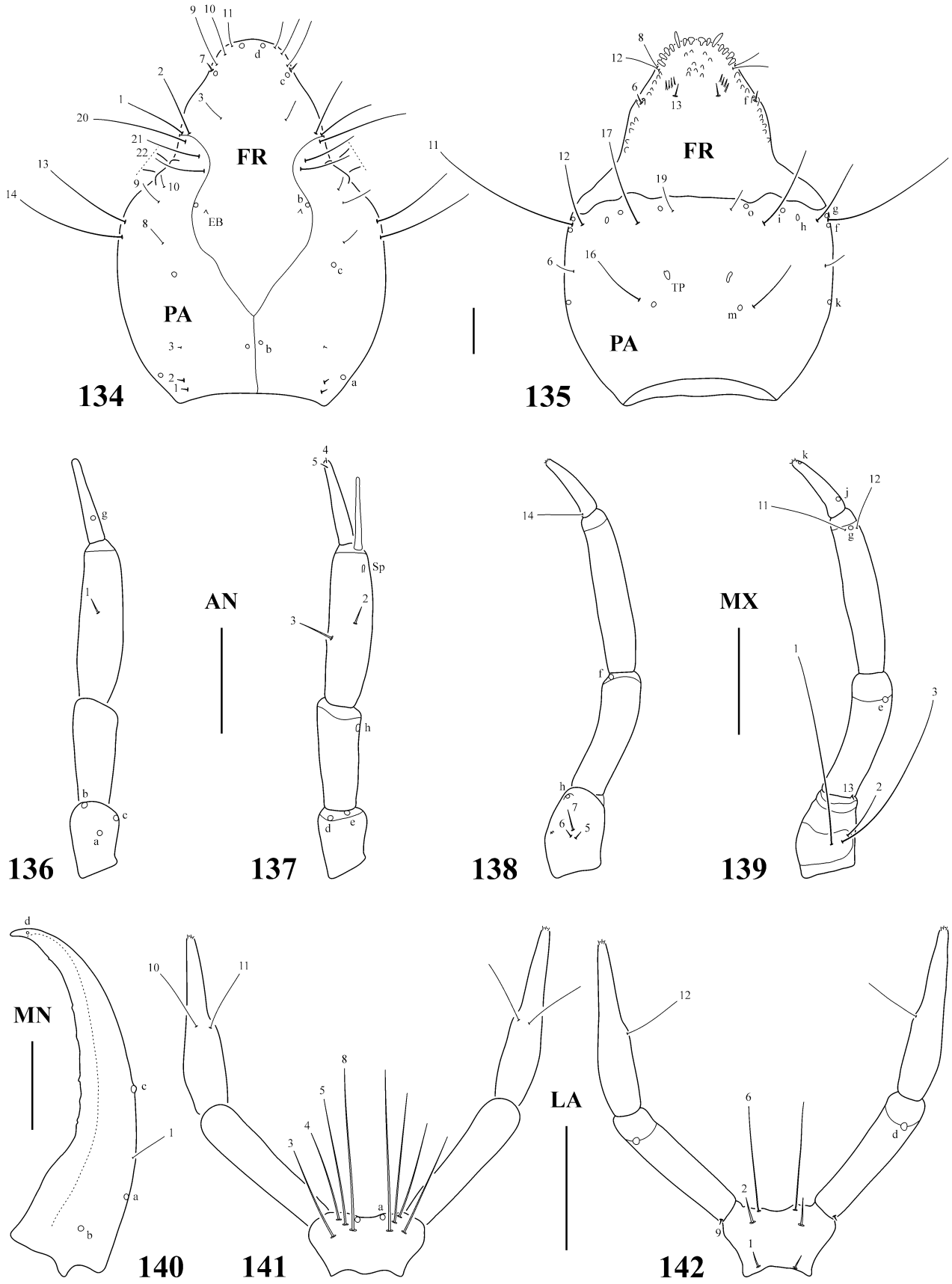
FIGURES 115–123. *Limbodessus millbilliensis*, first-instar larva. 115, cephalic capsule, dorsal aspect; 116, cephalic capsule, ventral aspect; 117, right antenna, dorsal aspect; 118, left antenna, ventral aspect; 119, right maxilla, dorsal aspect; 120, left maxilla, ventral aspect; 121, right mandible, dorsal aspect; 122, labium, dorsal aspect; 123, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.05 mm.



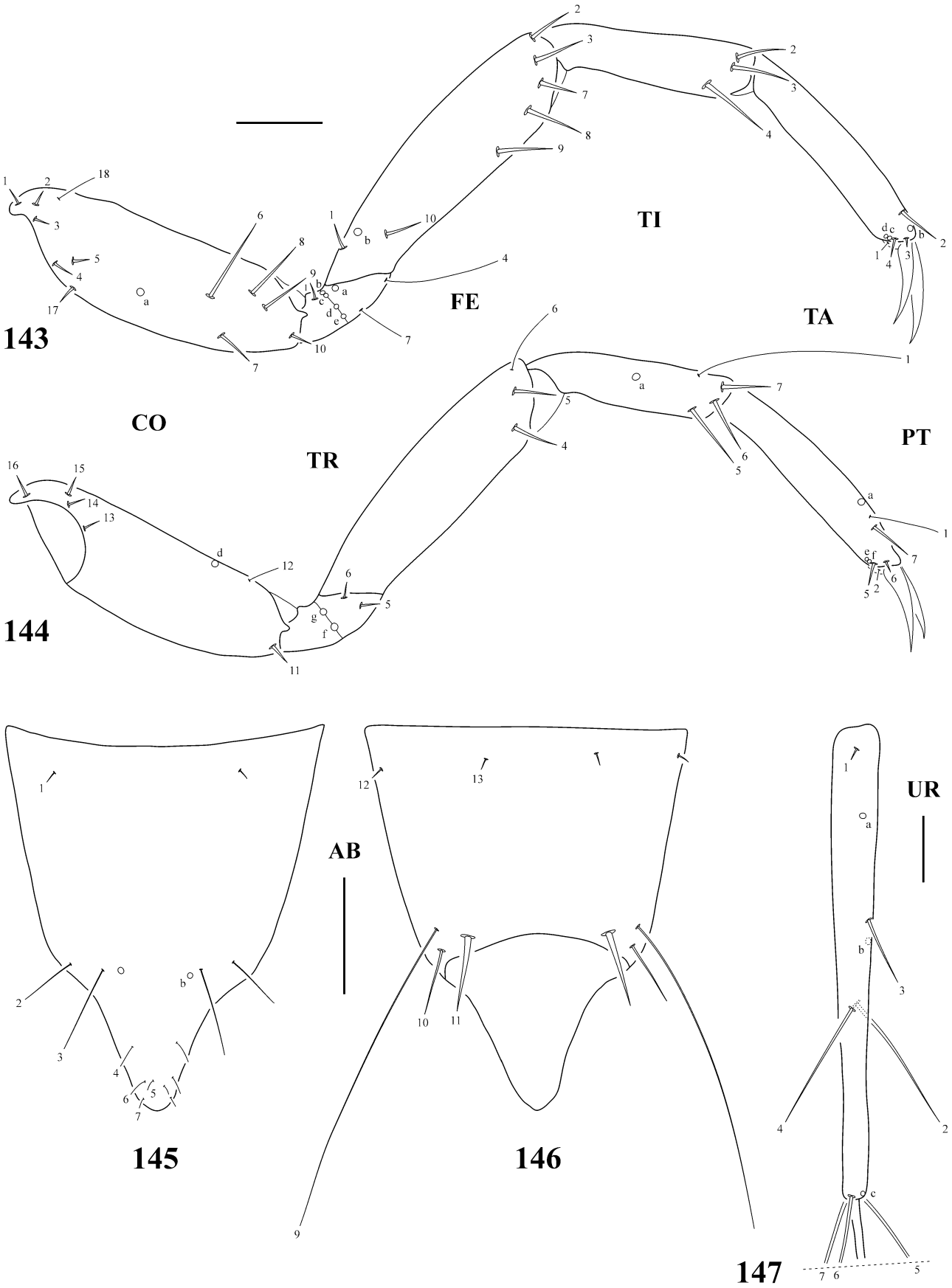
FIGURES 124–128. *Limbodessus millbilliensis*, first-instar larva. 124, left metathoracic leg, anterior aspect; 125, right metathoracic leg, posterior aspect; 126, abdominal segment VIII, dorsal aspect; 127, abdominal segment VIII, ventral aspect; 128, right urogomphus, dorsal aspect. Scale bars = 0.07 mm.



FIGURES 129–133. *Limbodessus millbilliensis*, third-instar larva. 129, head, dorsal aspect; 130, nasale, ventral aspect; 131, left prothoracic leg, anterior aspect; 132, right prothoracic leg, posterior aspect; 133, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.



FIGURES 134–142. *Limbodessus mirandaae*, first-instar larva. 134, cephalic capsule, dorsal aspect; 135, cephalic capsule, ventral aspect; 136, right antenna, dorsal aspect; 137, left antenna, ventral aspect; 138, right maxilla, dorsal aspect; 139, left maxilla, ventral aspect; 140, right mandible, dorsal aspect; 141, labium, dorsal aspect; 142, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.07 mm.



FIGURES 143–147. *Limbodessus mirandaae*, first-instar larva. 143, left metathoracic leg, anterior aspect; 144, right metathoracic leg, posterior aspect; 145, abdominal segment VIII, dorsal aspect; 146, abdominal segment VIII, ventral aspect; 147, right urogomphus, dorsal aspect. Scale bars = 0.07 mm.

***Limbodessus mirandaae* Watts & Humphreys, 2006**
(Figs 134–147)

Source of material. One specimen of instar I was used for the description (Table 1). The larva was collected at the following locality: **Australia, Carey palaeovalley**, Miranda West calcrete, Yacabindie Station, BES 10478 & 84, 6–VI–2004, coll. W. F. Humphreys and C. H. S. Watts. The larva studied was determined by comparing the sequence of a fragment of the CO1 gene with that of a known adult.

Diagnosis. No diagnosis is provided owing to a lack of specimens of instars II and III.

Instar I (Figs 134–147). Head (Figs 134–142). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 2.20–2.75 times longer than A1; A3 more than 2.25 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 less than 1.30 times longer than LP1. Legs (Figs 143–144). L3 less than 2.85 times longer than HW. Abdomen (Figs. 145–147). Chaetotaxy. Frontoclypeus with 14 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 3.

Instar II. Not available.

Instar III. Not available.

Remarks. This species was described on the basis of a single instar I with the second urogomphomere broken, which prevented the evaluation of urogomphal morphometry. The species is not diagnosed above because of lack of instars II and III. However, it can be separated from the other species described as instar I by the combination of characters given under the description.

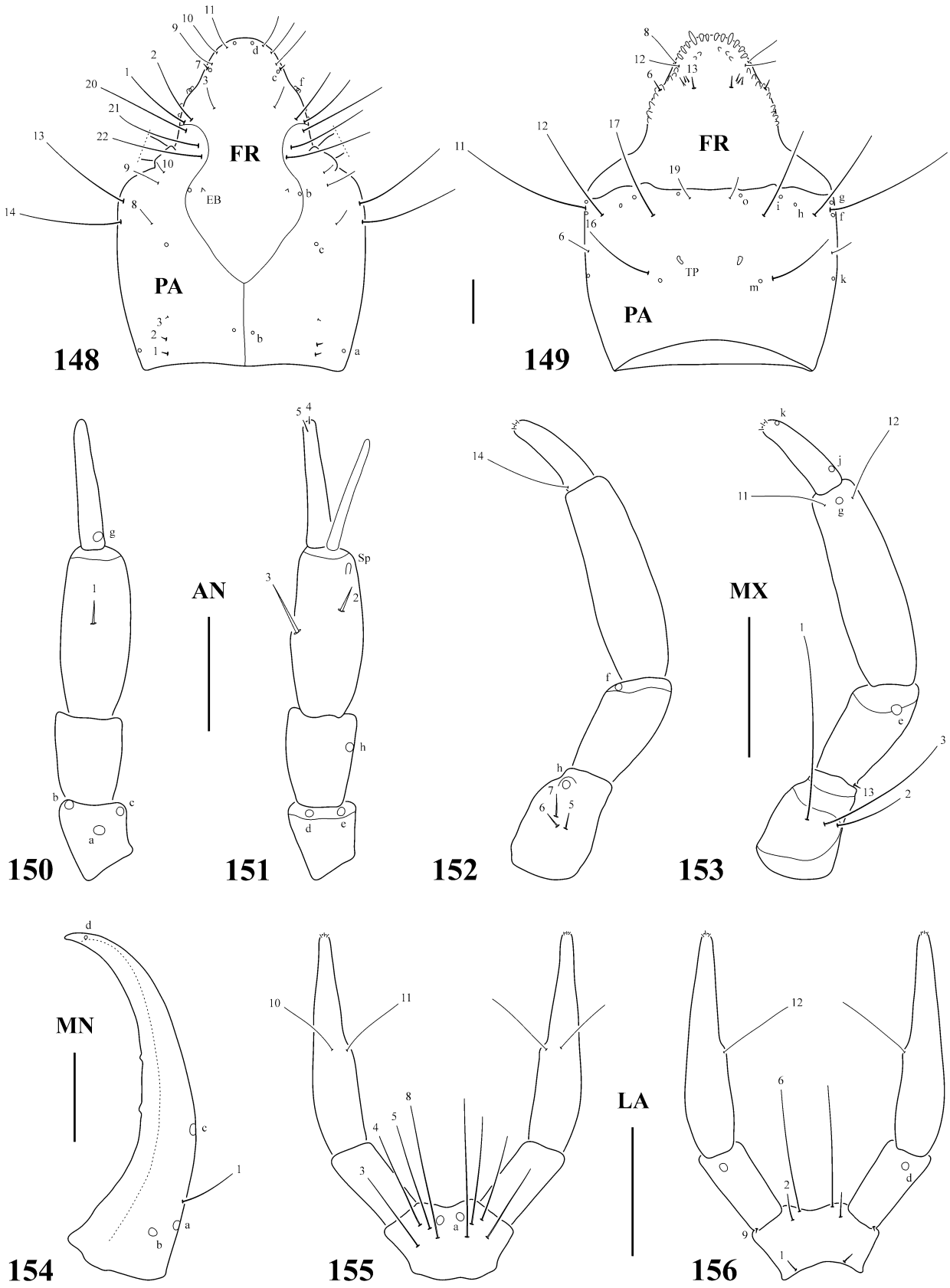
***Limbodessus morgani* (Watts & Humphreys, 2000)**
(Figs 148–161)

Source of material. One specimen of instar I and one of instar II were used for the description (Table 1). Larvae were collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Uramurdah Lake calcrete, NE Lake Way, No 7, site 285, BES 6450, 26.85444S, 120.33833E, 9-V-2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper.

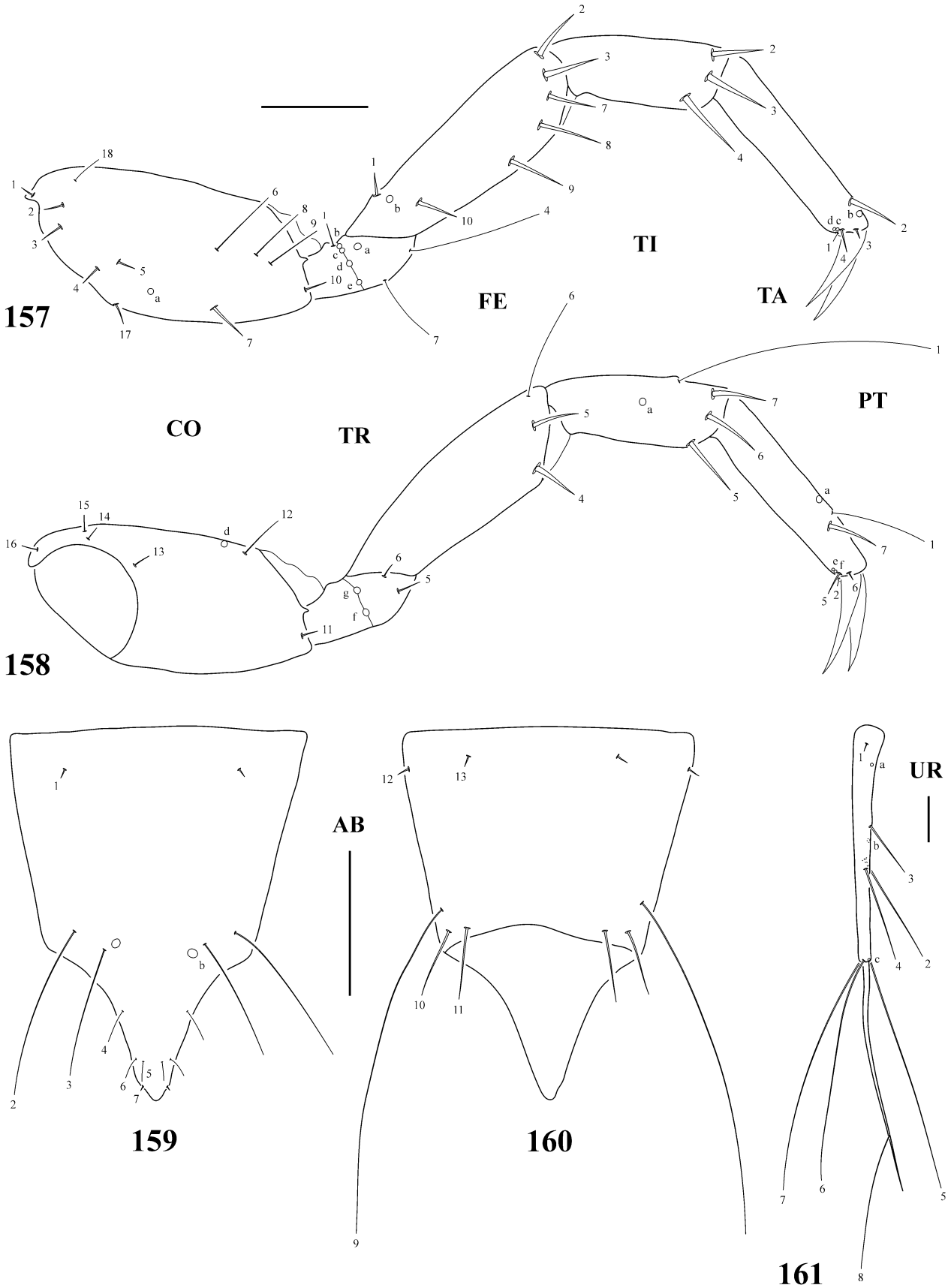
Diagnosis (instar II). Smaller species (HL less than 0.40 mm); head subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.75); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent.

Instar I (Figs 148–161). Head (Figs 148–156). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted contiguous to setae PA1 and PA2; A3 more than 2.80 times longer than A1; A3 less than 2.05 times longer than A2; MP2 more than 2.10 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 more than 2.40 times longer than LP1. Legs (Figs 157–158). L3 less than 2.85 times longer than HW. Abdomen (Figs 159–161). U more than 3.75 times longer than LAS; U less than 2.35 times longer than HW; U1 less than 1.05 times longer than U2. Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U absent. Measurements

Instar II. Head. A3 less than 2.50 times longer than A1; A4 more than 0.75 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 less than 2.05 times longer than MP3; LP2 more than 1.75 times longer than LP1. Legs. L3 less than 2.20 times longer than HW; CL(L3) more than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U less than 2.15 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 22 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on proCO absent; ventral secondary setae on mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on meso- and metaTI absent; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 6. Secondary leg setation detailed in Table 14.



FIGURES 148–156. *Limbodessus morgani*, first-instar larva. 148, cephalic capsule, dorsal aspect; 149, cephalic capsule, ventral aspect; 150, right antenna, dorsal aspect; 151, left antenna, ventral aspect; 152, right maxilla, dorsal aspect; 153, left maxilla, ventral aspect; 154, right mandible, dorsal aspect; 155, labium, dorsal aspect; 156, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.04 mm.



FIGURES 157–161. *Limbodessus morgani*, first-instar larva. 157, left metathoracic leg, anterior aspect; 158, right metathoracic leg, posterior aspect; 159, abdominal segment VIII, dorsal aspect; 160, abdominal segment VIII, ventral aspect; 161, right urogomphus, dorsal aspect. Scale bars = 0.05 mm.

Instar III. Not available.

Remarks. The absence of instar III specimens of *L. morgani* hampers the comparison with the other species described here, particularly regarding the chaetotaxic characters. *Limbodessus morgani* has a small size and belongs to the group of stygobitic species that lack secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*). Within this group, it can be separated by the following combination of characters: lateral margins of the nasale not inflated in dorsal view, and claws relatively longer as compared to tarsus (ratio CL/TA > 0.40). This last feature separates *L. morgani* from all other stygobitic species studied except *L. fridaywellensis*.

Limbodessus nambiensis Watts & Humphreys, 2006

(Figs 162–175)

Source of material. One specimen of instar I and one of instar II were used for the description (Table 1). Larvae were collected at the following localities: **Australia, Carey palaeovalley**, Nambi calcrete, MEB site 106, BES 10314, 28.23974S, 121.83632E, 21–III–2004, coll. W. F. Humphreys and S. J. B. Cooper; Nambi calcrete, MEB site 105, BES 10316, 28.24039S, 121.83721E, 21–III–2004, coll. W. F. Humphreys and S. J. B. Cooper. The larvae studied were determined by comparing the sequence of a fragment of the CO1 gene with that of a known adult.

