Zootaxa 4647 (1): 115–133
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4647.1.11
http://zoobank.org/urn:lsid:zoobank.org:pub:FF6B08B1-4FAC-4EE7-83CB-4328CF714350

A new species of *Podapolipus* (Acari: Heterostigmata: Podapolipidae) from an Australian gryllacridid cricket (Orthoptera), with keys to orthopteran-associated species of the genus

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Abstract

A new species of the ectoparasitic mite genus *Podapolipus* Rovelli & Grassi, 1888 from a recently described species of the raspy cricket genus *Chauliogryllacris* Rentz, in Rentz and John,1990 (Orthoptera: Gryllacrididae) is described. The main distinctions of *Podapolipus gryllacridi* **n. sp.** from its described congeners from orthopterans are the larval female and adult male having all dorsal and ventral idiosomatic setae, except the greatly elongated pair of scapular setae (and the caudal setae of the larval female), reduced to the size of microsetae; the larval female having separate tergites C and D; the male having an entire prodorsal shield, with apex of the aedeagus between bases of setae v_1; and the adult female having smooth dorsal shields. Novel biological features of this parasite include its adult females' dwelling in the hollow sternal apodemes of their host, and its larval females using their host's other parasite, a gamasine mite, as phoretic and facultative hyperparasitic hosts. Keys are presented for the larval females and adult males of *Podapolipus* species associated with orthopterans. Problems with the generic concept of *Podapolipus* and closely related genera are reviewed. This is the first record of a podapolipid associated with orthopterans of the family Gryllacrididae.

Keywords: mite-insect relationships; ectoparasites; Ensifera; mite-on-mite hyperparasitism, phoresy

Introduction

Parasitic associations with insects have arisen repeatedly and independently among many lineages of the trombidiform mite cohort (or hyporder) Heterostigmata, including at least five of its eight constituent superfamilies (Lindquist 1986, Kaliszewski *et al.* 1995, Walter *et al.* 2009). Within the cohort, the Podapolipidae is putatively the most highly derivative and specialized family (Lindquist 1986), consisting entirely of obligate parasitic mites representing about 30 genera and some 200 described species on insects. They are especially diverse (21 genera) on adults of holometabolous Coleoptera (10 families of beetles), but some have specialized on heterometabolous insects, especially Orthoptera and some Blattodea (Regenfuss 1968, Walter *et al.* 2009). Rarely, they have become specialized on insects of other orders, as *Locustacarus buchneri* (Stammer), a tracheal parasite of bumble bees, Hymenoptera (Stammer 1951), and the genus *Cydnipolipus* Kurosa and Husband, 1994 on cydnid bugs, Heteroptera (Kurosa & Husband 1994, Husband & Husband 2017). Many genera of podapolipids appear to be restricted to one family of host insects, as detailed by Walter *et al.* (2009). However, species of *Podapolipus* Rovelli and Grassi, 1888 parasitize hosts of three different orders of insects, the Blattodea, Orthoptera, and Coleoptera, even though each species is restricted to hosts of one of those orders (Husband 1989). Many species of *Podapolipus* noted from various taxa of Orthoptera remain undescribed (Husband 1986). Here, we present the first record of a podapolipid mite associated with raspy crickets of a species of the family Gryllacrididae, recently described as *Chauliogryllacris acaropenates* Rentz, Su & Béthoux, 2018, for us to proceed with studies of the mites (Rentz *et al.* 2018). *Podapolipus*

Accepted by Z.-Q. Zhang: 8 May 2019; published: 26 Jul. 2019

and its putative sister genus *Podapolipoides* Regenfuss, 1968 are widely considered to represent the most derivative subsets of podapolipids (Regenfuss 1973, Eickwort 1975), and they are distinguished from each other by attributes of questionable plasticity. Our observations of a new species of *Podapolipus* have prompted some commentary on these species-or genus-group aspects. In proposing a new species, our rationale for excluding it from other known described species has allowed us to present tentative keys to the larval female and male of those species of *Podapolipus* associated with orthopterans, which complement the keys to other species of the genus associated with beetles, presented by Hajiqanbar (2013). Keys to adult females of these genera are impractical, as their morphological structures are so reduced and pliable, with their bag-like idiosomas assuming variable sizes and shapes in accord with their extent of embryogenesis and location in structures of their hosts.

Materials and Methods

Collection. Numerous podapolipid mites were collected from three of the eight adult raspy crickets (Gryllacrididae), hand-collected in tropical rainforest of Queensland, Australia by David Rentz and Olivier Béthoux during late summer nights (see collection data in Table 1). Additional larval female podapolipid mites were found on adult female gamasine mites, identified as an undescribed species representing the poorly known genus *Berlesia* Canestrini 1884 of the superfamily Dermanyssoidea, removed as parasites from two of these crickets (Table 1).