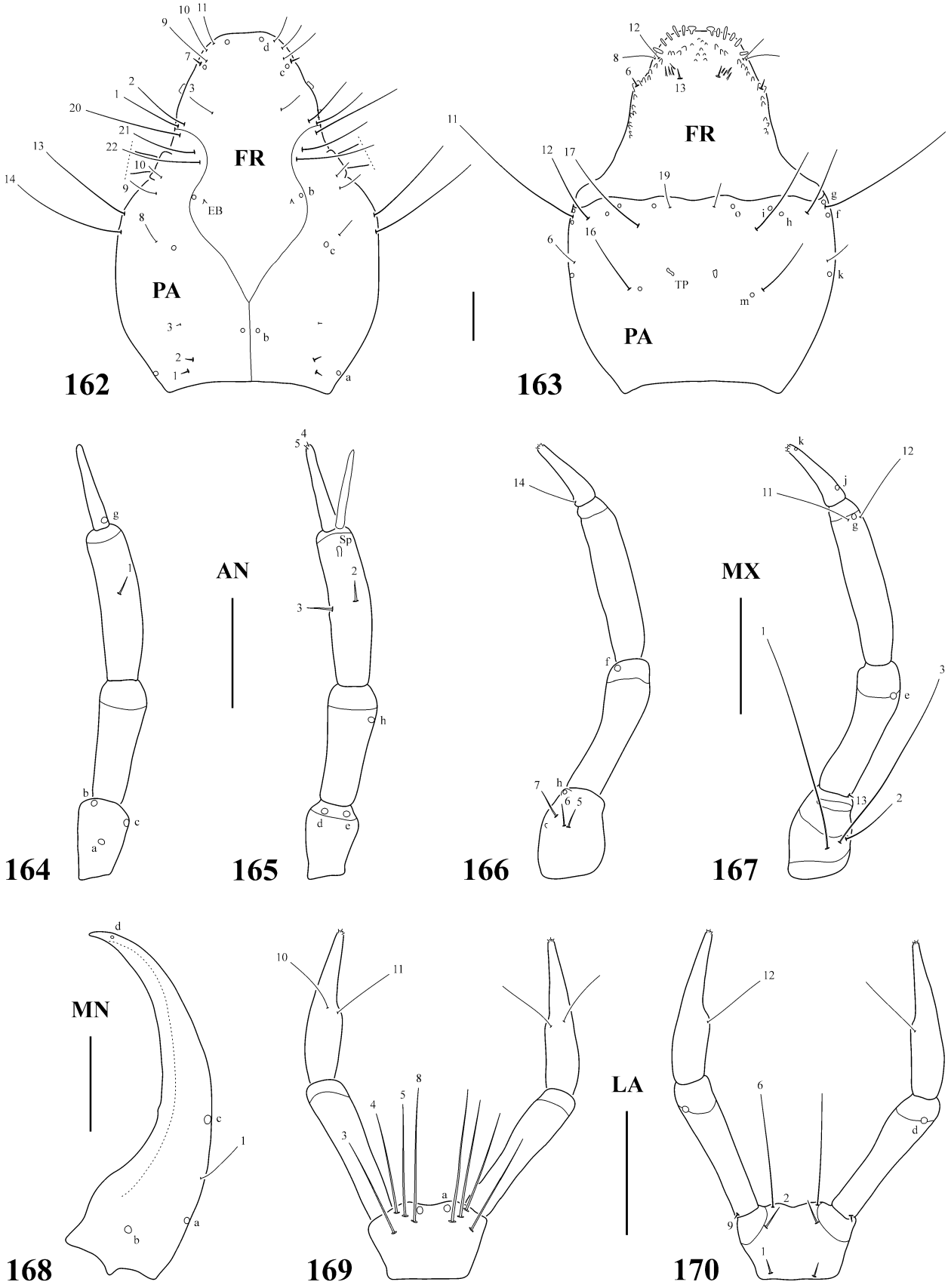
Diagnosis (instar II). Medium-sized species (instar II: HL 0.45–0.85 mm); head subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen moderately reduced (instar II: HW/OCW 0.80–2.10); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal numerous; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U present.

Instar I (Figs 162–175). Head (Figs 162–170). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 less than 2.15 times longer than A1; A3 more than 2.25 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 less than 1.30 times longer than LP1. Legs (Figs 171–172). L3 less than 2.85 times longer than HW. Abdomen (Figs 173–175). U 3.60–3.70 times longer than LAS; U less than 2.35 times longer than HW; U1 more than 1.45 times longer than U2. Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 3.

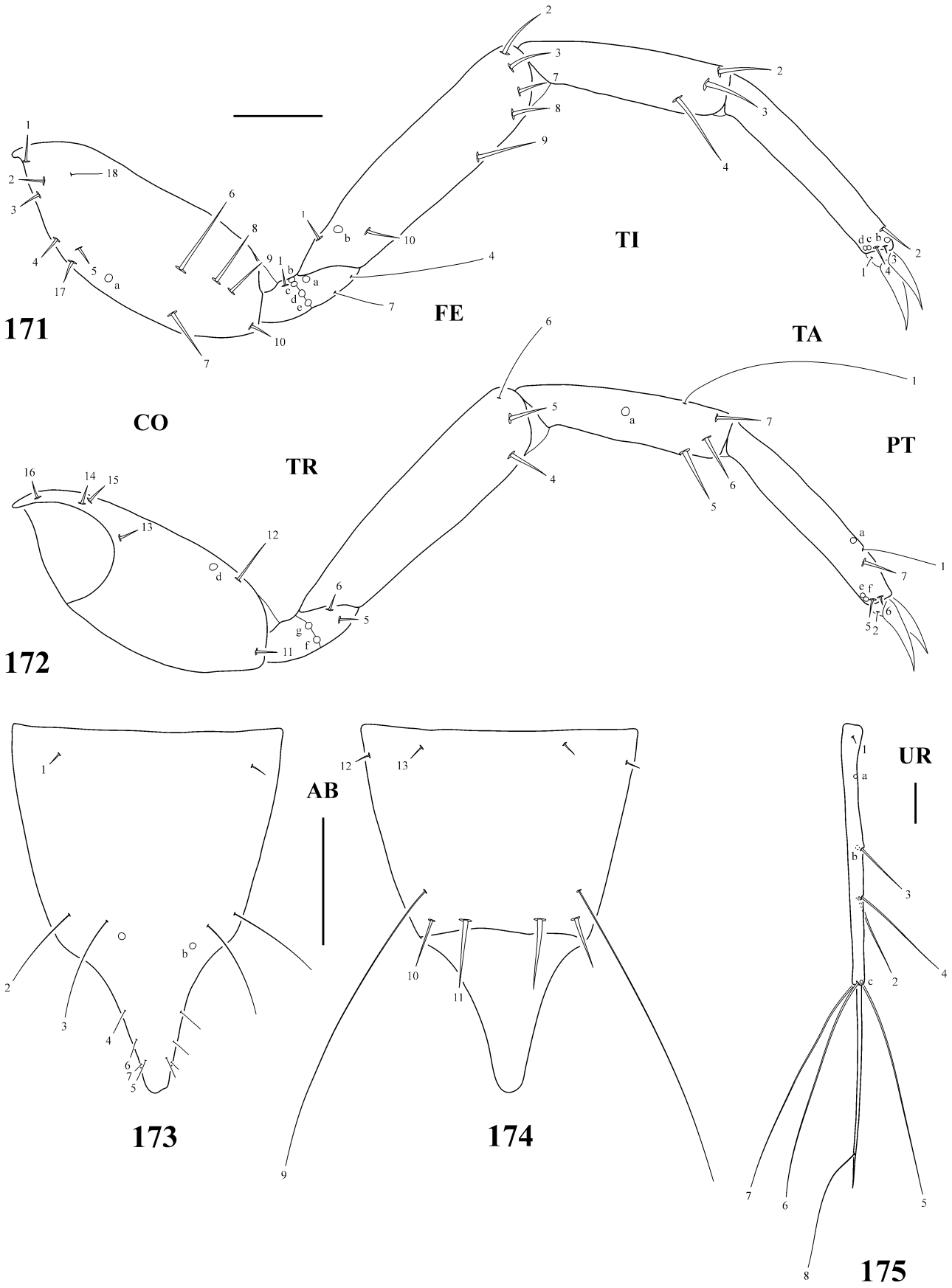
Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 less than 1.05 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 less than 0.90 times as long as LP1. Abdomen. U 3.00–4.00 times longer than LAS; U less than 2.15 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 36 lamellae clypeales distributed in a single row; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 6.

Instar III. Not available.

Remarks. The description of *L. nambiensis* is based on one well preserved instar I and one instar II in which the legs are lacking. For this reason, morphometric and chaetotaxic characters could not be evaluated. The absence of instar III specimens hampers the comparison with the other species described here, particularly regarding the chaetotaxic characters. *Limbodessus nambiensis* belongs to the group of stygobitic species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis*, *L. bigbellensis*, *L. cooperi*, *L. eberhardi*, *L. macrohinkleri*, *L. raesideensis*, *L. yandalensis*), and within this group it can be distinguished by the following combination of characters: smaller size, head subpentagonal, occipital suture present, and occipital foramen moderately reduced.



FIGURES 162–170. *Limbodessus nambiensis*, first-instar larva. 162, cephalic capsule, dorsal aspect; 163, cephalic capsule, ventral aspect; 164, right antenna, dorsal aspect; 165, left antenna, ventral aspect; 166, right maxilla, dorsal aspect; 167, left maxilla, ventral aspect; 168, right mandible, dorsal aspect; 169, labium, dorsal aspect; 170, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.07 mm.



FIGURES 171–175. *Limbodessus nambiensis*, first-instar larva. 171, left metathoracic leg, anterior aspect; 172, right metathoracic leg, posterior aspect; 173, abdominal segment VIII, dorsal aspect; 174, abdominal segment VIII, ventral aspect; 175, right urogomphus, dorsal aspect. Scale bars = 0.07 mm.

***Limbodessus ordinarius* Watts & Humphreys, 2009**
(Figs 176–179)

Source of material. Three specimens of instar II and three of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following locality: **Australia, Raeside palaeovalley**, Black Range North calcrete, MRB 160, BES 13224, 27.8286S, 119.3213E, 2–IV–2006, coll. W. F. Humphreys and S. J. B. Cooper.

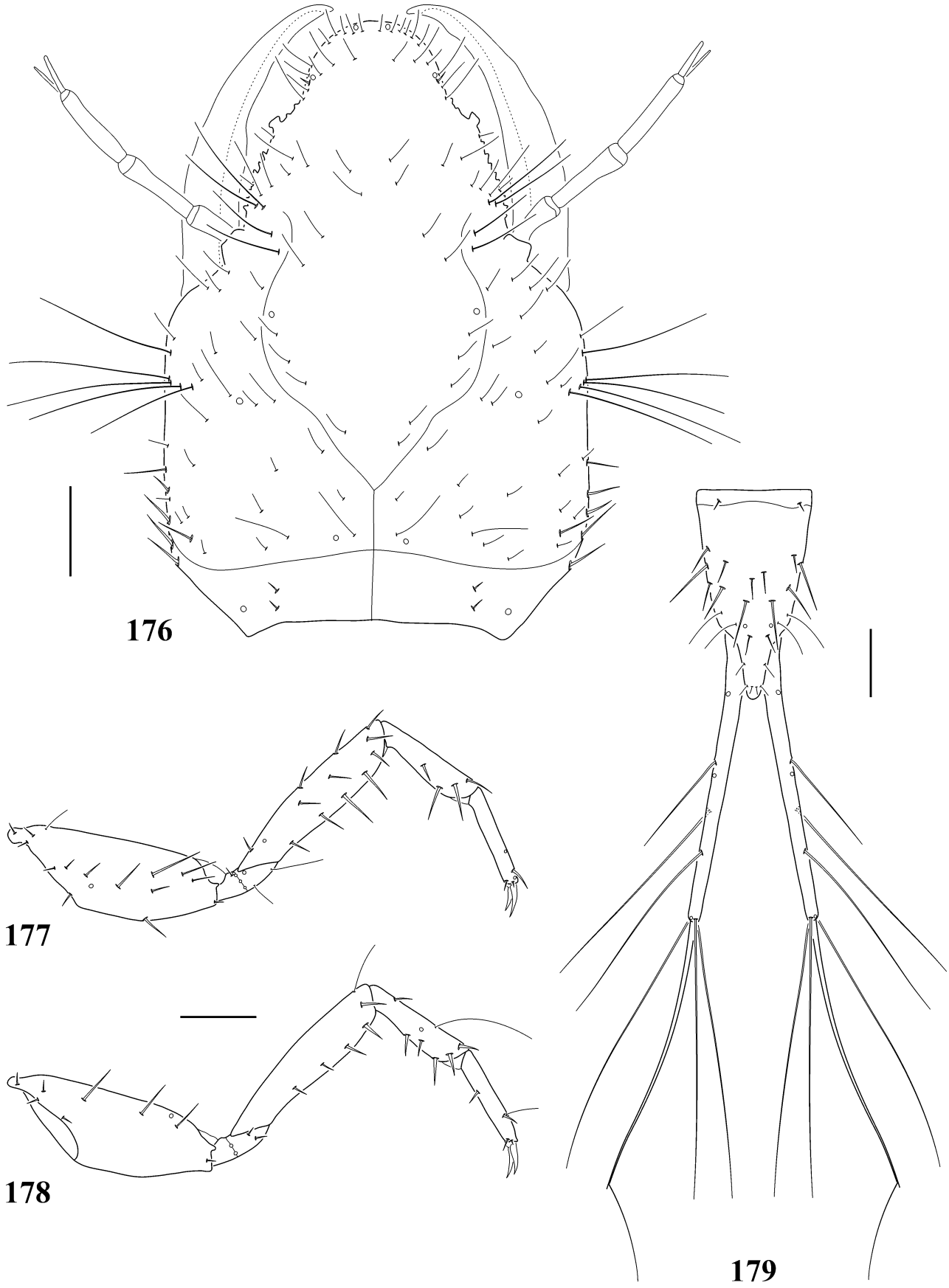
Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 176) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 179).

Instar I. Not available.

Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 less than 1.05 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U less than 2.15 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 26 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; mesoTI with less than 2 posterodorsal secondary setae; metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on proTI present; posteroventral secondary setae on meso- and metaTI absent; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 6. Secondary leg setation detailed in Table 14.

Instar III (Figs 176–179). Head (Fig. 176). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 177–178). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 179). U 2.40–3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 53 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI absent; anteroventral and posterodorsal secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal and posteroventral secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 11. Secondary leg setation detailed in Table 19.

Remarks. *Limbodessus ordinarius* belongs to the group of species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. pulpa*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 179), from which it is distinguished by the following combination of characters: lateral margins of the nasale not inflated in dorsal view (Fig. 176), absence of anterodorsal secondary setae on the protibia (Fig. 177), presence of anteroventral and posterodorsal secondary setae on the protibia (Figs 177–178), and absence of anteroventral secondary setae on the protarsus (Fig. 177).



FIGURES 176–179. *Limbodessus ordinarius*, third-instar larva. 176, head, dorsal aspect; 177, left prothoracic leg, anterior aspect; 178, right prothoracic leg, posterior aspect; 179, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.15 mm.

TABLE 17. Number and position of secondary setae on the legs of third-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. exilis*	*L. fridaywellensis*	*L. hillviewensis*	*L. hinkleri*
Coxa	A	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / – / –
	P	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / – / –
	PD	3–5 / 3–5 / 1–3	3 / 3 / 2	3 / 5 / 2	2 / – / –
	V	2 / 1 / 1	2 / 1 / 1	2 / 1 / 1	1 / – / –
	Total	5–7 / 4–6 / 2–4	5 / 4 / 3	5 / 6 / 3	3 / – / –
Trochanter	Pr	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / – / –
	Total	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / – / –
Femur	AD	1–2 / 2 / 2	0 / 1 / 0	2 / 2 / 2	4 / – / –
	AV	3 / 2 / 3–4	1 / 2 / 1	3 / 3 / 4	1 / – / –
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / – / –
	PV	2–3 / 2–3 / 4–5	2 / 3 / 3	3 / 4 / 4	3 / – / –
	Total	7 / 7–8 / 10	3 / 6 / 4	8 / 9 / 10	8 / – / –
Tibia	AD	1 / 1 / 1	1 / 1 / 1	1 / 1 / 1	1 / – / –
	AV	1 / 2–3 /2–4	0 / 1 / 2	0 / 3 / 3	0 / – / –
	PD	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / – / –
	PV	2 / 2 / 2–4	1 / 1 / 1	1 / 1 / 2	1 / – / –
	Total	4 / 6–7 / 6–10	2 / 4 / 5	2 / 6 / 7	2 / – / –
Tarsus	AD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / – / –
	AV	0 / 2 / 3	0 / 0 / 0	0 / 1 / 2	0 / – / –
	PD	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1	0 / – / –
	PV	0 / 0–1 / 1	0 / 0 / 0	0 / 0 / 0	0 / – / –
	Total	0 / 3–4 / 5	0 / 1 / 1	0 / 2 / 3	0 / – / –

Limbodessus palmulaoides Watts & Humphreys, 2006

(Figs 180–193)

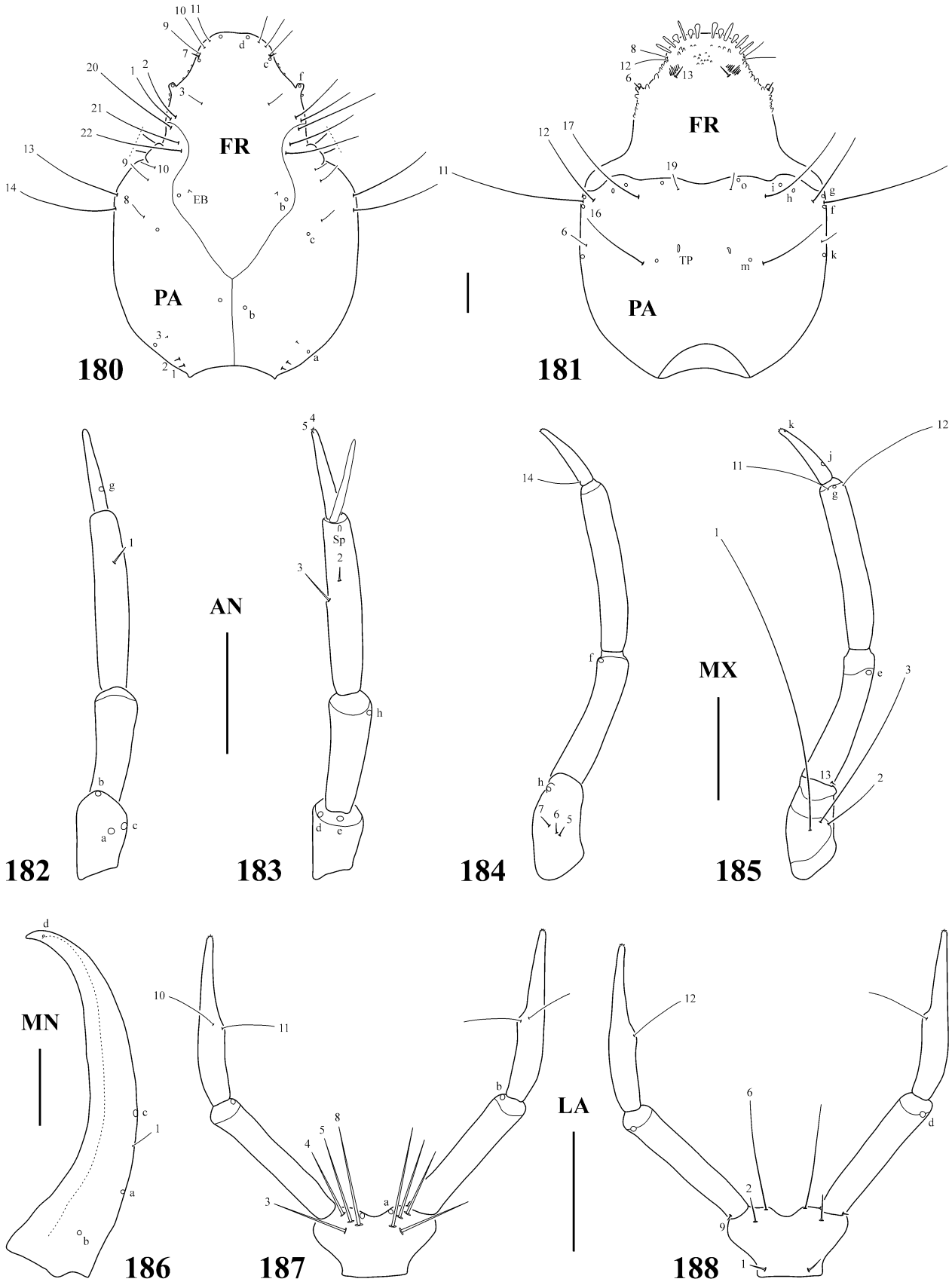
Source of material. One specimen of instar I was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Mounth Windarra calcrete, MEB site 73, BES 10292, 28.39652S, 122.19766E, 20–III–2004, coll. W. F. Humphreys and S. J. B. Cooper.

Diagnosis. No diagnosis is provided owing to a lack of specimens of instars II and III.

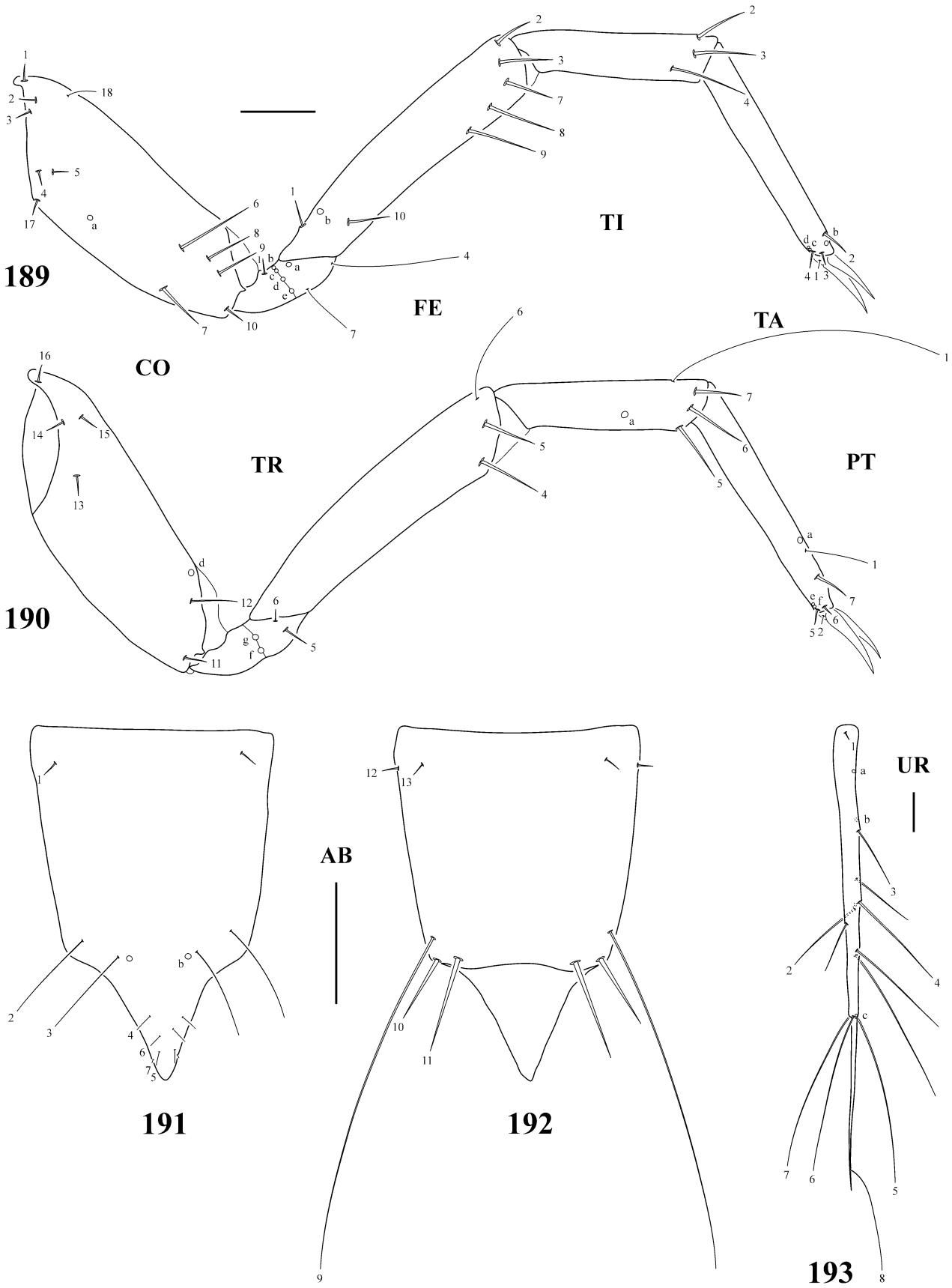
Instar I (Figs 180–193). Head (Figs 180–188). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 less than 2.15 times longer than A1; A3 (instar I): (0) less than 2.05 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 less than 1.30 times longer than LP1. Legs (Figs 189–190). L3 less than 2.85 times longer than HW. Abdomen (Figs 191–193). U more than 3.75 times longer than LAS; U less than 2.35 times longer than HW; U1 more than 1.45 times longer than U2. Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U present. Measurements and ratios that characterize the body shape are shown in Table 3.

Instar II. Not available.

Instar III. Not available.



FIGURES 180–188. *Limbodessus palmulaoides*, first-instar larva. 180, cephalic capsule, dorsal aspect; 181, cephalic capsule, ventral aspect; 182, right antenna, dorsal aspect; 183, left antenna, ventral aspect; 184, right maxilla, dorsal aspect; 185, left maxilla, ventral aspect; 186, right mandible, dorsal aspect; 187, labium, dorsal aspect; 188, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.10 mm.



FIGURES 189–193. *Limbodessus palmulaoides*, first-instar larva. 189, left metathoracic leg, anterior aspect; 190, right metathoracic leg, posterior aspect; 191, abdominal segment VIII, dorsal aspect; 192, abdominal segment VIII, ventral aspect; 193, right urogomphus, dorsal aspect. Scale bars = 0.10 mm.

Remarks. The species is not diagnosed above because of lack of instars II and III. However, it can be separated from all the other species described as instar I by the presence of additional setae on the urogomphus (Fig. 193), a unique feature within the taxa examined, and by the combination of characters given under the description.

Limbodessus pulpa (Watts & Humphreys, 1999)

(Figs 194–207)

Source of material. Two specimens of instar I and one of instar II were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Carey palaeovalley**, Paroo calcrete, GSWA 6 central, BES 5606, 26.43389S, 119.77667E, 7–V–2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper; Paroo calcrete, BES 5617, 7–V–2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper; Paroo calcrete, GSWA 6NE, BES 8132, 26.43389S, 119.77722E, 21–VIII–2001, coll. W. F. Humphreys, T. Karanovic and J. M. Waldock.

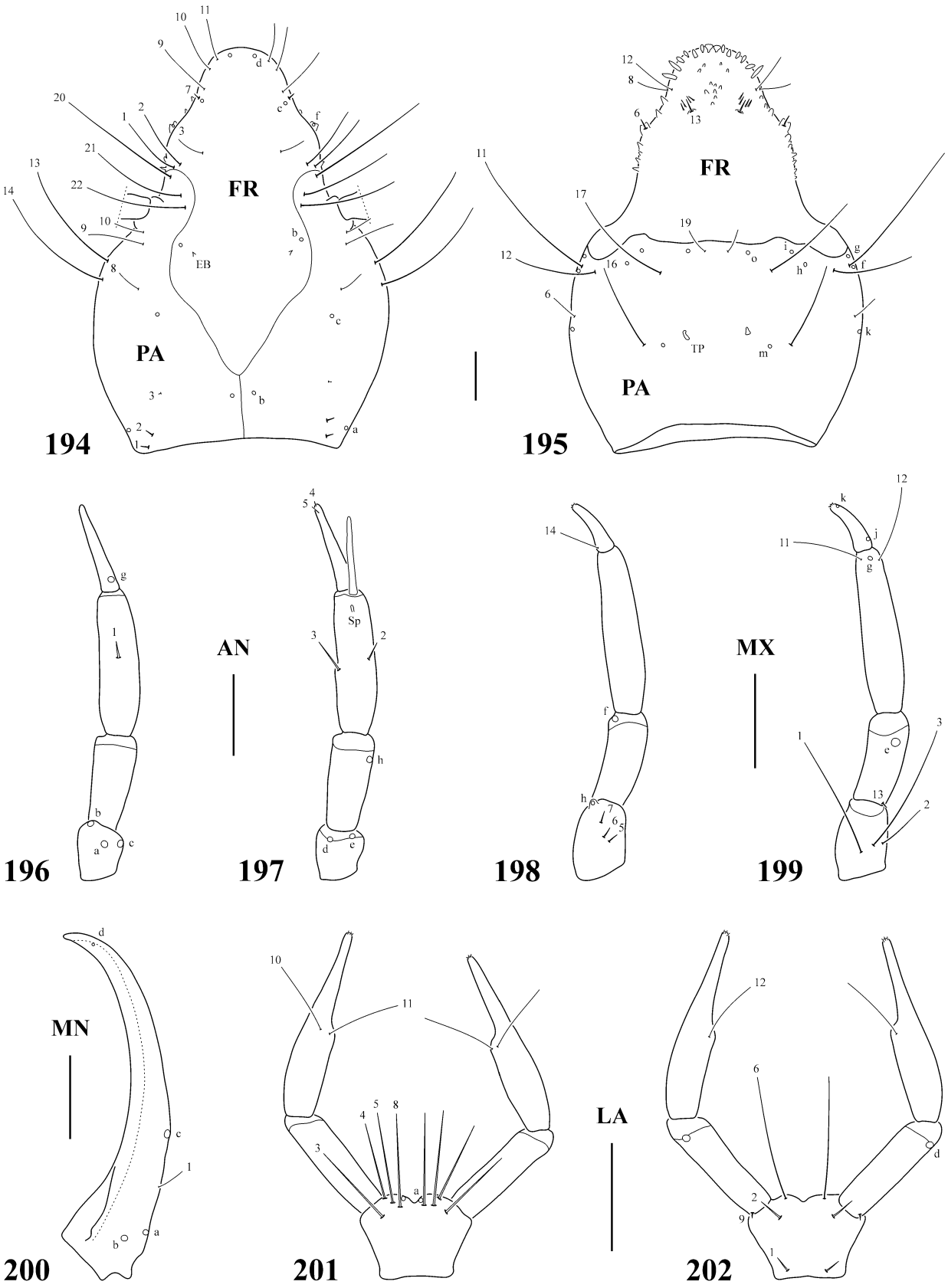
Diagnosis (instar II). Medium-sized species (instar II: HL 0.45–0.85 mm); head subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (instar II: HW/OCW less than 1.75); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent.

Instar I (Figs 194–207). Head (Figs 194–202). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 2.20–2.75 times longer than A1; A3 more than 2.25 times longer than A2; MP2 1.55–1.85 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 203–204). L3 less than 2.85 times longer than HW. Abdomen (Figs 205–207). U less than 3.45 times longer than LAS; U less than 2.35 times longer than HW; U1 1.10–1.40 times longer than U2. Chaetotaxy. Frontoclypeus with 14 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 4.

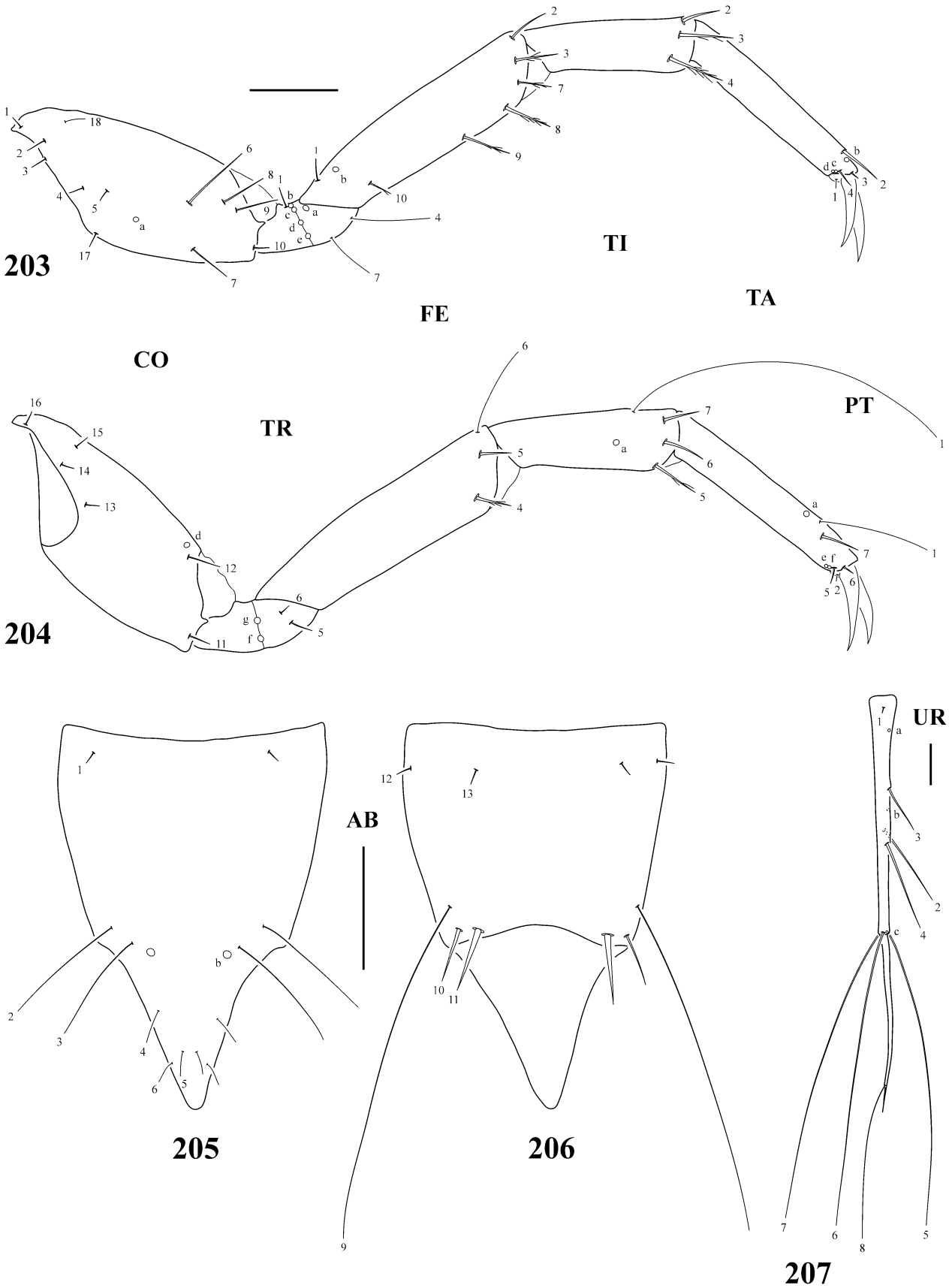
Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Chaetotaxy. Anteroventral margin of nasale with 29 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on meso- and metaTI absent; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 6. Secondary leg setation detailed in Table 14.

Instar III. Not available.

Remarks. The description of *L. pulpa* is based on two well preserved instar I and one instar II in which the second urogomphomere is broken. For this reason, morphometric characters could not be evaluated for the urogomphus of instar II. The absence of instar III specimens hampers the comparison with the other species described here, particularly regarding the chaetotaxic characters. *Limbodessus pulpa* belongs to the group of species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. raeae*, *L. windarraensis*, *L. yuinmeryensis*), and within this group is likely to be distinguished by the following combination of characters: lateral margins of the nasale not inflated in dorsal view, lateral margins of parietal curved, and claws relatively shorter as compared to tarsus (ratio CL/TA < 0.40). Watts & Humphreys (1999) described a *Limbodessus* larva identified as “Larva form 2” from the same locality (Paroo calcrete) where the specimens of *L. pulpa* described here were collected. A comparison with the drawings provided by Watts & Humphreys (1999) strongly suggests that the specimen identified as “Larva form 2” is indeed *L. pulpa*. A drawing of the habitus of this species was presented by Watts & Humphreys (1999).



FIGURES 194–202. *Limbodessus pulpa*, first-instar larva. 194, cephalic capsule, dorsal aspect; 195, cephalic capsule, ventral aspect; 196, right antenna, dorsal aspect; 197, left antenna, ventral aspect; 198, right maxilla, dorsal aspect; 199, left maxilla, ventral aspect; 200, right mandible, dorsal aspect; 201, labium, dorsal aspect; 202, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.05 mm.



FIGURES 203–207. *Limbodessus pulpa*, first-instar larva. 203, left metathoracic leg, anterior aspect; 204, right metathoracic leg, posterior aspect; 205, abdominal segment VIII, dorsal aspect; 206, abdominal segment VIII, ventral aspect; 207, right urogomphus, dorsal aspect. Scale bars = 0.06 mm.

***Limbodessus raeae* Watts & Humphreys, 2006**
(Figs 208–211)

Source of material. One specimen of instar III was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Hinkler Well calcrete, Lake Way Station, Dawson's Well, BES 14305, 28.8866S, 120.1621E, 17–IX–2006, coll. W. F. Humphreys and T. Moulds.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 208) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 211).

Instar I. Not available.

Instar II. Not available.

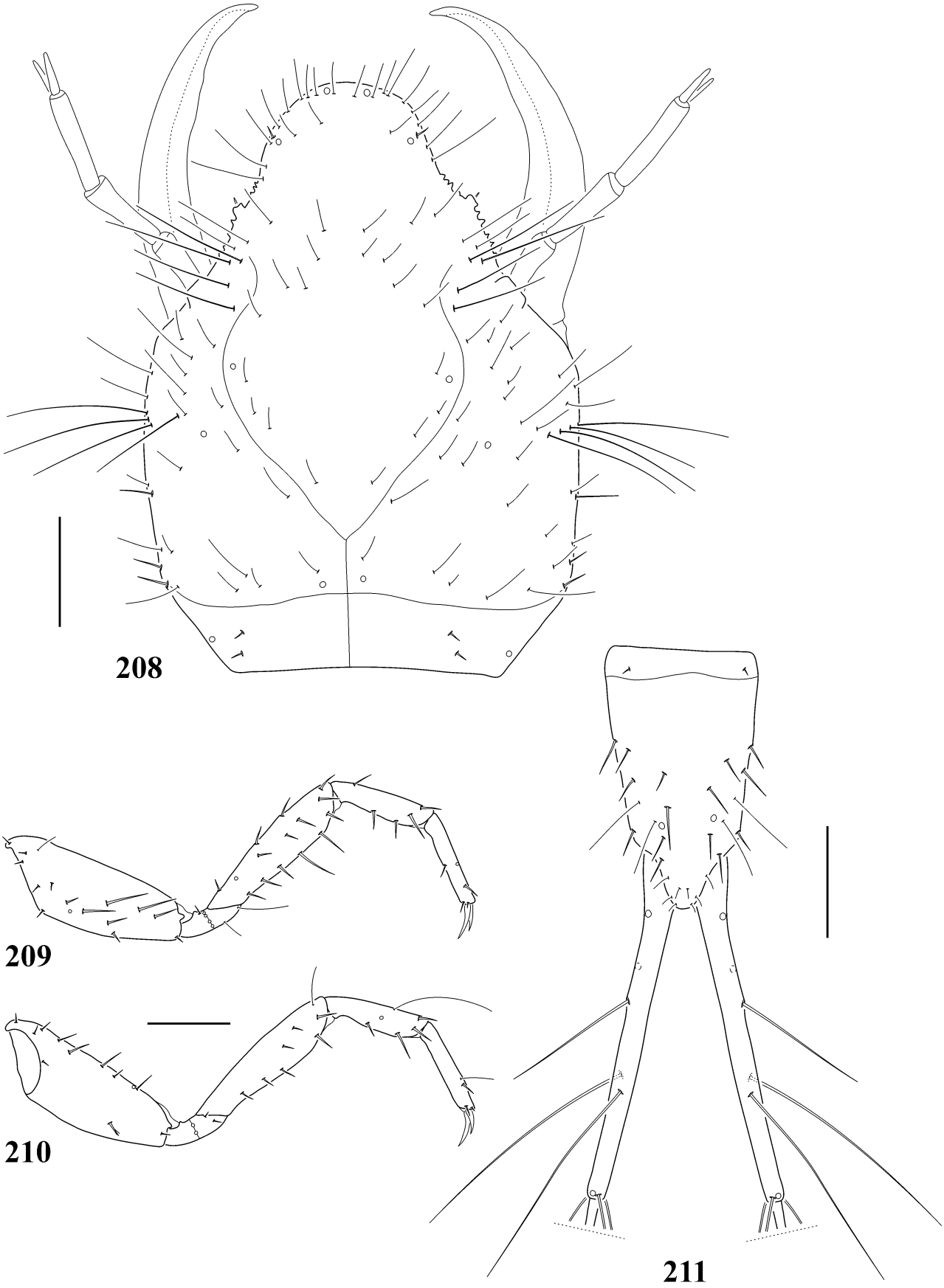
Instar III (Figs 208–211). Head (Fig. 208). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 209–210). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 211). Chaetotaxy. Anteroventral margin of nasale with 59 lamellae clypeales distributed in 2 rows; proCO with 1–4 anterior secondary setae; mesoCO with 1–5 anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal and anteroventral secondary setae on proTI present; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI absent; metaTI with less than 16 secondary setae; anterodorsal and posteroventral secondary setae on pro-, meso- and metaTA absent; anteroventral secondary setae on pro- and metaTA present; posterodorsal secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; proTA with 1–7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 11. Secondary leg setation detailed in Table 19.

Remarks. The description of *L. raeae* is based on a single instar III in which the mesothoracic legs and the second urogomphomere were broken, which prevented the evaluation of some morphometric and chaetotaxic characters. This species belongs to the group of stygobitic species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. windarraensis*, *L. yuinmeryensis*) (Fig. 211). Compared to these species, larvae of *L. raeae* can be distinguished by the lateral margins of the nasale not inflated in dorsal view (Fig. 208), the presence of anterior secondary setae on the pro- and mesocoxa (Fig. 209), the presence of anteroventral secondary setae on the protibia and the protarsus (Fig. 209), and the absence of posteroventral secondary setae on the tarsus (Fig. 210).

***Limbodessus raesideensis* (Watts & Humphreys, 2001)**
(Figs 212–215)

Source of material. Two specimens of instar II and two of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Raeside palaeovalley**, Lake Mason calcrete, Salt Well, BES 8353, 27.54S, 119.62417E, 24–VI–2000, coll. W. F. Humphreys and S. Hinze; Lake Mason calcrete, Salt Well, BES 14361, 27.586S, 119.5218E, 20–IX–2006, coll. W. F. Humphreys and T. Moulds.

Diagnosis (instar III). Larger species (HL more than 1.25 mm); head (Fig. 212) pyriform; nasale digitiform; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 numerous (25 or more); occipital foramen strongly reduced (HW/OCW more than 2.85); occipital suture present; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal numerous; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 robust; secondary setae on U present (Fig. 215).



FIGURES 208–211. *Limbodessus raeae*, third-instar larva. 208, head, dorsal aspect; 209, left prothoracic leg, anterior aspect; 210, right prothoracic leg, posterior aspect; 211, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.15 mm.

TABLE 18. Number and position of secondary setae on the legs of third-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. inornatus*	*L. leysi*	*L. masonensis*	*L. millbilliensis*
Coxa	A	10–13 / 10–18 / 17–26	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	P	3–7 / 14–16 / 18–22	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PD	7 / 4–6 / 5–8	2 / 2–3 / 1–2	3–5 / 3–4 / 1–3	3 / 3 / 2
	V	9–11 / 9–10 / 7–11	1–2 / 1 / 1	2 / 1 / 1–2	1 / 1 / 1
	Total	32–35 / 40–47 / 56–58	3–4 / 3–4 / 2–3	5–7 / 4–5 / 2–5	4 / 4 / 3
Trochanter	Pr	0 / 1 / 1–2	0–1 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	Total	0 / 1 / 1–2	0–1 / 1 / 1	0 / 1 / 1	0 / 1 / 1
Femur	AD	2 / 2–3 / 3–4	2 / 2–3 / 2	2 / 2 / 2–3	2 / 2 / 2
	AV	8–9 / 9 / 9–11	3–4 / 1–4 / 3–4	3–5 / 4 / 4–5	3–4 / 3–4 / 4–5
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PV	5 / 7–9 / 10–13	1–3 / 2–3 / 4	4 / 5 / 4–5	3 / 3 / 4–5
	Total	15–16 / 18–21 / 23–27	6–9 / 7–9 / 9–10	9–11 / 11 / 11–12	8–9 / 8–9 / 10–12
Tibia	AD	0 / 1 / 3	0 / 1 / 1	1 / 1–2 / 1	1 / 1 / 1
	AV	0 / 2–3 / 2–3	1 / 1–2 / 1–3	0 / 2 / 2–3	0 / 2 / 2–3
	PD	1 / 2 / 2–3	0–1 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	PV	1–2 / 2–3 / 4–6	0–1 / 1–2 / 0–2	1 / 1 / 1	1 / 1 / 1–2
	Total	2–3 / 7–9 / 11–15	1–3 / 5 / 5	2 / 5–6 / 5–6	2 / 5 / 5–7
Tarsus	AD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	AV	0 / 2 / 3–4	1 / 2 / 2	0 / 1 / 1–2	0 / 2 / 2–3
	PD	0 / 2 / 2–3	0 / 1 / 1	0 / 1 / 1	0 / 1 / 1
	PV	1 / 2 / 4	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	Total	1 / 6 / 9–11	1 / 3 / 3	0 / 2 / 2–3	0 / 3 / 3–4

Instar I. Not available.

Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 less than 1.05 times longer than MP1; MP2 more than 3.20 times longer than MP3; LP2 less than 0.90 times as long as LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U less than 2.15 times longer than HW; U1 more than 1.65 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 70 lamellae clypeales distributed in 1–2 rows; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with more than 3 posteroventral secondary setae; metaFE with more than 11 secondary setae; anterodorsal secondary setae on proTI absent; anteroventral, posterodorsal and posteroventral secondary setae on proTI present; anterodorsal and posteroventral secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; metaTI with more than 5 secondary setae; anterodorsal secondary setae on proTA absent; anteroventral and posteroventral secondary setae on proTA present; posterodorsal and posteroventral secondary setae on meso- and metaTA present; metaTA with more than 5 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 7. Secondary leg setation detailed in Table 15.

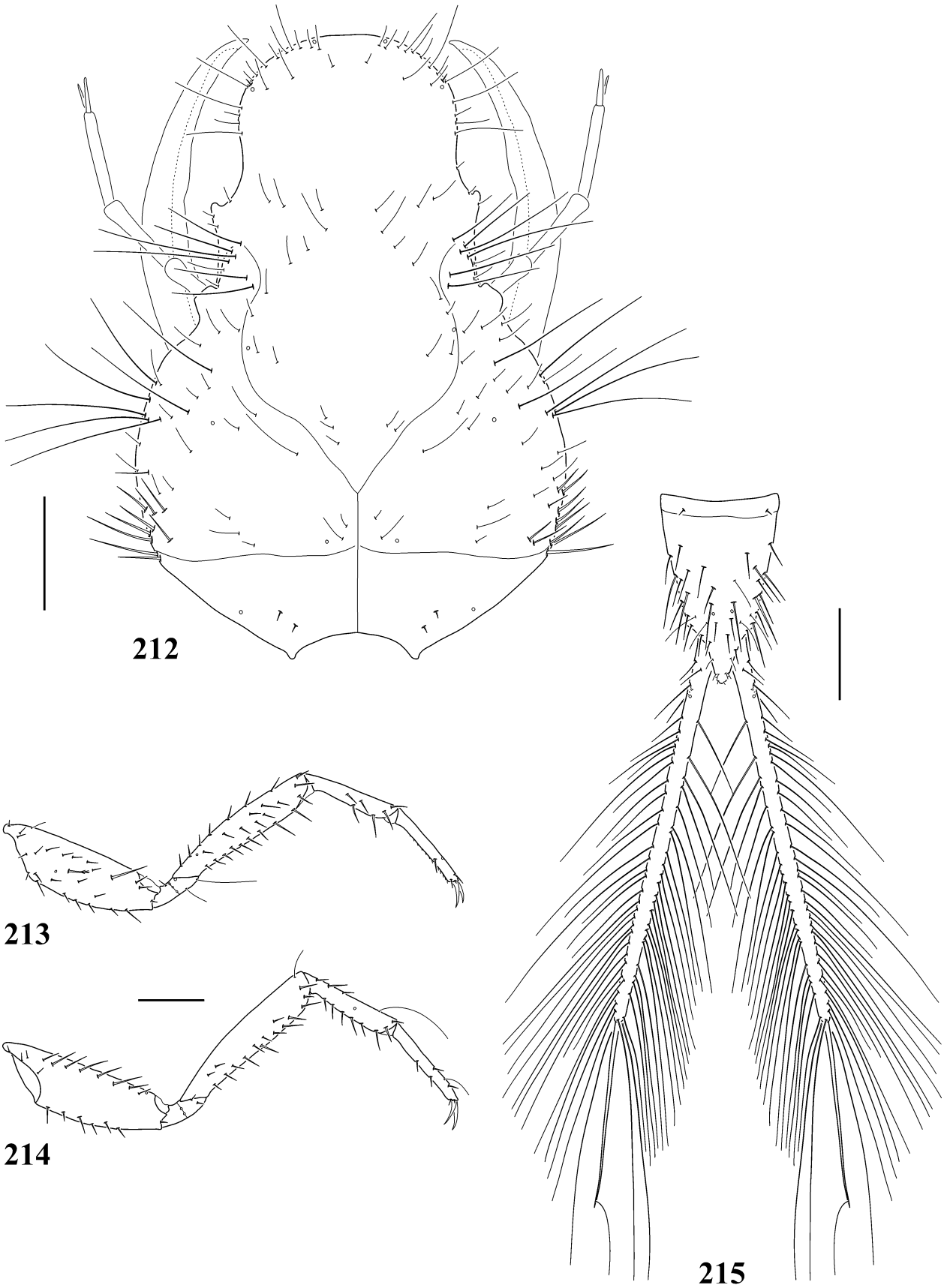
Instar III (Figs 212–215). Head (Fig. 212). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP more than 1.75 times longer than labial palpus; MP2 3.20–4.00 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 213–214). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 215). U more than 3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 1.80–2.60 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 134 lamellae clypeales

distributed in 2 rows; proCO with more than 7 anterior secondary setae; mesoCO with 1–5 anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with more than 21 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with more than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE present; metaFE with more than 30 secondary setae; anterodorsal secondary setae on proTI absent; anteroventral and posterodorsal secondary setae on proTI present; mesoTI with more than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with more than 18 secondary setae; anterodorsal secondary setae on proTA absent; anterodorsal secondary setae on meso- and metaTA present; anteroventral and posterodorsal secondary setae on pro-, meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with 1–5 posteroventral secondary setae; proTA with 1–7 secondary setae; mesoTA with more than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 11. Secondary leg setation detailed in Table 19.

Remarks. *Limbodessus raesideensis* is a very characteristic stygobitic species that belongs to the group of species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis*, *L. bigbellensis*, *L. cooperi*, *L. eberhardi*, *L. macrohinkleri*, *L. nambiensis*, *L. yandalensis*) (Fig. 215). Within this group, it can be distinguished by the following combination of characters: head pyriform (Fig. 212), occipital suture present (Fig. 212), occipital foramen strongly reduced (Fig. 212), presence of anterior secondary setae on the coxa (Fig. 213), presence of posterodorsal secondary setae on the meso- and metafemur, femur with more than 30 secondary setae, and absence of anterodorsal secondary setae on the protibia and protarsus (Fig. 213).

TABLE 19. Number and position of secondary setae on the legs of third-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. ordinarius*	*L. praelargus*	*L. raeae*	*L. raesideensis*
Coxa	A	0–1 / 0 / 0	11 / 13 / 16	1 / 1 / 0	8–9 / 3–4 / 2–3
	P	0 / 0 / 0	1 / 11 / 13	0 / 0 / 0	0 / 0 / 0
	PD	1–2 / 1–3 / 1–2	8 / 5 / 8	4 / 4 / 1	7 / 6 / 4–5
	V	1–2 / 1 / 1	7 / 6 / 8	3 / 1 / 1	7–8 / 7 / 5–6
	Total	3–4 / 2–4 / 2–3	27 / 35 / 45	8 / 6 / 2	22–24 / 16–17 / 12–13
Trochanter	Pr	0 / 1 / 1–2	0 / 0 / 2	0 / 1 / 1	0–1 / 1 / 1
	Total	0 / 1 / 1–2	0 / 0 / 2	0 / 1 / 1	0–1 / 1 / 1
Femur	AD	2 / 2 / 2	2 / 2 / 3	2 / – / 3	6 / 4 / 3–5
	AV	3–4 / 3–4 / 5–6	8 / 8 / 9	5 / – / 4	14–16 / 14–16 / 13–14
	PD	0 / 0 / 0	0 / 0 / 0	0 / – / 0	0 / 1–2 / 2–4
	PV	3–4 / 5 / 4–6	2 / 6 / 9	5 / – / 3	10–14 / 10–11 / 11–14
	Total	9 / 10–11 / 11–14	12 / 16 / 21	12 / – / 10	30–36 / 30–32 / 31–35
Tibia	AD	0 / 1 / 1	1 / 1 / 2	1 / – / 1	0 / 1–3 / 2
	AV	1–2 / 2 / 3–5	0 / 2 / 3	1 / – / 2	3 / 6–7 / 6–7
	PD	1 / 1 / 1	0 / 2 / 2	0 / – / 1	3–4 / 3–4 / 4–5
	PV	1–2 / 2–3 / 3	1 / 2 / 3	1 / – / 3	5 / 5–6 / 7
	Total	4 / 6–7 / 8–10	2 / 7 / 10	3 / – / 7	11–12 / 17–18 / 19–21
Tarsus	AD	0 / 0 / 0	0 / 0 / 0	0 / – / 0	0 / 1–3 / 0–1
	AV	0 / 2 / 2–3	0 / 2 / 3	1 / – / 3	1–2 / 4–5 / 5–6
	PD	0 / 1 / 1	0 / 3 / 3	0 / – / 1	1 / 0–2 / 1–4
	PV	0–1 / 0 / 0	1 / 1 / 3	0 / – / 0	2 / 2–3 / 4–5
	Total	0–1 / 3 / 3–4	1 / 6 / 9	1 / – / 4	4–5 / 9–11 / 11–15



FIGURES 212–215. *Limbodessus raesideensis*, third-instar larva. 212, head, dorsal aspect; 213, left prothoracic leg, anterior aspect; 214, right prothoracic leg, posterior aspect; 215, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.30 mm.

***Limbodessus windarraensis* (Watts & Humphreys, 1999)**
(Figs 216–233)

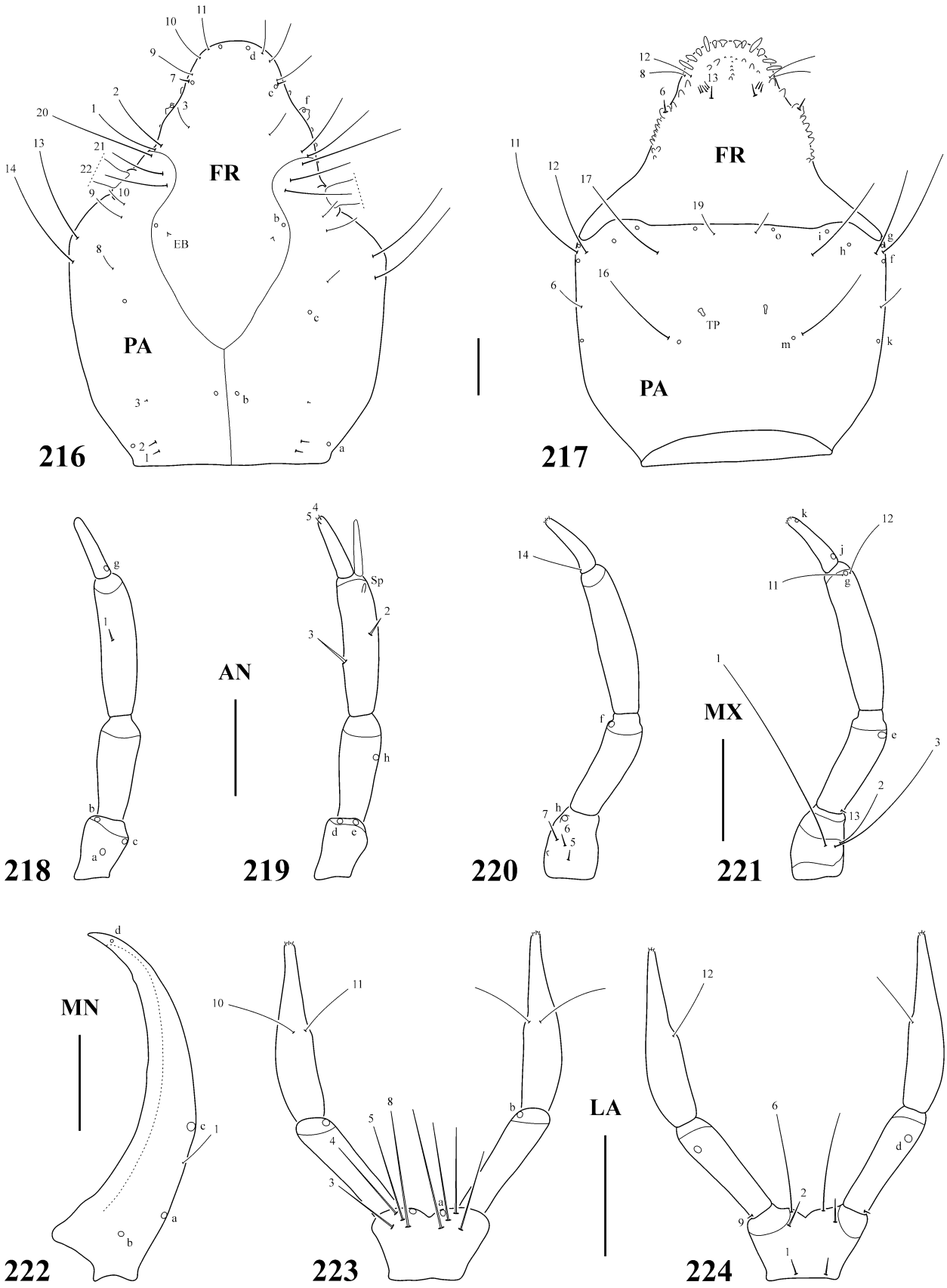
Source of material. One specimen of instar I, one of instar II and one of instar III were used for the description (Table 1). Larvae were collected in association with adults at the following localities: **Australia, Carey palaeovalley**, Mount Windarra calcrete, Leverton Downs Station, MEB site 90, BES 10305, 28.39120S, 122.20378E, 20–III–2004, coll. W. F. Humphreys and S. J. B. Cooper; Mount Windarra calcrete, Leverton Downs Station, MEB site 95 bore line, BES 10307, 28.40192S, 122.19969E, 20–III–2004, coll. W. F. Humphreys and S. J. B. Cooper.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 230) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 233).

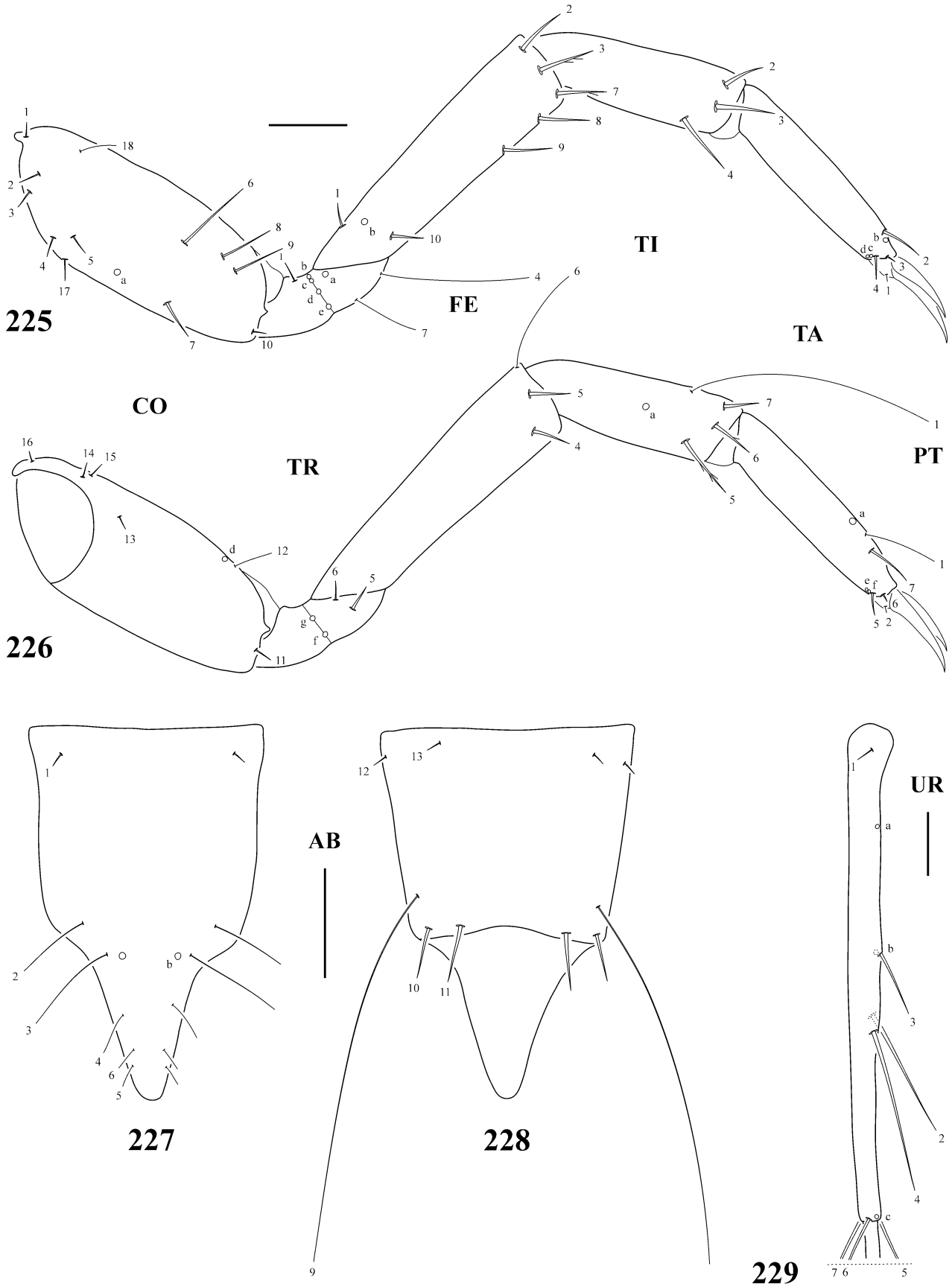
Instar I (Figs 216–229). Head (Figs 216–224). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 2.20–2.75 times longer than A1; A3 more than 2.25 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 225–226). L3 less than 2.85 times longer than HW. Abdomen (Figs 227–229). Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 4.

Instar II. Head. A3 more than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U less than 2.15 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 26 lamellae clypeales distributed in a single row; anterior secondary setae on proCO present; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTI present; anteroventral and posterodorsal secondary setae on proTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on pro-, meso- and metaTI absent; metaTI with less than 5 secondary setae; anterodorsal secondary setae on proTA absent; anteroventral secondary setae on proTA present; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on pro-, meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 7. Secondary leg setation detailed in Table 15.

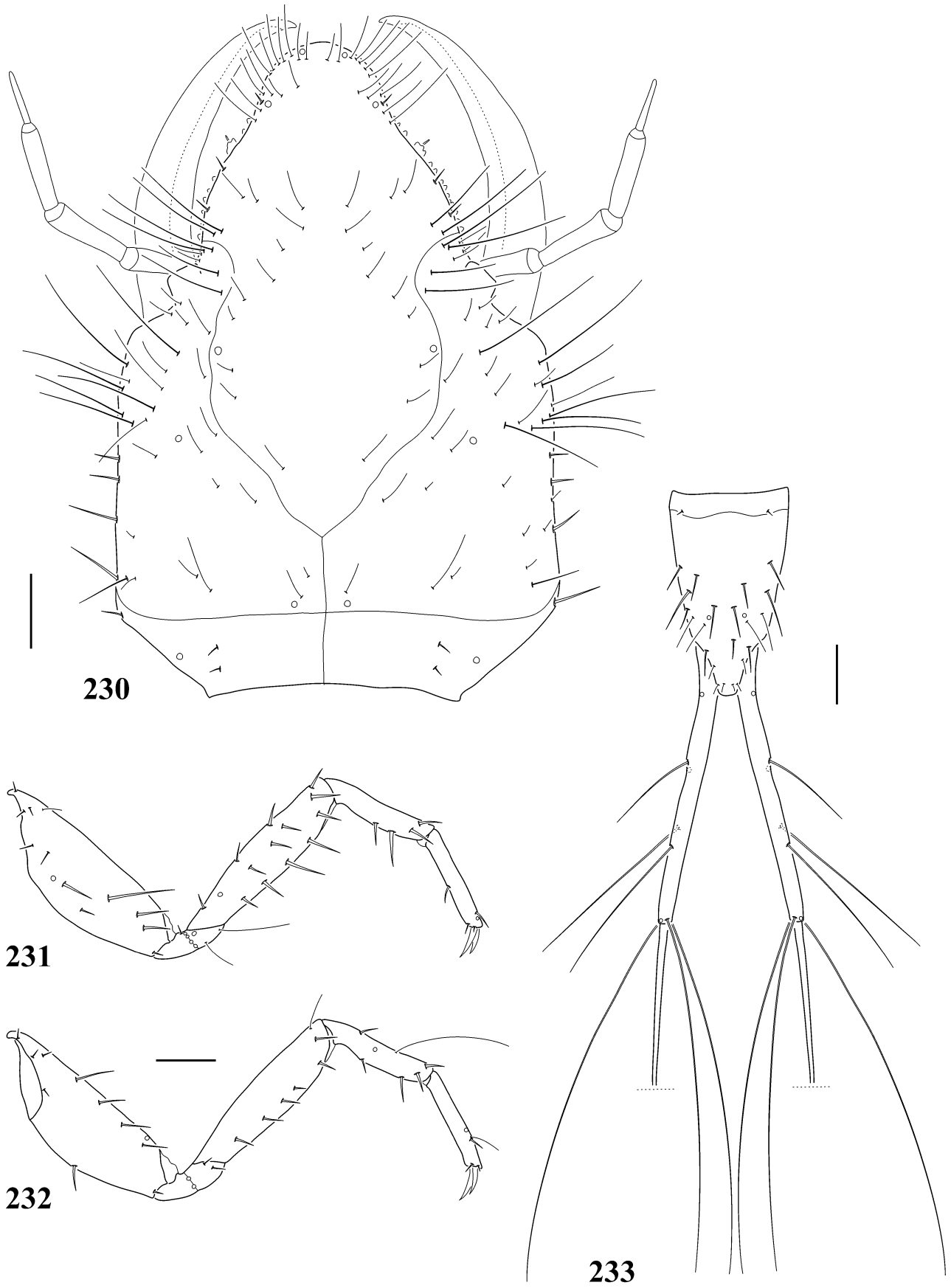
Instar III (Figs 230–233). Head (Fig. 230). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN more than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 231–232). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 233). Chaetotaxy. Anteroventral margin of nasale with 52 lamellae clypeales distributed in 2 rows; proCO with 1–4 anterior secondary setae; mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal secondary setae on proTI absent; anteroventral and posterodorsal secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; metaTI with less than 16 secondary setae; anterodorsal and posteroventral secondary setae on pro-, meso- and metaTA absent; anteroventral secondary setae on pro-, meso- and metaTA present; posterodorsal secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; proTA with 1–7 secondary setae; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 12. Secondary leg setation detailed in Table 20.



FIGURES 216–224. *Limbodessus windarraensis*, first-instar larva. 216, cephalic capsule, dorsal aspect; 217, cephalic capsule, ventral aspect; 218, right antenna, dorsal aspect; 219, left antenna, ventral aspect; 220, right maxilla, dorsal aspect; 221, left maxilla, ventral aspect; 222, right mandible, dorsal aspect; 223, labium, dorsal aspect; 224, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.06 mm.



FIGURES 225–229. *Limbodessus windarraensis*, first-instar larva. 225, left metathoracic leg, anterior aspect; 226, right metathoracic leg, posterior aspect; 227, abdominal segment VIII, dorsal aspect; 228, abdominal segment VIII, ventral aspect; 229, right urogomphus, dorsal aspect. Scale bars = 0.05 mm.



FIGURES 230–233. *Limbodessus windarraensis*, third-instar larva. 230, head, dorsal aspect; 231, left prothoracic leg, anterior aspect; 232, right prothoracic leg, posterior aspect; 233, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Remarks. The instars I and III of *L. windarraensis* examined had the second urogomphomere broken, which prevented the evaluation of urogomphal morphometry. This species belongs to the group of stygobitic species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. yuinmeryensis*) (Fig. 233), from which it can be distinguished by the following combination of characters: lateral margins of the nasale not inflated in dorsal view (Fig. 230), presence of anterior secondary setae on the procoxa (Fig. 231), metacoxa with four secondary setae, presence of anteroventral and posterodorsal secondary setae on the protibia (Figs 231–232), presence of anteroventral secondary setae on the protarsus (Fig. 231), and absence of posteroventral secondary setae on the tarsus (Fig. 231).

Limbodessus yandalensis Watts & Humphreys, 2006

(Figs 234–237)

Source of material. One specimen of instar III was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Carey palaeovalley**, Yandal calcrete, MEB site 128, BES 10345, 27.76413S, 121.02592E, 23–III–2004, coll. W. F. Humphreys and S. J. B. Cooper.

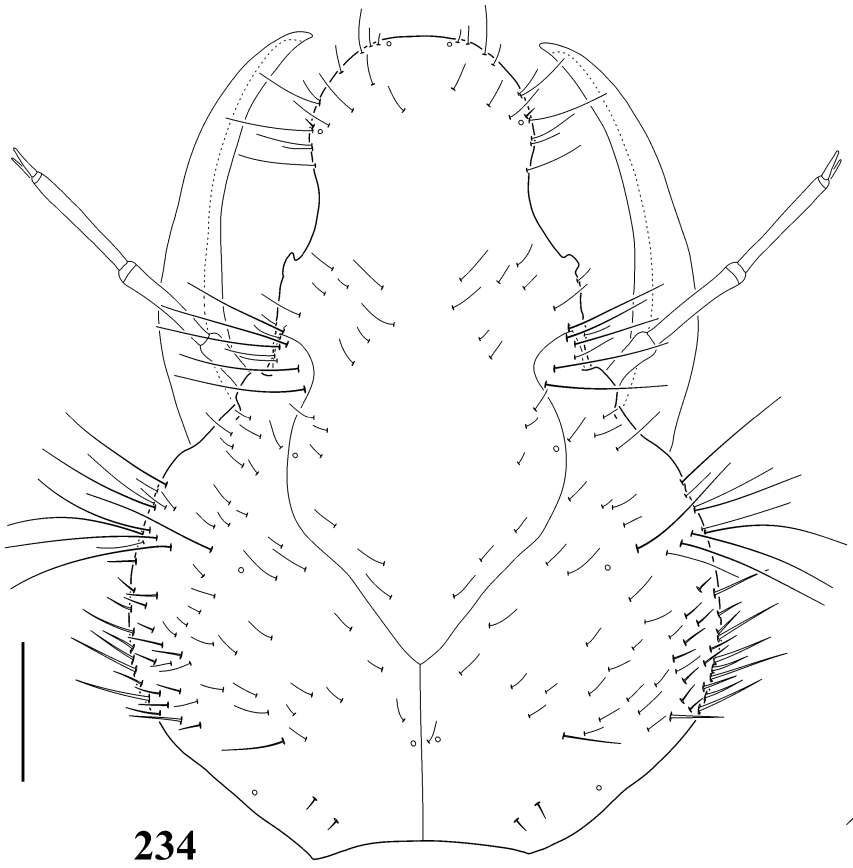
Diagnosis (instar III). Larger species (HL more than 1.25 mm); head (Fig. 234) pyriform; nasale digitiform; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale well developed; slender spinulae anterior to seta FR13 numerous (25 or more); occipital foramen strongly reduced (HW/OCW more than 2.85); occipital suture absent; lateral margins of parietal curved; secondary spiniform setae on lateral margins of parietal numerous; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U present (Fig. 237).

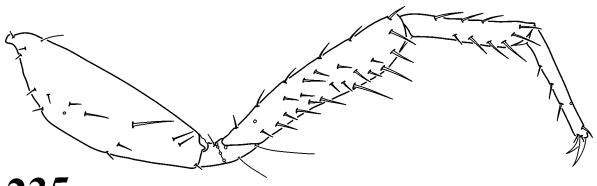
Instar I. Not available.

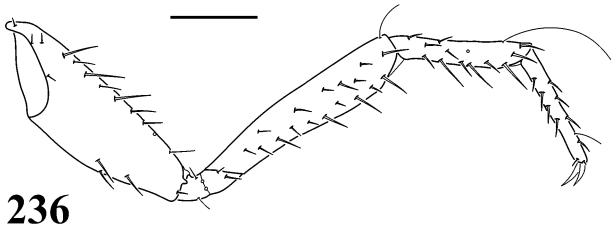
Instar II. Not available.

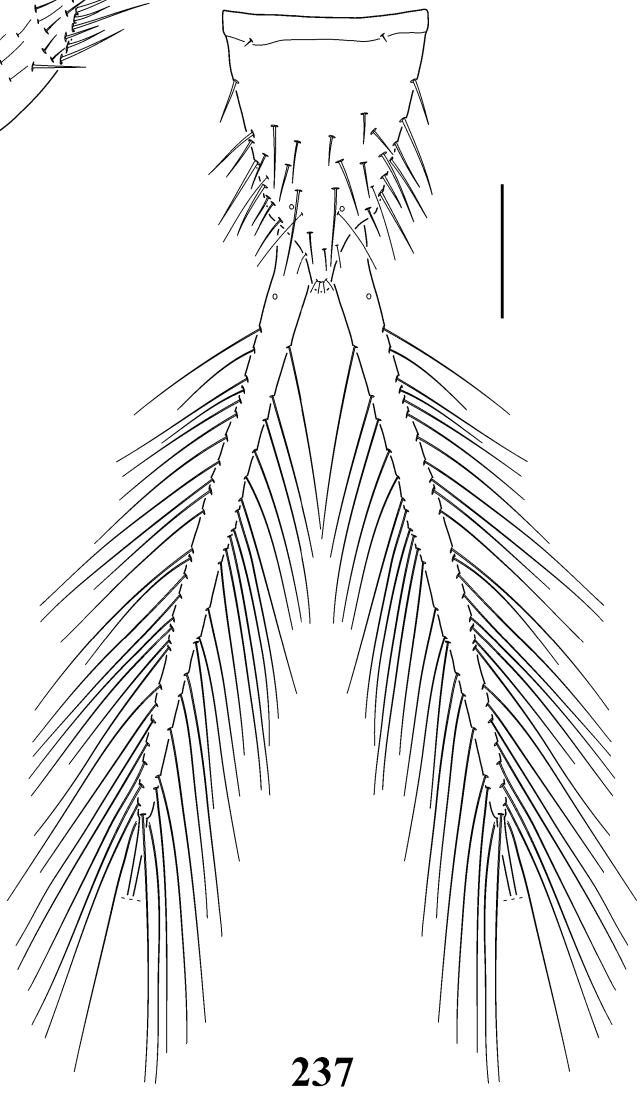
Instar III (Figs 234–237). Head (Fig. 234). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 more than 4.30 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 235–236). L3 2.25–2.85 times longer than HW. Chaetotaxy (Fig. 237). Anteroventral margin of nasale with 206 lamellae clypeales distributed in 3 rows; proCO with 1–4 anterior secondary setae; mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with 12–15 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with more than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with more than 30 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI present; mesoTI with more than 4 anteroventral secondary setae; metaTI with more than 9 anteroventral secondary setae; metaTI with more than 18 secondary setae; anterodorsal secondary setae on pro-, meso- and metaTA absent; anteroventral and posterodorsal secondary setae on pro-, meso- and metaTA present; posteroventral secondary setae on pro- and mesoTA present; metaTA with more than 8 posteroventral secondary setae; proTA with more than 9 secondary setae; mesoTA with more than 7 secondary setae; metaTA with more than 18 secondary setae; secondary setae on U present. Measurements and ratios that characterize the body shape are shown in Table 12. Secondary leg setation detailed in Table 20.

Remarks. The only specimen of *L. yandalensis* examined had the second urogomphomere broken, which prevented the evaluation of urogomphal morphometry. *Limbodessus yandalensis* is a very characteristic stygobitic species that belongs to the group of species characterized by the presence of secondary setae on the urogomphus (*L. barwidgeeensis*, *L. bigbellensis*, *L. cooperi*, *L. eberhardi*, *L. macrohinkleri*, *L. nambiensis*, *L. raesideensis*) (Fig. 237). Within this group, *L. yandalensis* can be distinguished by the following combination of characters: head pyriform (Fig. 234), occipital suture abesent (Fig. 234), occipital foramen strongly reduced (Fig. 234), presence of anterior secondary setae on the procoxa (Fig. 235), absence of posterodorsal secondary setae on the meso- and metafemur, presence of anterodorsal secondary setae on the protibia (Fig. 235), and absence of anterodorsal secondary setae on the protarsus (Fig. 235).









FIGURES 234–237. *Limbodessus yandalensis*, third-instar larva. 234, head, dorsal aspect; 235, left prothoracic leg, anterior aspect; 236, right prothoracic leg, posterior aspect; 237, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.30 mm.

TABLE 20. Number and position of secondary setae on the legs of third-instar larvae of species of *Limbodessus*. Numbers between slash marks refer to pro-, meso- and metathoracic leg, respectively. A = anterior, D = dorsal, P = posterior, Pr = proximal, V = ventral, Total = total number of secondary setae on the segment (excluding primary setae).

Segment	Position	*L. shuckardii*	*L. windarraensis*	*L. yandalensis*	*L. yuinmeryensis*
Coxa	A	3–4 / 3–4 / 2–4	1 / 0 / 0	1 / 0 / 0	0 / 0 / 0
	P	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PD	5 / 6–8 / 4–6	3 / 3 / 3	7 / 7 / 8	2–3 / 3 / 2
	V	3–4 / 2 / 1–6	1 / 1 / 1	5 / 3 / 0	2 / 1 / 1
	Total	12 / 12–13 / 9–14	5 / 4 / 4	13 / 10 / 8	4–5 / 4 / 3
Trochanter	Pr	0 / 1 / 1	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
	Total	0 / 1 / 1	0 / 1 / 1	1 / 1 / 1	0 / 1 / 1
Femur	AD	2 / 2–3 / 2–3	2 / 2 / 2	4 / 6 / 6	1–2 / 2 / 2
	AV	5–8 / 6–7 / 6–9	4 / 3 / 6	15 / 12 / 14	3 / 3–4 / 3–5
	PD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	PV	2–3 / 4–6 / 6–7	4 / 5 / 5	14 / 13 / 13	3–4 / 3 / 3–5
	Total	10–12 / 12–15 / 15–18	10 / 10 / 13	33 / 31 / 33	8 / 8–9 / 10
Tibia	AD	1 / 1 / 1	0 / 1 / 1	3 / 1 / 1	1 / 1 / 1
	AV	0–1 / 2–3 / 3–4	1 / 2 / 3	3 / 9 / 10	1 / 2–3 / 2–3
	PD	0 / 1 / 1–2	1 / 1 / 1	2 / 5 / 5	0 / 1 / 1
	PV	2 / 1–2 / 3–4	1 / 1 / 1	7 / 9 / 9	1 / 1–2 / 2
	Total	3–4 / 5–7 / 9–10	3 / 5 / 6	15 / 24 / 25	3 / 6 / 6–7
Tarsus	AD	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0
	AV	0 / 1 / 2	1 / 2 / 2	3 / 5 / 7	0 / 1 / 2
	PD	0 / 1 / 1	0 / 1 / 1	3 / 5 / 6	0 / 1 / 1
	PV	1 / 1 / 1	0 / 0 / 0	4 / 5 / 9	0 / 0 / 0
	Total	1 / 3 / 4	1 / 3 / 3	10 / 15 / 22	0 / 2 / 3

Limbodessus yarrabubbaensis Watts & Humphreys, 2009

(Figs 238–251)

Source of material. One specimen of instar I was used for the description (Table 1). The larva was collected in association with adults at the following locality: **Australia, Murchison palaeovalley**, Yarrabubba South calcrete, MEB site 72, BES 13100, 27.0668S, 118.6795E, 21–X–2005, coll. W. F. Humphreys and R. Leys.

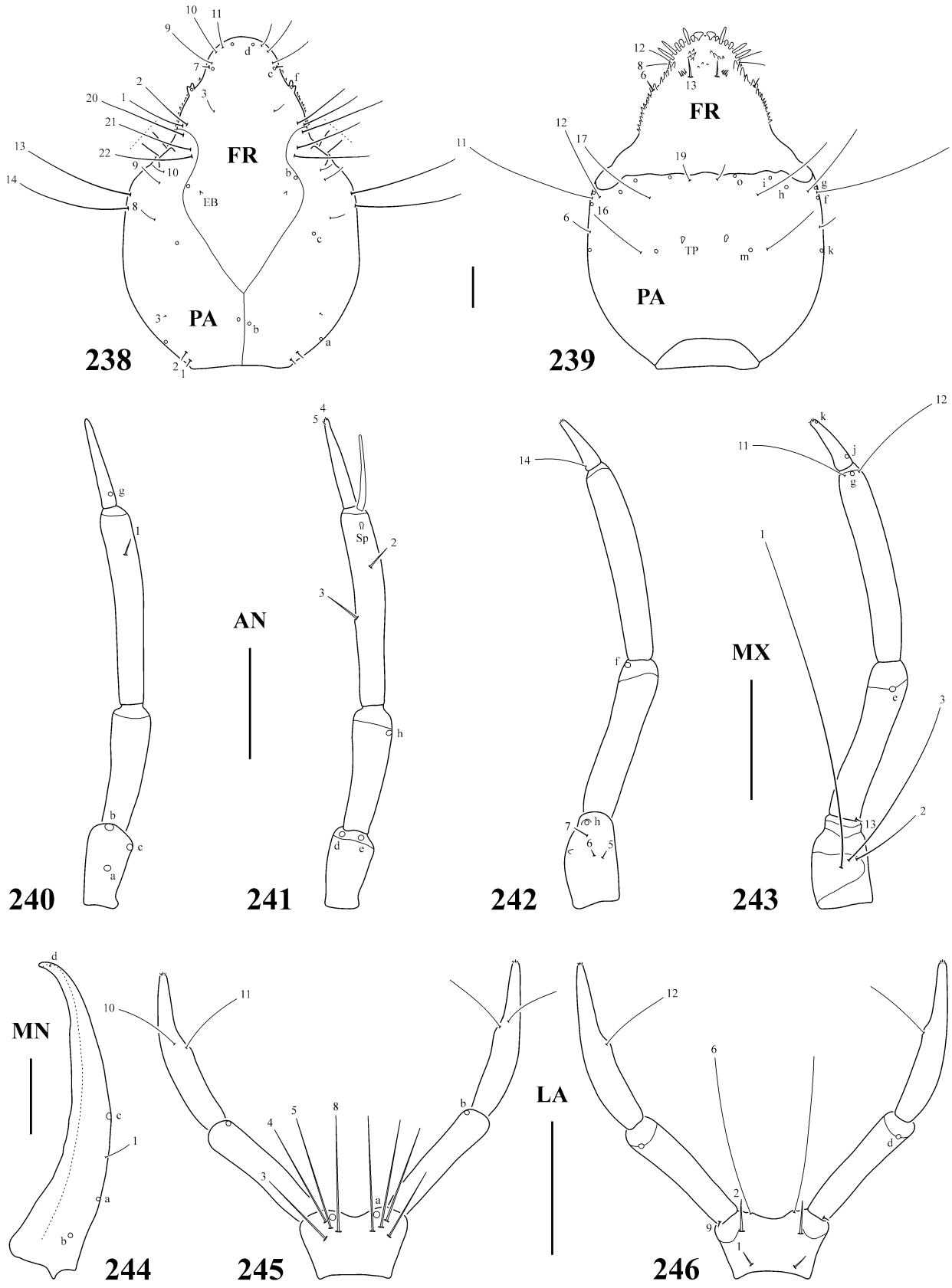
Diagnosis. No diagnosis is provided owing to a lack of specimens of instars II and III.

Instar I (Figs 238–251). Head (Figs 238–246). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted far from setae PA1 and PA2; A3 2.20–2.75 times longer than A1; A3 more than 2.25 times longer than A2; MP2 less than 1.45 times longer than MP1; MP2 more than 3.30 times longer than MP3; LP2 less than 1.30 times longer than LP1. Legs (Figs 247–248). L3 less than 2.85 times longer than HW. Abdomen (Figs 249–251). U 3.60–3.70 times longer than LAS; U less than 2.35 times longer than HW; U1 more than 1.45 times longer than U2. Chaetotaxy. Frontoclypeus with 14 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 4.

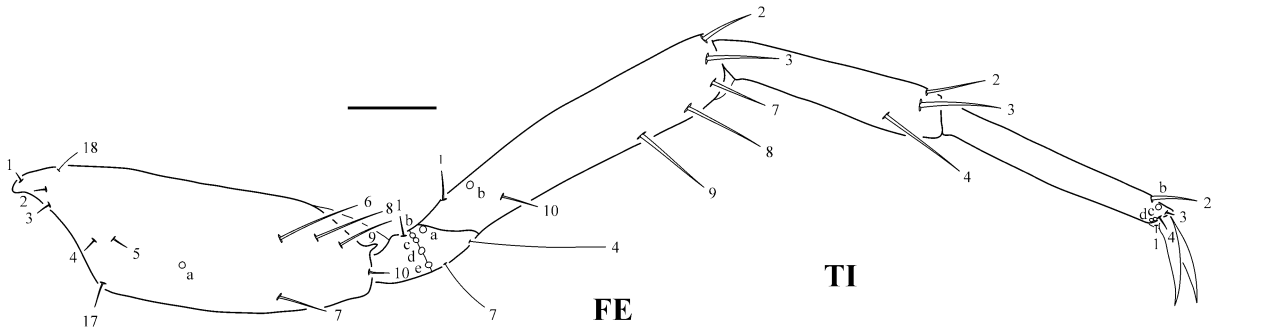
Instar II. Not available.

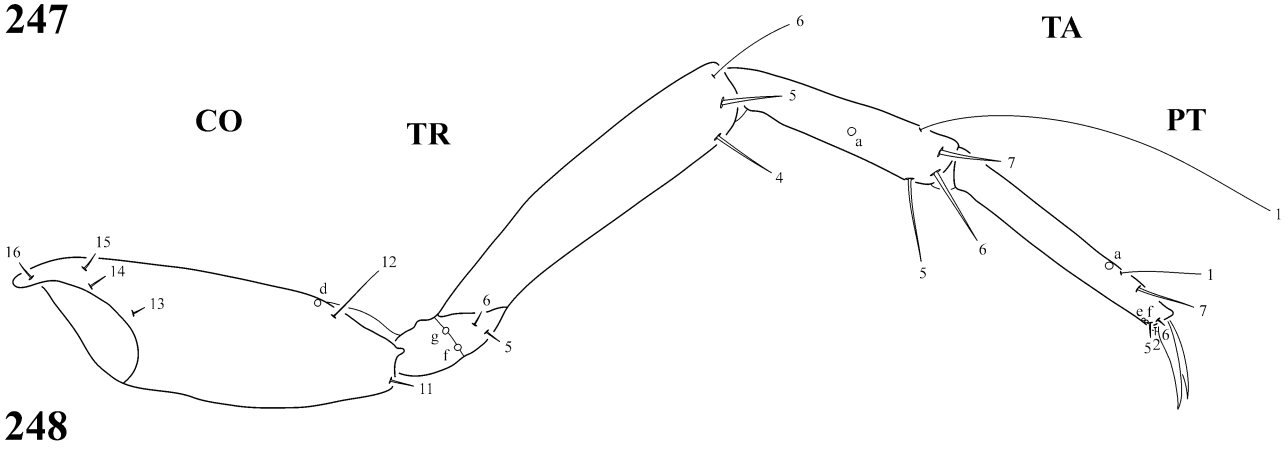
Instar III. Not available.

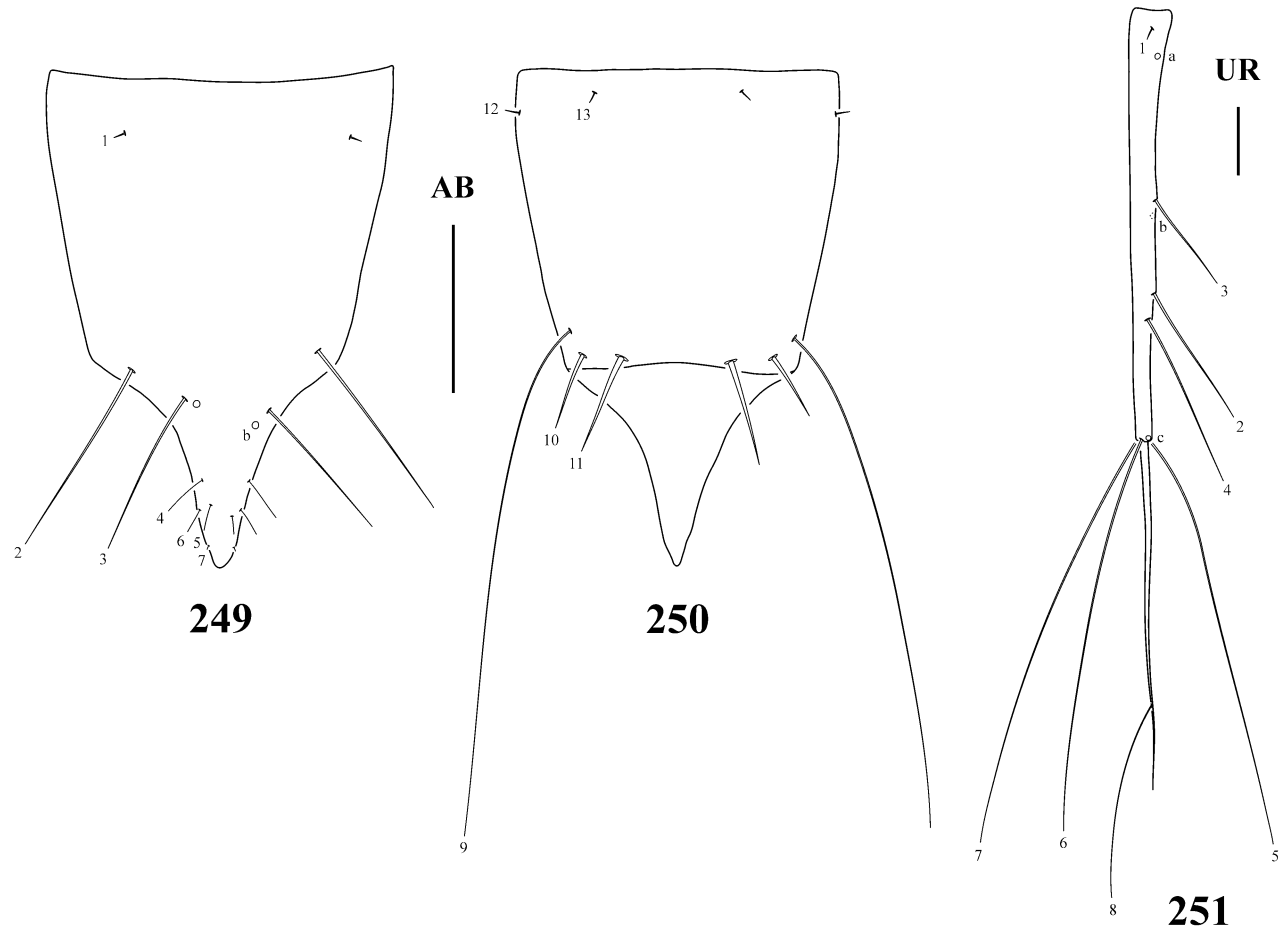
Remarks. The species is not diagnosed above because of lack of instars II and III. However, it can be separated from the other species described as instar I by the combination of characters given under the description.



FIGURES 238–246. *Limbodessus yarrabubbaensis*, first-instar larva. 238, cephalic capsule, dorsal aspect; 239, cephalic capsule, ventral aspect; 240, right antenna, dorsal aspect; 241, left antenna, ventral aspect; 242, right maxilla, dorsal aspect; 243, left maxilla, ventral aspect; 244, right mandible, dorsal aspect; 245, labium, dorsal aspect; 246, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.10 mm.







FIGURES 247–251. *Limbodessus yarrabubbaensis*, first-instar larva. 247, left metathoracic leg, anterior aspect; 248, right metathoracic leg, posterior aspect; 249, abdominal segment VIII, dorsal aspect; 250, abdominal segment VIII, ventral aspect; 251, right urogomphus, dorsal aspect. Scale bars = 0.10 mm.

***Limbodessus yuinmeryensis* (Watts & Humphreys, 2003)**
(Figs 252–269)

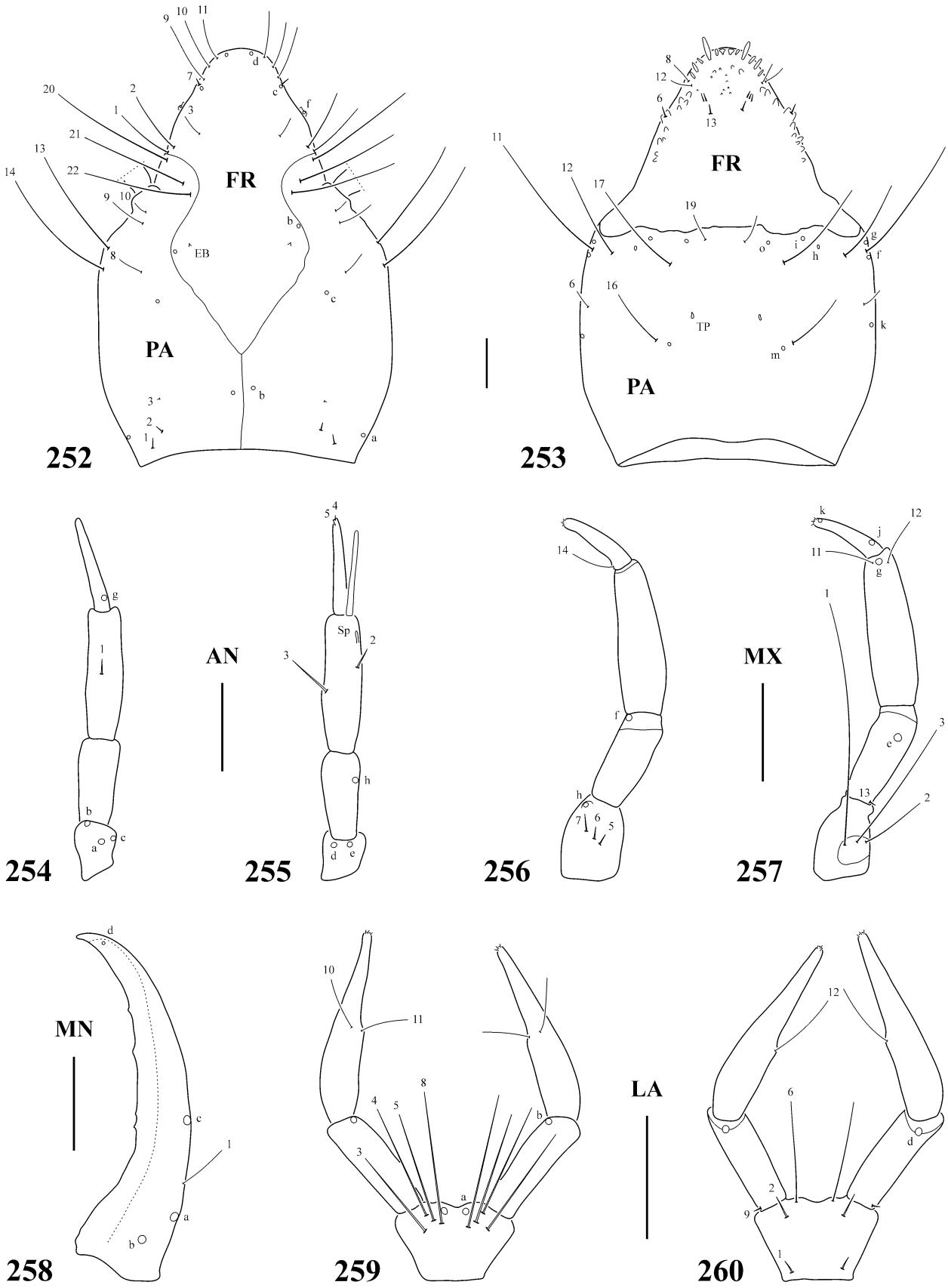
Source of material. Two specimens of instar I, two of instar II and two of instar III were used for the description (Table 1). The larvae were collected in association with adults at the following localities: **Australia, Raeside palaeovalley**, Yuinmery calcrete, New Well, BES 6654, 28.54972S, 119.09111E, 15-V-2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper; Yuinmery calcrete, Nine mile Well, BES 8061, 28.54306S, 119.13333E, 15-V-2001, coll. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper; Yuinmery calcrete, Youanmi Station, Ram(New) Well, BES 14372, 27.8286S, 119.3213E, 20-IX-2006, coll. W. F. Humphreys and T. Moulds; Yuinmery calcrete, Youanmi Station, Ram(New) Well, BES 14373, 27.8286S, 119.3213E, 20-IX-2006, coll. W. F. Humphreys and T. Moulds.

Diagnosis (instar III). Medium-sized species (HL 0.55–1.15 mm); head (Fig. 266) subpentagonal; nasale subtriangular; half-circle of dense spinulae on lateroventral margins of nasale absent; hole-like structure on ventrodistal surface of nasale absent; lateral margins of nasale not inflated in dorsal view; lateral branches of nasale minute; slender spinulae anterior to seta FR13 scarce (20 or less); occipital foramen well developed (HW/OCW less than 1.90); occipital suture present; lateral margins of parietal straight; secondary spiniform setae on lateral margins of parietal scarce; seta AN2 present; distal half of MN broad; setae LA3, LA4, LA5 and LA8 hair-like; secondary setae on U absent (Fig. 269).

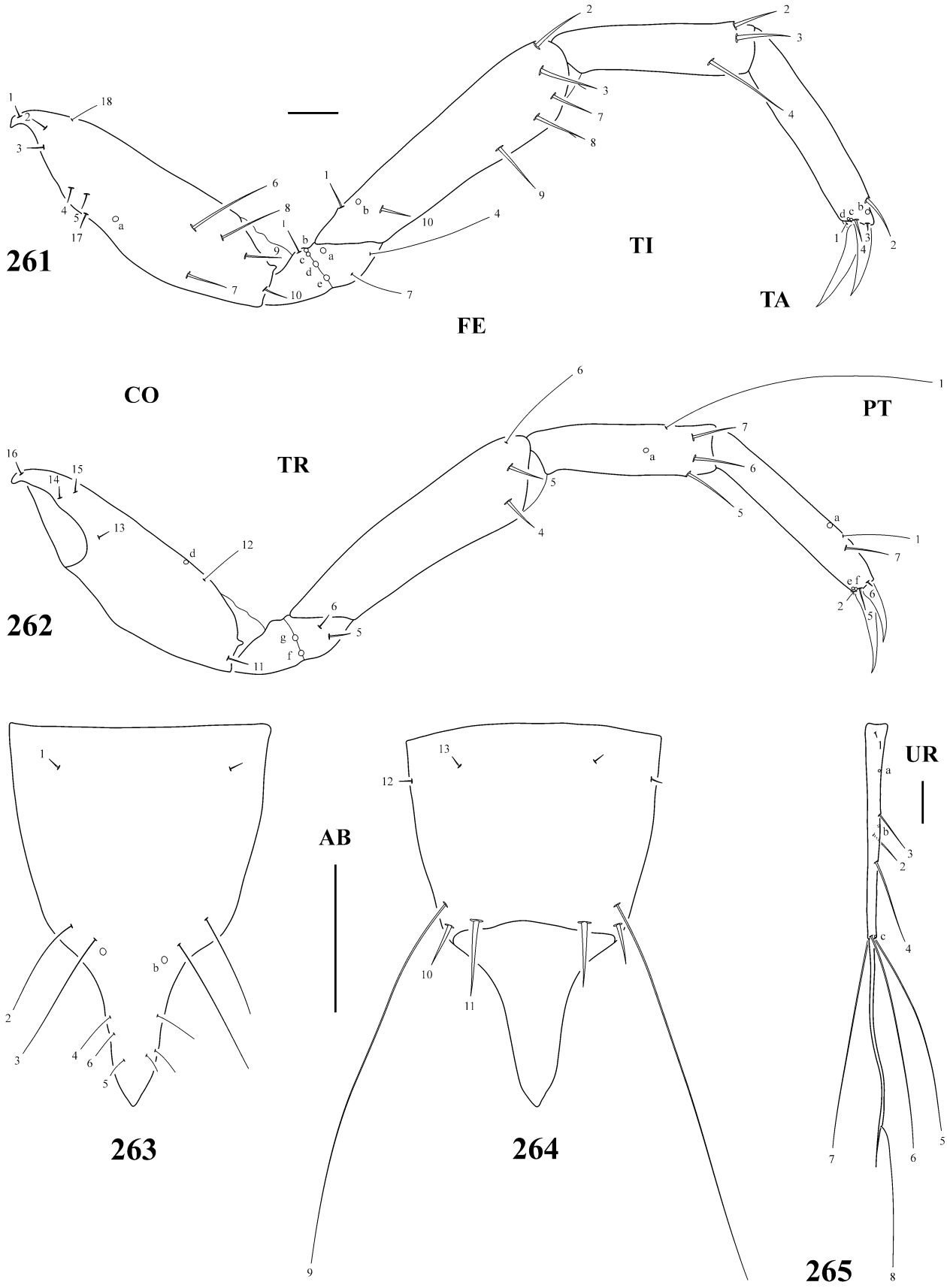
Instar I (Figs 252–265). Head (Figs 252–260). Cephalic capsule not strongly elongate (HL/HW less than 1.55); seta PA3 inserted contiguous to setae PA1 and PA2; A3 (1) 2.20–2.75 times longer than A1; A3 more than 2.25 times longer than A2; MP2 1.55–1.85 times longer than MP1; MP2 1.95–2.65 times longer than MP3; LP2 1.40–2.00 times longer than LP1. Legs (Figs 261–262). L3 less than 2.85 times longer than HW. Abdomen (Figs 263–265). U more than 3.75 times longer than LAS; U more than 2.45 times longer than HW; U1 less than 1.05 times longer than U2. Chaetotaxy. Frontoclypeus with 12 lamellae clypeales; additional setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 4.

Instar II. Head. A3 less than 2.50 times longer than A1; A4 less than 0.70 times as long as A3; MN less than 4.70 times longer than broad; MP2 1.05–1.45 times longer than MP1; MP2 2.10–2.95 times longer than MP3; LP2 1.00–1.70 times longer than LP1. Legs. L3 2.25–2.95 times longer than HW; CL(L3) less than 0.40 times as long as TA. Abdomen. U 3.00–4.00 times longer than LAS; U more than 2.25 times longer than HW; U1 less than 1.45 times longer than U2. Chaetotaxy. Anteroventral margin of nasale with 24 lamellae clypeales distributed in a single row; anterior secondary setae on proCO absent; meso- and metaCO with less than 5 posterodorsal secondary setae; ventral secondary setae on pro- and mesoCO present; proFE with less than 3 posteroventral secondary setae; metaFE with less than 11 secondary setae; anterodorsal, anteroventral and posterodorsal secondary setae on proTI absent; anterodorsal secondary setae on meso- and metaTI present; meso- and metaTI with less than 2 posterodorsal secondary setae; posteroventral secondary setae on pro- and metaTI present; posteroventral secondary setae on mesoTI absent; metaTI with less than 5 secondary setae; secondary setae on proTA absent; posterodorsal secondary setae on meso- and metaTA present; posteroventral secondary setae on meso- and metaTA absent; metaTA with less than 4 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 7. Secondary leg setation detailed in Table 15.

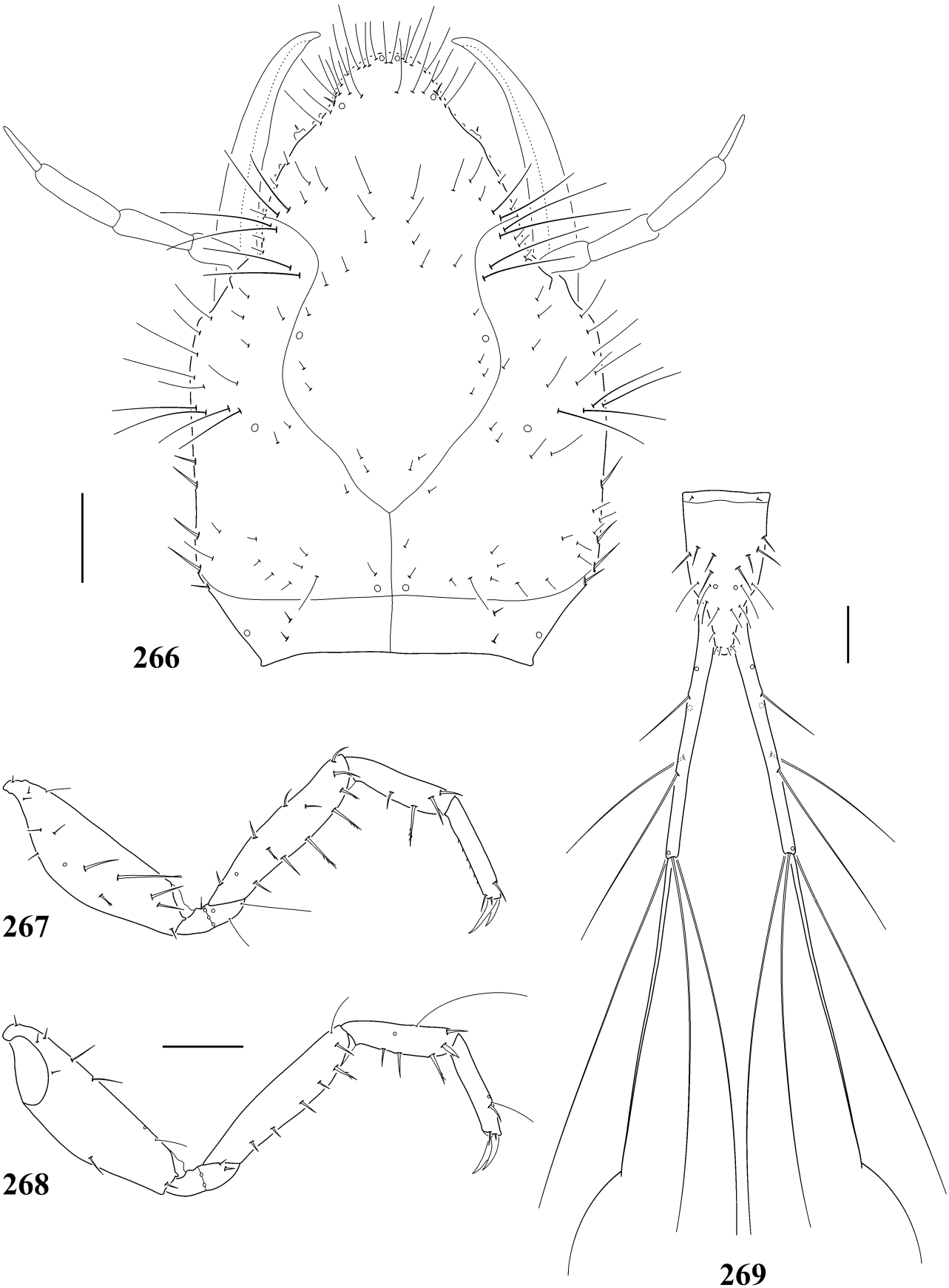
Instar III (Figs 266–269). Head (Fig. 266). A3 less than 2.25 times longer than A1; A3 less than 1.45 times longer than A2; MN less than 4.85 times longer than broad; MP less than 1.75 times longer than labial palpus; MP2 2.10–3.10 times longer than MP3; LP2 more than 0.65 times as long as LP1. Legs (Figs 267–268). L3 2.25–2.85 times longer than HW. Abdomen (Fig. 269). U more than 3.10 times longer than LAS; U 1.55–2.25 times longer than HW; U1 0.70–1.40 times as long as U2. Chaetotaxy. Anteroventral margin of nasale with 40 lamellae clypeales distributed in 2 rows; pro- and mesoCO without anterior secondary setae; pro-, meso- and metaCO without posterior secondary setae; proCO with less than 11 secondary setae; metaCO with less than 20 secondary setae; anterodorsal secondary setae on pro- and metaFE present; metaFE with less than 12 anteroventral secondary setae; posterodorsal secondary setae on meso- and metaFE absent; metaFE with 9–27 secondary setae; anterodorsal and anteroventral secondary setae on proTI present; mesoTI with less than 4 anteroventral secondary setae; metaTI with less than 9 anteroventral secondary setae; posterodorsal secondary setae on proTI absent; metaTI with less than 16 secondary setae; secondary setae on proTA absent; anterodorsal and posteroventral secondary setae on meso- and metaTA absent; anteroventral and posterodorsal secondary setae on meso- and metaTA present; mesoTA with less than 7 secondary setae; metaTA with less than 16 secondary setae; secondary setae on U absent. Measurements and ratios that characterize the body shape are shown in Table 12. Secondary leg setation detailed in Table 20.



FIGURES 252–260. *Limbodessus yuinmeryensis*, first-instar larva. 252, cephalic capsule, dorsal aspect; 253, cephalic capsule, ventral aspect; 254, right antenna, dorsal aspect; 255, left antenna, ventral aspect; 256, right maxilla, dorsal aspect; 257, left maxilla, ventral aspect; 258, right mandible, dorsal aspect; 259, labium, dorsal aspect; 260, labium, ventral aspect. EB, egg burster; Sp, spinula; TP, tentorial pit. Scale bars = 0.05 mm.



FIGURES 261–265. *Limbodessus yuinmeryensis*, first-instar larva. 261, left metathoracic leg, anterior aspect; 262, right metathoracic leg, posterior aspect; 263, abdominal segment VIII, dorsal aspect; 264, abdominal segment VIII, ventral aspect; 265, right urogomphus, dorsal aspect. Scale bars = 0.07 mm.



FIGURES 266–269. *Limbodessus yuinmeryensis*, third-instar larva. 266, head, dorsal aspect; 267, left prothoracic leg, anterior aspect; 268, right prothoracic leg, posterior aspect; 269, abdominal segment VIII and urogomphi, dorsal aspect. Scale bars = 0.10 mm.

Remarks. *Limbodessus yuinmeryensis* belongs to the group of species characterized by the absence of secondary setae on the urogomphus (*L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L. hillviewensis*, *L. hinkleri*, *L. leysi*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. ordinarius*, *L. pulpa*, *L. raeae*, *L. windarraensis*) (Fig. 269). Larvae of this species can be distinguished from those of any species of that group by the following combination of characters: lateral margins of the nasale not inflated in dorsal view (Fig. 266), presence of anteroventral secondary setae on the protibia (Fig. 267), absence of anteroventral secondary setae on the protarsus (Fig. 267), and absence of posteroventral secondary setae on the tarsus (Fig. 268).

Key to larvae of *Limbodessus*

The key presented here was prepared to distinguish both species and instars of the *Limbodessus* taxa known so far as larvae. However, as this genus is very speciose and diverse, and the larvae of many species are still unknown, the present key should be considered preliminary. The main purpose at this point is to recognize and evaluate the characters potentially useful to separate species and instars within the genus and to establish a template to which larvae described in the future can be incorporated.

1. Egg bursters present (e.g. Fig. 31); secondary setae on cephalic capsule absent (e.g. Figs 31–32) (instar I) 2
- Egg bursters absent (e.g. Fig. 8); secondary setae on cephalic capsule present (e.g. Fig. 8) 13
2. Larger species (HL more than 0.65 mm); occipital foramen strongly reduced (HW/OCW more than 2.20) (Figs 31–32, 180–181, 238–239) 3
- Smaller species (HL less than 0.55 mm); occipital foramen not strongly reduced (HW/OCW less than 2.00) (Figs 49–50, 89–90, 115–116, 134–135, 148–149, 162–163, 194–195, 216–217, 252–253) 5
3. Additional setae on urogomphus present (Fig. 193); nasale with 12 lamellae clypeales (Fig. 181) . . . . . *L. palmulaoides* Watts & Humphreys
- Additional setae on urogomphus absent (Figs 44, 251); nasale with 14 lamellae clypeales (Figs 32, 239) 4
4. Nasale longer (Fig. 31); ratio A3/A2 less than 1.40; ratio MP2/MP3 less than 2.50; ratio L3/HW more than 2.90 . . . . . *L. bigbellensis* (Watts & Humphreys)
- Nasale shorter (Fig. 238); ratio A3/A2 more than 1.50; ratio MP2/MP3 more than 3.30; ratio L3/HW less than 2.70 . . . . . *L. yarrabubbaensis* Watts & Humphreys
5. Ratio HW/OCW 1.75–1.95 6
- Ratio HW/OCW less than 1.70 7
6. Nasale with 12 lamellae clypeales (Fig. 217); ratio LP2/LP1 more than 1.45 . . . . . *L. windarraensis* (Watts & Humphreys)
- Nasale with 14 lamellae clypeales (Fig. 135); ratio LP2/LP1 less than 1.30 . . . . . *L. mirandaae* Watts & Humphreys
7. Nasale with 14 lamellae clypeales (Figs 116, 195) 8
- Nasale with 12 lamellae clypeales (Figs 50, 90, 149, 163, 253) 9
8. Nasale with a hole-like structure on ventrodistal surface; ratio A3/A1 more than 2.75 . . *L. millbilliensis* Watts & Humphreys
- Nasale without a hole-like structure on ventrodistal surface; ratio A3/A1 less than 2.65 . . . . . *L. pulpa* (Watts & Humphreys)
9. Smaller species (HL less than 0.35 mm); ratio MP2/MP1 more than 2.10; ratio LP2/LP1 more than 2.40 . . . . . *L. morgani* (Watts & Humphreys)
- Larger species (HL more than 0.35 mm); ratio MP2/MP1 less than 1.90; ratio LP2/LP1 less than 2.00 10
10. Nasale with a strongly developed half-circle of dense spinulae on lateroventral margins (Fig. 90) *L. leysi* Watts & Humphreys
- Nasale without a strongly developed half-circle of dense spinulae on lateroventral margins (Figs. 50, 163, 253) 11
11. Ratio HW/OCW more than 1.60; ratio LP2/LP1 less than 1.20 . . . . . *L. nambiensis* Watts & Humphreys
- Ratio HW/OCW less than 1.45; ratio LP2/LP1 more than 1.40 12
12. Ratio A3/A1 more than 2.80; ratio MP2/MP3 = 1.80 . . . . . *L. challaensis* (Watts & Humphreys)
- Ratio A3/A1 less than 2.70; ratio MP2/MP3 = 2.00 . . . . . *L. yuinmeryensis* (Watts & Humphreys)
13. Spiracles on mesothorax and abdominal segments I-VII absent (instar II) 14
- Spiracles on mesothorax and abdominal segments I-VII present (instar III) 27
14. Stemmata present; two rows of secondary hair-like setae present on ventral surface of parietal; epigean species 15
- Stemmata absent; two rows of secondary hair-like setae on ventral surface of parietal absent; stygobitic species 16
15. Legs longer (L3 1.15–1.30 mm); secondary setae on protarsus present; metatibia and metatarsus with more than 5 secondary setae . . . . . *L. amabilis* (Clark)
- Legs shorter (L3 0.95–1.05 mm); secondary setae on protarsus absent; metatibia and metatarsus with less than 4 secondary setae . . . . . *L. shuckardii* (Clark)
16. Secondary setae on urogomphus present 17
- Secondary setae on urogomphus absent 20
17. Smaller species (HL less than 0.90 mm); nasale with less than 50 lamellae clypeales; ratio MP2/MP3 less than 2.80 . . . . . *L. nambiensis* Watts & Humphreys
- Larger species (HL more than 1.00 mm); nasale with more than 60 lamellae clypeales; ratio MP2/MP3 more than 3.20 . . 18

18. Occipital foramen not strongly reduced (HW/OCW 1.90–2.00) (Fig. 27) ..... *L. barwidgeeensis* Watts & Humphreys
- Occipital foramen strongly reduced (HW/OCW more than 2.60) (Fig. 107) 19
19. Occipital suture absent (Fig. 107); nasale with more than 200 lamellae clypeales; ratio A3/A1 more than 2.50 ..... *L. macrohinkleri* Watts & Humphreys
- Occipital suture present; nasale with less than 100 lamellae clypeales; ratio A3/A1 less than 2.20 ..... *L. raesideensis* (Watts & Humphreys)
20. Protibia without secondary setae 21
- Protibia with 1–3 secondary setae 24
21. Seta AN2 absent; ratio HW/OCW more than 1.75 ..... *L. hinkleri* (Watts & Humphreys)
- Seta AN2 present; ratio HW/OCW less than 1.75 22
22. Nasale with a hole-like structure on ventrodistal surface; lateral margins of nasale inflated in dorsal view ..... *L. millbilliensis* Watts & Humphreys
- Nasale without a hole-like structure on ventrodistal surface; lateral margins of nasale not inflated in dorsal view 23
23. Smaller species (HL less than 0.45 mm); nasale with less than 25 lamellae clypeales; ratio MP2/MP3 less than 2.20; ratio LP2/LP1 more than 1.60 ..... *L. morgani* (Watts & Humphreys)
- Larger species (HL more than 0.45 mm); nasale with more than 25 lamellae clypeales; ratio MP2/MP3 more than 2.70; ratio LP2/LP1 less than 1.30 ..... *L. pulpa* (Watts & Humphreys)
24. Protarsus with 1 secondary seta; protibia with 3 secondary setae. ..... *L. windarraensis* (Watts & Humphreys)
- Protarsus without secondary setae; protibia with 1 secondary seta 25
25. Ratio MP2/MP1 less than 1.05; ratio U/HW less than 2.15 ..... *L. ordinarius* Watts & Humphreys
- Ratio MP2/MP1 more than 1.10; ratio U/HW more than 2.20 26
26. Ratio A3/A1 more than 2.20; ratio MP2/MP3 more than 2.40; ratio L3/HW more than 2.45 ..... *L. masonensis* (Watts & Humphreys)
- Ratio A3/A1 less than 2.20; ratio MP2/MP3 less than 2.40; ratio L3/HW less than 2.45 .... *L. yuinmeryensis* (Watts & Humphreys)
27. Stemmata present (Figs 8, 12, 14, 18, 22); two rows of secondary hair-like setae present on ventral surface of parietal (Fig. 23); epigean species 28
- Stemmata absent (Figs 45, 63, 67, 69, 73, 77, 81, 85, 103, 111, 129, 176, 208, 212, 230, 234, 266); two rows of secondary hair-like setae on ventral surface of parietal absent; stygobitic species 32
28. Secondary setae on urogomphus absent (Figs 11, 13, 26) 29
- Secondary setae on urogomphus present (Figs 17, 21) 31
29. Smaller species (HL less than 0.62 mm). ..... *L. compactus* (Clark)
- Larger species (HL more than 0.62 mm) 30
30. Legs longer (L3 1.67–1.69 mm); anterodorsal secondary setae on tarsus present (Fig. 9) ..... *L. amabilis* (Clark)
- Legs shorter (L3 1.38–1.42 mm); anterodorsal secondary setae on tarsus absent (Fig. 24). ..... *L. shuckardii* (Clark)
31. Legs longer (L3 1.94–2.01 mm); urogomphus longer (U 1.62–1.66 mm); metacoxa with more than 50 secondary setae ..... *L. inornatus* (Sharp)
- Legs shorter (L3 1.73 mm); urogomphus shorter (U 1.35 mm); metacoxa with less than 50 secondary setae ..... *L. praelargus* (Lea)
32. Occipital foramen reduced (HW/OCW more than 1.95) (Figs 45, 67, 69, 212, 234); secondary setae on urogomphus present (Figs 48, 68, 215, 237); metatarsus with more than 10 secondary setae 33
- Occipital foramen well developed (HW/OCW less than 1.90) (Figs 63, 73, 77, 81, 85, 103, 111, 129, 176, 208, 230, 266); secondary setae on urogomphus absent (Figs 66, 76, 80, 84, 88, 106, 114, 133, 179, 211, 233, 269); metatarsus with less than 6 secondary setae 37
33. Nasale with less than 110 lamellae clypeales 34
- Nasale with more than 120 lamellae clypeales 35
34. Nasale with 55–65 lamellae clypeales; lateral projections of nasale visible in dorsal view (Fig. 45); ratio HW/OCW more than 2.80 ..... *L. bigbellensis* (Watts & Humphreys)
- Nasale with 90–100 lamellae clypeales; lateral projections of nasale not visible in dorsal view (Fig. 67); ratio HW/OCW less than 2.10 ..... *L. cooperi* Watts & Humphreys
35. Occipital suture absent (Fig. 234) ..... *L. yandalensis* Watts & Humphreys
- Occipital suture present (Figs 69, 212) 36
36. Nasale broad (Fig. 212); femur with more than 30 secondary setae (Figs 213–214) ... *L. raesideensis* (Watts & Humphreys)
- Nasale narrow (Fig. 69); femur with less than 20 secondary setae (Figs 70–71) ..... *L. eberhardi* (Watts & Humphreys)
37. Lateral margins of nasale inflated in dorsal view (Figs 85, 103, 129) 38
- Lateral margins of nasale not inflated in dorsal view (Figs 77, 81, 176, 230, 266) 40
38. Nasale with a half-circle of dense spinulae on lateroventral margins (Fig. 103); nasale without a hole-like structure on ventrodistal surface ..... *L. leysi* Watts & Humphreys
- Nasale without a half-circle of dense spinulae on lateroventral margins (Figs 85, 129); nasale with a hole-like structure on ventrodistal surface (Fig. 130) 39
39. Seta AN2 present; distal half of mandible narrow (Fig. 129); nasale with 50–60 lamellae clypeales ..... *L. millbilliensis* Watts & Humphreys
- Seta AN2 absent; distal half of mandible broad (Fig. 85); nasale with 30–40 lamellae clypeales .. *L. hinkleri* (Watts & Humphreys)
40. Nasale with less than 45 lamellae clypeales 41
- Nasale with more than 45 lamellae clypeales 42
41. Smaller species (HL 0.45 mm); metathoracic claw 0.45–0.50 times as long as metatarsus .....

. . . . . *L. fridaywellensis* (Watts & Humphreys)
- Larger species (HL 0.67 mm); metathoracic claw 0.30–0.35 times as long as metatarsus . . . . . *L. yuinmeryensis* (Watts & Humphreys)
42. Nasale with more than 55 lamellae clypeales . . . . . *L. raeae* Watts & Humphreys
- Nasale with less than 55 lamellae clypeales 43
43. Mandible more than 5.00 times longer than broad 44
- Mandible less than 4.80 times longer than broad 45
44. Anteroventral secondary setae on protibia absent (Fig. 64); secondary setae on protarsus absent (Figs 64–65) . . . . . *L. challaensis* (Watts & Humphreys)
- Anteroventral secondary setae on protibia present (Fig. 231); secondary setae on protarsus present (Figs 231–232) . . . . . *L. windarraensis* (Watts & Humphreys)
45. Secondary setae on protarsus present (Fig. 178) . . . . . *L. ordinarius* Watts & Humphreys
- Secondary setae on protarsus absent 46
46. Anteroventral secondary setae on protibia present (Fig. 74); posteroventral secondary setae on metatarsus present . . . . . *L. exilis* Watts & Humphreys
- Anteroventral secondary setae on protibia absent; posteroventral secondary setae on metatarsus absent 47
47. Mesofemur with 11 secondary setae; ratio MP/LP more than 1.50 . . . . . *L. masonensis* (Watts & Humphreys)
- Mesofemur with 9 secondary setae; ratio MP/LP less than 1.50 . . . . . *L. hillviewensis* (Watts & Humphreys)

Character analysis

In total, 100 characters derived from the larval morphology, morphometry and chaetotaxy were included, of which 88 were coded as binary and 12 as multistate (Table 21). The analysis of the data matrix (Table 22) using TNT resulted in 200 most parsimonious trees of 386 steps. The strict consensus was calculated (Fig. 270), in which the tribe Bidessini as well as the stygobitic species of *Limbodessus* are resolved as monophyletic groups. As several Bidessini taxa collapsed in a polytomy, little can be said about the intergeneric relationships within this tribe. However, the monophyly of *Limbodessus* is not supported as long as the genus *Allodessus* is resolved as sister to *Limbodessus inornatus*, and both are sister to *L. praelargus*. The support obtained was poor in general, with only a few clades receiving moderate support (Fig. 270).

TABLE 21. Characters used for the cladistic analysis.

No.	Character and states
(00)	Head (instars I–III): (0) subpentagonal; (1) pyriform; (2) subovate
(01)	Half-circle of dense spinulae on lateroventral margins of nasale (instars I–III): (0) absent; (1) present
(02)	Hole-like structure on ventrodistal surface of nasale (instars I–III): (0) absent; (1) present
(03)	Lateral margins of nasale (instars I–III): (0) not inflated in dorsal view; (1) inflated in dorsal view
(04)	Lateral projections of nasale (instars I–III): (0) absent; (1) very small, inconspicuous; (2) well developed, short, not bifid apically; (3) strongly developed, bifid apically
(05)	Slender spinulae anterior to seta FR13 (instar III): (0) absent; (1) scarce (20 or less); (2) numerous (25 or more)
(06)	Egg bursters (instar I): (0) located medially; (1) located basally
(07)	Seta FR2 (instars I–III): (0) inserted close to frontal line; (1) inserted far from frontal line
(08)	Seta FR6 (instars I–III): (0) not distinctly developed; (1) strongly developed
(09)	Pore FRb (instars I–III): (0) present; (1) absent
(10)	Number of lamellae clypeales (instar III): (0) less than 60; (1) more than 60
(11)	Parietal (at level of occipital suture) (instar I): (0) not constricted; (1) constricted
(12)	Parietal (at level of occipital suture) (instars II–III): (0) not constricted; (1) constricted
(13)	Occipital suture (Instar I): (0) present; (1) absent
(14)	Occipital suture (instars II–III): (0) present; (1) absent
(15)	Occipital foramen (instar III): (0) large; (1) reduced
(16)	Lateral margin of parietal (instars I–III): (0) curved; (1) straight

..... *continued on the next page*

TABLE 21. (Continued)

No.	Character and states
(17)	Seta PA3 (instars I–III): (0) inserted contiguously to setae PA1 and PA2; (1) inserted far from setae PA1 and PA2
(18)	Seta PA18 (instars I–III): (0) present; (1) absent
(19)	Pore PAc (instars I–III): (0) inserted medially (not passing the level of stemmata); (1) inserted distally (anterior to the stemmata); (2) absent
(20)	Pore PAd (instars I–III): (0) present; (1) absent
(21)	Pore PAe (instars I–III): (0) present; (1) absent
(22)	Pore PAj (instars I–III): (0) present; (1) absent
(23)	Pore PAm (instars I–III): (0) present; (1) absent
(24)	Secondary spiniform setae on lateral margin of parietal (instar III): (0) scarce; (1) numerous
(25)	Row of secondary hair-like setae on ventral surface of parietal (instar III): (0) absent; (1) present
(26)	A1 (instar III): (0) shorter than A2; (1) subequal in length to A2
(27)	Secondary setae on A2 (instars II–III): (0) absent; (1) present
(28)	Ventral spinula on A3 (instars I–III): (0) present; (1) absent
(29)	Seta AN2 (instars I–III): (0) present; (1) absent
(30)	Seta AN3 (instars I–III): (0) inserted distally; (1) inserted submedially
(31)	Pore ANf (instars I–III): (0) present; (1) absent
(32)	Pore ANh (instars I–III): (0) present; (1) absent
(33)	Additional ventroapical pores on antennomere 3 (instars I–III): (0) present; (1) absent
(34)	Mandible (instar III): (0) moderately elongate; (1) strongly elongate
(35)	Distal half of mandible (instars I–III): (0) broad; (1) narrow
(36)	Sensillum MN2 (instars I–III): (0) setiform; (1) pore-like
(37)	Pore MNa (instars I–III): (0) inserted at about the same level as pore MNb; (1) inserted distally to pore MNb
(38)	Maxillary cardo (instars I–III): (0) not fused to stipes; (1) fused to stipes
(39)	Galea (instars I–III): (0) elongate, finger-like; (1) short, finger-like; (2) absent, if present at most bulge-like
(40)	Maxillary palpomere 3 (instar III): (0) elongate (MP2/MP3 < 3.10); (1) short (MP2/MP3 > 3.40)
(41)	Seta MX4 (instars I–III): (0) present; (1) absent
(42)	Setae MX5 and MX6 (instars I–III): (0) present; (1) absent
(43)	Seta MX7 (instars I–III): (0) present; (1) absent
(44)	Setae MX8 and MX9 (instars I–III): (0) present; (1) absent
(45)	Seta MX10 (instars I–III): (0) present; (1) absent
(46)	Prementum (instars I–III): (0) broader to as long as broad; (1) longer than broad
(47)	Lateral spinulae on prementum (instars I–III): (0) absent; (1) present
(48)	Labial palpus (instar III): (0) elongate (MP/LP < 2.00); (1) short (MP/LP > 2.00)
(49)	Seta LA2 (instars I–III): (0) present; (1) absent
(50)	Seta LA3 (instars I–III): (0) present; (1) absent
(51)	Seta LA8 (instars I–III): (0) inserted distally or subdistally; (1) inserted proximally
(52)	Setae LA3, LA4, LA5 and LA8 (instars I–III): (0) hair-like; (1) robust
(53)	Seta LA9 (instars I–III): (0) present; (1) absent
(54)	Seta LA10 (instars I–III): (0) inserted medially; (1) inserted distally; (2) absent
(55)	Seta LA12 (instars I–III): (0) inserted medially; (1) inserted distally; (2) absent
(56)	Pore LAb (instars I–III): (0) present; (1) absent
(57)	Claws (instar III): (0) elongate (CL/TA > 0.40); (1) short (CL/TA < 0.40)

..... *continued on the next page*

TABLE 21. (Continued)

No.	Character and states
(58)	Seta TR2 (instars I–III): (0) present; (1) absent
(59)	Pore FEa (instars I–III): (0) present; (1) absent
(60)	Seta TI7 (instars I–III): (0) short, spiniform; (1) elongate, setiform
(61)	Anterior secondary setae on procoxa (instar III): (0) absent; (1) present
(62)	Anterior secondary setae on mesocoxa (instar III): (0) absent; (1) present
(63)	Anterior secondary setae on metacoxa (instar III): (0) absent; (1) present
(64)	Secondary setae on coxa (instar III): (0) absent; (1) present
(65)	Posterodorsal secondary setae on meso- and metafemur (instar III): (0) absent; (1) present
(66)	Anterodorsal secondary setae on protibia (instar III): (0) absent; (1) present
(67)	Anteroventral secondary setae on protibia (instar III): (0) absent; (1) present
(68)	Posterodorsal secondary setae on protibia (instar III): (0) absent; (1) present
(69)	Anterodorsal secondary setae on protarsus (instar III): (0) absent; (1) present
(70)	Anterodorsal secondary setae on meso- and metatarsus (instar III): (0) absent; (1) present
(71)	Anteroventral secondary setae on protarsus (instar III): (0) absent; (1) present
(72)	Anteroventral secondary setae on mesotarsus (instar III): (0) absent; (1) present
(73)	Posterodorsal secondary setae on protarsus (instar III): (0) absent; (1) present
(74)	Posterodorsal secondary setae on meso- and metatarsus (instar III): (0) absent; (1) present
(75)	Posteroventral secondary setae on pro- and mesotarsus (instar III): (0) absent; (1) present
(76)	Posteroventral secondary setae on metatarsus (instar III): (0) absent; (1) present
(77)	Secondary setae on protarsus (instar III): (0) absent; (1) present
(78)	Natatory setae on legs (instars I–III): (0) absent; (1) present
(79)	Spiracles on mesothorax and abdominal segments I–VII (instar III): (0) present; (1) absent
(80)	Abdominal tergites I–VII (instar I): (0) with anterior transverse carina; (1) without anterior transverse carina
(81)	Ventral surface of abdominal segments II–III (instar III): (0) membranous; (1) sclerotised
(82)	Ventral surface of abdominal segments IV–V (instar III): (0) membranous; (1) sclerotised
(83)	Ventral surface of abdominal segment VI (instars I–III): (0) membranous; (1) sclerotized
(84)	Siphon (instars I–III): (0) very short; (1) short to moderately long; (2) very long, urogomphomere-like
(85)	Seta AB2 (instars I–III): (0) setiform; (1) pore-like; (2) absent
(86)	Seta AB4 (instars I–III): (0) not distinctly developed; (1) very elongate, strongly developed
(87)	Seta AB5 (instars I–III): (0) not distinctly developed; (1) strongly developed
(88)	Seta AB6 (instars I–III): (0) short (1) elongate
(89)	Seta AB9 (instars I–III): (0) inserted dorsolaterally; (1) inserted ventrolaterally
(90)	Seta AB10 (instars I–III): (0) setiform; (1) spiniform
(91)	Pore ABa (instars I–III): (0) present; (1) absent
(92)	Pore ABc (instars I–III): (0) present; (1) absent
(93)	Secondary ventral setae on siphon (instar III): (0) absent; (1) present
(94)	Urogomphus (instar III): (0) short (U/HW < 3.00); (1) elongate (U/HW > 3.60)
(95)	Setae UR2, UR3 and UR4 (instar I): (0) inserted contiguous; (1) not inserted contiguous; (2) only UR2 and UR3 contiguous; (3) only UR3 and UR4 contiguous; (4) only UR2 and UR4 contiguous
(96)	Seta UR5 (instars I–III): (0) elongate, setiform; (1) short, spiniform
(97)	Seta UR8 (instars I–III): (0) inserted terminally on U2; (1) inserted subapically on U2; (2) inserted medially on U2; (3) inserted proximally on U2; (4) absent; (5) inserted on U1
(98)	Pore URb (instars I–III): (0) proximal to seta UR2; (1) contiguous to seta UR2; (2) distal to seta UR2; (3) absent
(99)	Secondary setae on urogomphus (instars II–III): (0) absent; (1) present

TABLE 22. Data matrix used for the cladistic analysis. Missing data coded '?'

	0000000000	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8888888888	9999999999
Species	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
Laccophilus obliquatus	2000001000	0011100002	0000001010	1001000000	0000000010	1010220100	0111101001	1110000110	1000100001	0010010501
Allodessus bistrigatus	0000110000	0001000010	1110010000	1101001112	0100110000	0010000011	0111100010	0010111100	1000100001	1110010101
Amarodytes duponti	0000110000	0000000110	1110010000	1101001012	0100110000	0000000011	0111101100	0010100000	1000100001	1110010101
Anodocheilus maculatus	0000110000	0001000110	1110010010	1101001012	0100110000	0000000011	0111101000	0010100000	1000100001	1110010100
Hydroglyphus balkei	000011?000	000?000110	1110010000	1101001112	0100110000	0010000011	0000100010	0011100100	?000100001	1110010100
Hypodessus cruciatus	0000110000	0001000110	1110010000	1101001012	0100110000	0000000011	0111101010	0010111100	1000100001	1110010100
Limbodessus amabilis	000011?000	000?000110	1110010000	1101001112	0100110000	0000000011	0111001101	1000011100	1000100001	1110?10?10
Limbodessus barwidgeeensis	100011?000	100?001110	1110100000	1101001112	1100110000	0010000111	0?00000110	1011111100	1000100001	1110??0??1
Limbodessus bigbellensis	1000110000	1001011110	1110000000	1101001112	1100110000	0010000111	0000001111	0010111100	1000100001	1110010101
Limbodessus challaensis	0000110000	0001001110	1110000000	1101001112	0100110000	0000000111	0000001000	0010100000	1000100001	1110040100
Limbodessus compactus	000011?000	000?000110	111001000?	1101001112	0100110000	0000000?11	0?????????	????????00	1000100001	1110?10?00
Limbodessus cooperi	000011?000	100?001110	1110100000	1101001112	1100110000	0000000111	000000????	1???1?1?00	1000100001	11100?0??1
Limbodessus eberhardi	100012?000	100?010110	1110000000	1101001112	1100110000	0000000111	0000001110	1111111100	1000100001	1110??0??1
Limbodessus exilis	000011?000	000?001110	1110000000	1101001112	0100110000	0000000111	0000001100	0010101000	1000100001	1110?10?00
Limbodessus fridaywellensis	000011?000	000?001110	1110000000	1101001112	0100110000	0000000011	0000001000	0000100000	1000100001	1110040100
Limbodessus hillviewensis	000011?000	000?001110	1110000000	1101001112	0100110000	0000000111	0000001000	0010100000	1000100001	1110?10?10
Limbodessus hinkleri	011110?000	000?0?1110	1110000001	1101001112	0100110000	0000000?11	00??0?1000	?0?0?0?000	1000100001	1110?10?00
Limbodessus inornatus	000011?000	000?000110	1110010000	1101001112	0100110000	0010000011	0111100010	0010111100	1000100001	11100?01?1
Limbodessus leysi	0101110000	0001001110	1110000000	1101001112	0100110000	0000000111	0000000110	0110100100	1000100001	1110040100
Limbodessus macrohinkleri	100011?000	100?110110	1110100000	1101001112	1100110000	0000000111	0100000110	0111111100	1000100001	11100?01?1
Limbodessus masonensis	000011?000	000?001110	1110000000	1101001112	0100110000	0000000111	0000001000	0010100000	1000100001	1110010100
Limbodessus millbilliensis	0011100000	0001001110	1110000000	1101011112	0100110000	0000000111	0000001000	0010100000	1000100001	1110010110
Limbodessus morgani	0000110000	0001001110	1110000000	1101001112	0100110000	0000000011	0000000000	0010100000	1000100001	1110040100
Limbodessus nambiensis	0000110000	0001001110	1110100000	1101001112	0100110000	0000000?11	0?????????	????????00	1000100001	1110040101
Limbodessus ordinarius	000011?000	000?001110	1110000000	1101001112	0100110000	0000000111	0000000110	0010100100	1000100001	1110010100
Limbodessus praelargus	000011?000	000?000110	1110010000	1101001112	0100110000	0010000011	0111101000	0010111100	1000100001	11100?01?1
Limbodessus pulpa	0000110000	0001000110	1110000000	1101001112	0100110000	0000000111	0000000000	0010100000	1000100001	1110?10100
Limbodessus raeae	000011?000	000?001110	1110000000	1101001112	0100110000	0000000111	0110001100	01?0100100	1000100001	1110?40?00
Limbodessus raesidensis	100012?000	100?010110	1110100000	1101001112	1100110000	0010000111	0111010110	1111111100	1000100001	11100?01?1
Limbodessus shuckardii	000011?000	000?000110	1110010000	1101001112	0100110000	0000000011	0111001100	0010111100	1000100001	1110010110
Limbodessus windarraensis	0000110000	0001001110	1110000000	1101001112	0100110000	0000000111	0100000110	0110100100	1000100001	1110?40?00
Limbodessus yandalensis	100012?000	100?110110	1110100000	1101001112	1100110000	0000000111	0100001110	0111111100	1000100001	1110??0??1
Limbodessus yuinmeryensis	0000110000	0001001110	1110000000	1101001112	0100110000	0000000111	0000001100	0010100000	1000100001	1110010100
Liodessus flavofasciatus	0000110000	0001000110	1110010010	1101001012	0100110000	0000000011	0111100110	0111100100	1000100001	1110010100
Antiporus uncifer	10002?0000	00010?0110	10001?0010	1101?11112	?100110100	0000000010	0111111101	1110011110	0000000001	0100110121
Canthyporus kenyensis	00011?0000	?001000010	11000?0010	1001?11102	?00011101?1	0000000001	0111100000	0000000000	?000101111	1100?00410

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TABLE 22. (Continued)

Species	0000000000 0123456789	1111111111 0123456789	2222222222 0123456789	3333333333 0123456789	4444444444 0123456789	5555555555 0123456789	6666666666 0123456789	7777777777 0123456789	8888888888 0123456789	9999999999 0123456789
Heterosternuta wickhami	00001?0000	?0010?0110	11000?0000	1001?01?02	?100110100	00?0000010	0111100110	0011110101	1000000001	0100020111
Hydrocolus paugus	00001?0000	?0010?0110	11000?0100	1001?01?02	?100110100	00?0000000	0111101000	0000000000	1000100001	0100020110
Hydroporus columbianus	00001?0000	?0010?0110	11000?0000	1001?01?02	?100110?0	00?0000?00	0111101110	0000000000	1000100001	0100?20110
Laccornellus lugubris	0000120100	00?1001010	1000100010	1001011101	1000010101	0000000001	0111111010	1000100000	0??0101010	100?000410
Neoporus undulatus	00000?0000	?0010?0110	11000?0000	1001?01?02	?100110100	00?0000010	0111101100	1011111111	1000100001	0100020121
Oreodytes scitulus	00001?0000	?1100?0110	11000?0000	0101?01112	?100110000	00?0000000	0111101110	0000000000	0000000001	0100010?1
Scarodytes halensis	00011?0000	0110000110	11000?0000	0101??1?12	?100110100	0000000000	0111101000	1011011110	000010000?	0100020?1
Stictonectes canariensis	00001?0000	?0010?0110	10001?0000	1101?01?02	?000110000	0000000000	0111100010	1011111100	0000100001	0100020110
Hydrovatus caraibus	1000011100	0001100010	1111000010	1011010111	1000010001	1100000011	0111100000	0000000000	0111101110	1101000410
Herophydrus musicus	00011?0000	0001000110	10000?0010	?101??1?02	?000110100	00?0000010	0111111110	1011111100	???0100001	0100020?20
Hygrotus sayi	00001?0000	?0010?0110	10000?0010	1101??1?02	?000110?20	00?0000?10	0111110010	1011111110	1000100001	0100020210
Andex insignis	10001?0001	?001000111	1110100000	1111?11112	?000111000	0100010111	1111101101	1110011110	0011110111	1100031311
Desmopachria concolor	1000010001	0001000111	1110010000	1111011112	1110111000	0100111011	1000101101	1110011110	1111110111	1101001331
Hyphydrus ovatus	10000?0001	?001000111	1110000000	?111?11?12	?000111010	0100010011	1111101101	1110011110	0011110111	1101031301
Microdytes uenoi	10001?0001	?001000011	1110000000	?111?11?12	?000111000	0100010011	0111101101	1110011110	0111110111	1100000311
Pachydrus obesus	1000200001	0001000010	1000001010	1010011112	0111010000	0100011011	1000100100	0110000110	0001120001	1101020211
Laccornis latens	0000020000	1001000010	0000110010	0001011?01	0000010000	0000000101	0111100000	0000000000	0000100001	0000000010
Celina parallela	0000020100	0010000100	0000000010	1001000101	0000000000	1000000000	0111101111	1111111100	0000100011	0101000010
Derovatellus lentus	1000300010	0001000100	1010001000	1100111112	0101110111	0011220010	1????????1	1?1????110	1000220101	1100110011
Vatellus haagi	1000300010	0001000100	1011001100	1100111112	0101110111	0011220110	1111111111	1001111110	1000220011	1100110011

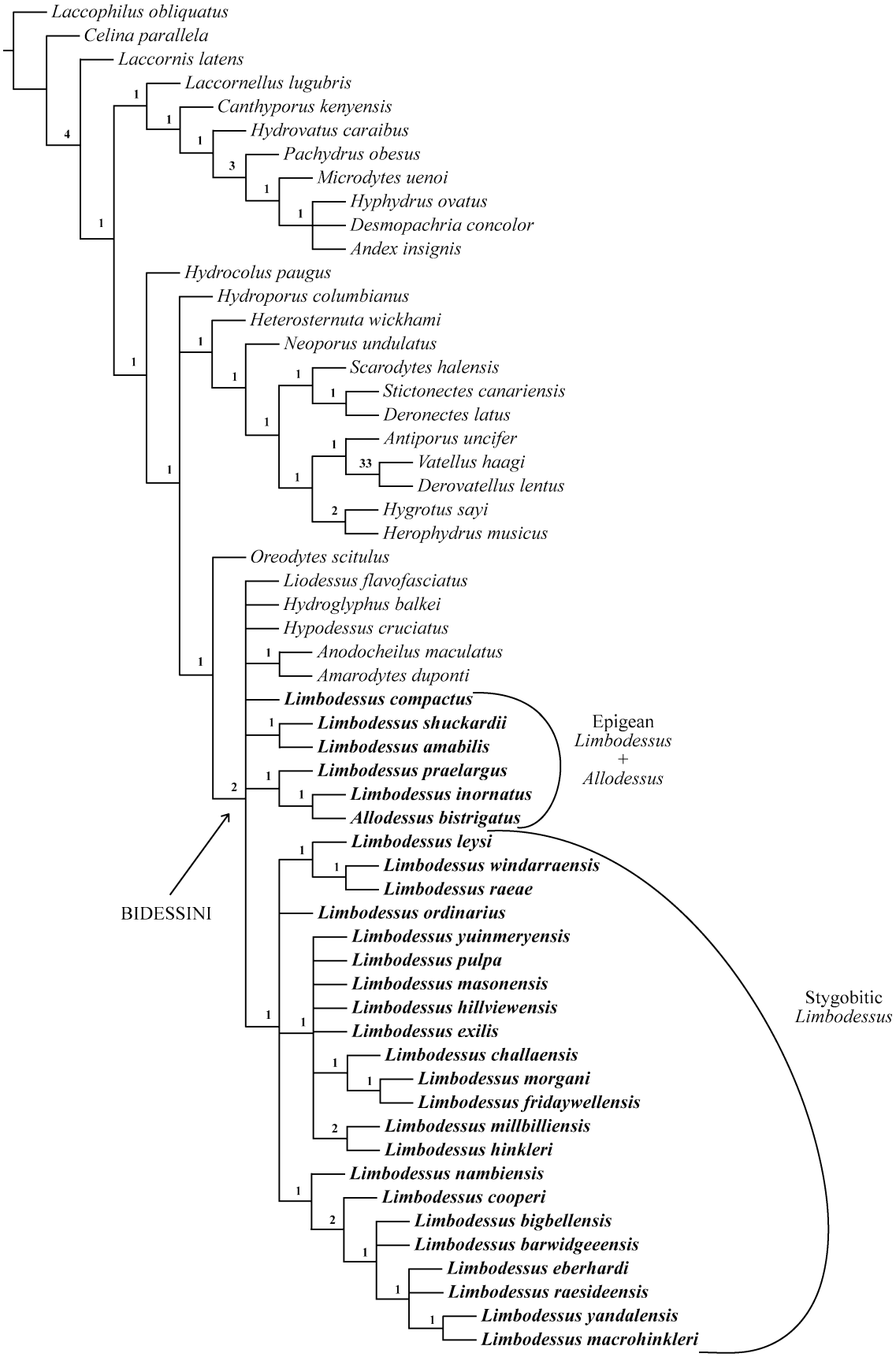

FIGURE 270. Consensus cladogram with Bremer support values indicated on each branch.

Discussion

Relationships to other genera

The larvae of *Limbodessus* lack the primary pore ABc on the last abdominal segment (character 92.1). This character state is unique within the subfamily Hydroporinae and has been proposed as a synapomorphy of the tribe Bidessini (Michat & Alarie 2008). The seta UR8 inserted subapically on the second urogomphomere (character 97.1) is another shared character of *Limbodessus* and the other Bidessini genera known in detail. This last character state, however, should not be viewed as strong evidence of a monophyletic origin of the Bidessini since it is present also in several genera of the tribe Hydroporini (Michat & Alarie 2008).

One interesting finding of this study is the presence of secondary setae on the urogomphi of some epigean and stygobitic species of *Limbodessus*. Prior to this study the absence of secondary urogomphal setae was used to distinguish larvae of *Limbodessus* from those of *Allodessus*, suggesting a more distant phylogenetic relationship between these two taxa. Contrary to recent phylogenetic analysis based on sequence data, which placed *Limbodessus* as the sister group of *Allodessus* (Leys *et al*. 2003; Balke & Ribera 2004; Hendrich & Balke 2009), our study suggests that *Limbodessus* is paraphyletic in regard of *Allodessus*, which reinforces the hypothesis of Hendrich *et al*. (2009) and Leys *et al*. (2012) based on molecular data sets. Indeed the consensus tree obtained in our study (Fig. 270) shows a sister group relationship between *A. bistrigatus* and *L. inornatus*, both sister to *L. praelargus*, giving support to the hypothesis that *Limbodessus* is paraphyletic as long as *Allodessus* is included.

As shown in this paper, *Limbodessus* is highly variable in regard to larval morphology, which makes it difficult to find characters that unambiguously separate the genus from all other Bidessini. However, the presence of a ventroapical spinula on the third antennomere distinguishes *Limbodessus* from *Anodocheilus* Babington, 1841 and *Liodessus* Guignot, 1939 (Michat & Torres 2006; Alarie *et al*. 2007), and the presence of pore PAk on the parietal separates *Limbodessus* from *Amarodytes* Régimbart, 1900 (Michat & Alarie 2006).

The separation between epigean and stygobitic species of *Limbodessus* is simpler because all known stygobitic species lack stemmata, lack two rows of secondary setae on the ventral surface of the parietal (character 25.0), and have the claws much shorter than the tarsi (character 57.1), whereas in all known epigean species the stemmata are well developed, two more or less defined rows of secondary hair-like setae are present on the ventral surface of the parietal, and the claws are relatively longer as compared to the tarsi.

Phylogenetic analysis of Limbodessus—morphology and convergent evolution

Our phylogenetic analysis supports a monophyletic origin of the stygobitic species of *Limbodessus* (Fig. 270). This finding is in conflict with previous phylogenetic analyses based on molecular data (Leys *et al*. 2003, 2012) which strongly support a polyphyletic origin of the stygobitic *Limbodessus*, and postulated that the majority of the species evolved within the different aquifers after independent colonization by a restricted number of widespread ancestral epigean species. Our result is supported by the absence of two rows of secondary hair-like setae on the ventral surface of the parietal (character 25.0), and the presence of short claws as compared to the tarsi (character 57.1). However, these characters as well as the absence of stemmata, the presence of a soft cuticle and a strongly reduced pigment (not included in our analysis) are seen as having a lesser evolutionary meaning because they are common attributes exhibited by all subterranean taxa (see also Alarie *et al*. 2009b and Michat *et al*. 2010) and most likely represent convergent traits acquired by independent evolution rather than shared apomorphies. As suggested for adult *Paroster* Sharp, 1882 (Leys & Watts 2008) the wide variation in larval body shape and size acquired, presumably by independent evolution, makes it difficult to assess relationships of the stygobitic species with their surface congeners using cladistics based on morphology and weakens our support of a monophyletic origin (see also Balke & Ribera 2004).

Identification of character states related to an underground existence

Our analysis splits the stygobitic species into three groupings, with *L. ordinarius* occupying an isolated unresolved position (Fig. 270). One contains relatively large, more modified species that show certain unusual characters (*L. barwidgeeensis*, *L. bigbellensis*, *L. cooperi*, *L. eberhardi*, *L. macrohinkleri*, *L. nambiensis*, *L. raesideensis* and *L. yandalensis*). *Limbodessus palmulaoides* and *L. yarrabubbaensis* might also belong to this group given their large size and the reduced occipital foramen, but they were only examined as instar I and could not be included in the phylogenetic analysis. The other two groupings, one composed of *L. challaensis*, *L. exilis*, *L. fridaywellensis*, *L.*

hillviewensis, *L. hinkleri*, *L. masonensis*, *L. millbilliensis*, *L. morgani*, *L. pulpa* and *L. yuinmeryensis*, and the other by *L. leysi*, *L. windarraensis* and *L. raeae*, include smaller species less deviated from the ancestral (epigean) condition. These two groups along with *L. ordinarius* form a polytomy that probably reflects the lack of characters useful to resolve relationships within the group.

In addition to large size the larvae of that group also have, with the possible exception of *L. cooperi* and *L. nambiensis*, a more or less pyriform head with a digitiform nasale (character 0.1), a strongly reduced occipital foramen (character 15.1) (Figs 27, 45, 69, 107, 212, 234), a longer second maxillary palpomere as compared to third palpomere (character 40.1), a large number of lamellae clypeales (generally more than 100 in instar III against about 50 in the smaller species which is similar to the number observed in the epigean species), and secondary setae on the urogomphus (character 99.1) (Figs 30, 48, 68, 110, 215, 237). This last character is also found in some epigean *Limbodessus* but the presence in all the larger stygobitic species but not in the smaller ones is suggestive of similar selection pressures in the different aquifers.

In contrast to the larger species, the smaller species are more similar to the epigean ones both in size and morphology. Characters common to all of them are: a subpentagonal head capsule (character 0.0), more typical of Bidessini, with a broad subtriangular nasale; occipital foramen (character 15.0) not reduced (Figs 63, 73, 77, 81, 111, 176, 208, 230, 266); and absence of posteroventral secondary setae on the tarsus (characters 75.0 and 76.0). In addition, all these smaller species have a lower number of lamellae clypeales (character 10.0) and lack secondary setae on the urogomphus (character 99.0) (Figs 66, 76, 80, 84, 114, 179, 211, 233, 269). Since both these characters are also found in some epigean *Limbodessus* they cannot be said to have necessarily evolved underground but the fact that they differ in all cases from the larger larvae is suggestive of some sort of selection pressure acting on the smaller species that is absent in the larger ones.

Other characters partially correlated with small size and not seen in epigean *Limbodessus* larvae are: the lateral margins of the nasale inflated in dorsal view (character 3.1, *L. leysi*, *L. millbilliensis* and *L. hinkleri*) (Figs 85, 103, 129), *L. leysi* is further modified in that the lateroventral margins of the nasale bear dense spinulae and appear strongly serrate (Fig. 103); the presence of a hole-like structure (of unknown function) on the ventrodistal surface of the nasale (character 2.1, *L. millbilliensis* and *L. hinkleri*) (Fig. 130); the absence of slender spinulae anterior to seta FR13 (character 5.0, *L. millbilliensis* and *L. hinkleri*); a very narrow distal half of the mandible (character 35.1, *L. millbilliensis*); and the absence of the primary seta AN2 on the antenna (character 29.1, *L. hinkleri*).

In summary, the larvae of the stygobitic species of *Limbodessus* have evolved a large range of body shapes and aberrant character states in contrast to the narrow range of morphologies seen in the larvae of the epigean species. As discussed above, some characters such as the absence of stemmata are present in most (or all) stygobitic species and are clearly the result of convergent evolution reflecting the underground lifestyle. Other characters are restricted to particular species, or groups of species, and would also seem to have evolved by convergent evolution. Alarie *et al*. (2009b) reached a similar conclusion studying stygobitic *Paroster*. Although these character clusters have an uncertain phylogenetic signal they do reflect selection pressures which presumably are similar between different aquifers. Our data identify the following characters as being possible adaptations to a stygobitic life: increase or decrease in overall size, strongly reduced occipital foramen, head either pyriform with a digitiform nasale or subpentagonal with a broad subtriangular nasale, inflated lateral margins of the nasale, an increase in the number of lamellae clypeales, dense spinulae on the margins of the nasale, a hole-like structure on the ventrodistal surface of the nasale, a comparatively long second maxillary palpomere, and absence of posteroventral secondary setae on the tarsus.

Possible reasons for evolution of characters

Our study suggests that the larger species of stygobitic *Limbodessus* have deviated the most from the epigean groundplan. We have little idea what might be driving the evolution of these species towards a larger size and comparatively more significant morphological modifications as compared to the larvae of the smaller stygobitic species. It is possible that the enlargement of the head capsule seen in many of the larger species might have resulted from an increased role for the cephalic appendages in the absence of stemmata, and hence an increased ability to catch prey in a non-visual manner (Alarie *et al*. 2009b). The large number of lamellae clypeales may also be related to an increased ability of the nasale to detect and catch prey in the dark (see Friis *et al*. 2003). A reduced occipital foramen may serve this purpose by increasing the mobility of the head (Michat *et al*. 2010). The presence of secondary setae on the urogomphus may help the larger larvae to position in the surface film to allow air exchange through the spiracles, or they may increase the ability of the larvae to sense water movements.

Size itself possibly has a relationship to prey size (Amphipods, Copepods, Isopods and Ostracods mainly, Tessa Bradford, pers. com.) although how this might operate is unclear. One pertinent observation is that adults in any given calcrete do not overlap in size (Watts & Humphreys 2009). This is true of third instar larvae also but obviously not so when first and second instars are included. Clearly the larvae of the larger species would be expected to be preying on larger prey and vice versa. The possibility of cannibalism cannot be ruled out.

Another possible explanation for the fact that the amount of modification from the hypothetical ancestral form is quite variable is differing times spent underground. Within the data are three sets of sympatric sister species: *L. masonensis* and *L. raesideensis*; *L. pulpa* and *L. eberhardi*; *L. raeae*, *L. macrohinkleri* and *L. hinkleri* (Leys *et al*. 2012). Each of these three sets includes large and small species which have spent a presumably identical amount of time underground (Leys *et al*. 2012), indicating that, in these three cases at least, the evolution of disparate morphologies is not related to different times underground.

Chaetotaxy

Whereas the larval morphology of the stygobitic *Limbodessus* species has undergone significant modifications with respect to the epigean species, the primary chaetotaxy apparently has remained as a very conservative expression of the phenotype. Indeed, a comparison of the primary sensilla of the stygobitic *Limbodessus* species with those of the epigean Bidessini known in detail (Alarie *et al*. 2007; Michat & Alarie 2006, 2008; Michat & Torres 2006; Michat *et al*. 2011) reveals no significant differences. Except for the absence of the seta AN2 in *L. hinkleri* and the presence of additional setae on the urogomphus in *L. palmulaoides*, all the primary chaetotaxic features that characterize the tribe Bidessini are found in *Limbodessus*. Secondary chaetotaxy, on the other hand, shows variation among the species, the most obvious being the variable number of lamellae clypeales (character 10), the presence or absence of secondary setae on the urogomphus (character 99), and the different number of secondary setae on the leg segments (characters 61–77).

Summary

Australian stygobitic dytiscids belong to five distinct genera: *Exocelina* Broun, 1886 (subfamily Copelatinae, 2 species described) and four genera in the subfamily Hydroporinae: *Carabhydrus* Watts, 1878 (1 species) and *Paroster* (34 species) in the tribe Hydroporini and *Limbodessus* (60 species) and *Neobidessodes* Hendrich & Balke, 2009 (2 species) in the tribe Bidessini (Watts & Humphreys 2009; Leys *et al*. 2010). Whereas the larvae of stygobitic *Paroster*, *Neobidessodes*, and *Limbodessus* were described recently (Alarie *et al*. 2009b; Michat *et al*. 2010; this paper), those of *Exocelina* and *Carabhydrus* remain unknown. This rich and diverse fauna of stygobitic diving beetles found in Australia in a relatively short time period gives support to the idea that, at a global scale, subterranean biodiversity is high (Gibert & Deharveng 2002). This, together with the fact that extensive subterranean areas are still undersampled in the World, highlights the great potential of subterranean ecosystems as a source of new biological information regarding invertebrates in general and diving beetles in particular.

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