Preparation and observation. Crickets were killed in a multi-use cyanide chamber. Two of them were prepared for dry storage, and one put in 75% ethanol. Two dry-preserved crickets were temporarily re-hydrated in a humidity chamber to allow for expansion of wings and body parts. The ethanol-preserved cricket had to be slightly dried in order to evaporate a liquid film, whose glistening otherwise concealed the minute pale-colored parasites. Crickets were examined under a dissection microscope at 20–60x externally, then dissected to investigate the respiratory, auditory, reproductive and apodematal cavities, while recording numbers and positions of mites encountered (see Table 1). Mites from the ethanol-preserved host were transferred to 75% ethanol; mites in a dry state were removed and either placed in 75 % ethanol or mounted directly into small drops of Hoyer's medium sandwiched between a larger (18 mm square) and a smaller (13 mm round) cover slip, to optimize focal clearance for high magnification viewing from either surface. Edges of smaller round cover slips were sealed with Glpt insulating varnish. Some of the specimens initially placed in ethanol were subsequently also mounted in the same manner noted above, and some were mounted on regular microslides with cover slips. Sandwiched cover slip preparations of mites were affixed to microslides for investigation.

Photomicrophagy and imaging. Compound microscopes Nikon E-800 and Zeiss AxioImager A2 with water-immersion (Nikon, 40x and 60x), dry and oil-immersion (Zeiss) brightfield, polarized and differential interference contrast illumination were used. Stacks of images, comprising multiple focal planes, were obtained with digital cameras: a Nikon D 7000 on Nikon microscope, and a Zeiss Axiocam 506 color on a Zeiss microscope. Images were corrected for noise and color balance with Adobe Photoshop Lightroom 5.7.1. Resulting stacks were combined using Helicon Focus Pro 5.0 (Helicon Soft Ltd.) mainly using algorithm A but always with manual addition of significant details from individual focal planes to the resulting image. Draft line drawings were made using a drawing tube attached to a Reichert Zetopan compound microscope using 500 X (dry) or 1250 X (oil immersion) magnifications, then drawings finished with the aid of InkScape (v. 0.48 r9654) and Wacom Intuos 4 drawing tablet. Adult female drawings were made from the live video directed by AmScope M-900 camera from the Nikon microscope as described by Sidorchuk & Vorontsov (2014).

Two scanning electron micrography (SEM) procedures were applied. For the first, mites were dehydrated in graded ethanols, then in hexamethyldisilazane, air-dried and gold-sputtered. Images were taken in the Palaeontological Institute, RAS, with VEGA\\TESCAN equipment at 20 kV. In the second procedure, mites were transmitted to isobutanol, dried in freeze drying device JFD 320, silver-sputtered, and imaging done at 20 kV on JEOL–JSM-6510LV microscope in Tyumen University.

Terminology and systematics. Terminology of structures for the idiosoma and legs, and application of the systems of setal notation are derived from a series of studies by Grandjean (1934, 1935, 1940, 1946) that are applicable to acariform mites in general; their application follows Lindquist (1977, 1986) for the superfamilies of Heterostigmata. Leg setal sigla in parentheses indicate both setae of a pseudosymmetric pair. Systematic concepts of the superfamilies of heterostigmatic mites follow those presented by Lindquist (1986) and Walter *et al.* (2009), with secondary modifications by Khaustov (2004, 2008) for the Pygmephoroidea and Scutacaroidea. Identification of the cricket was made by David Rentz and Olivier Béthoux, who subsequently described the species (Rentz *et al.* 2018).

Measurements. Measurements of structures, given as ranges in micrometers, were made with stage-calibrated ocular micrometer or digitally, in pixels, from the micrometric scale-calibrated live feed from AmScope digital camera via ToupView software, then recalculated to micrometers. Idiosomatic lengths exclude the anterior sheath or collar of soft cuticle which envelops the base of the gnathosomatic capsule (and varies much in extent, as a result of slide preparation). Setae that are hardly any longer than the diameter of their alveolus are termed "microsetae". Lengths of elongated setae are based on maximum measurements viewed under oil immersion, as otherwise they may appear considerably shorter, due to fineness of attenuation.

TABLE 1. Collection data for parasitic mites on gryllacridid crickets.

crickets	**specimen code**	**remarks**	**Mesostigmata: Gamasina**	***Podapolipus gryllacridi* nov. sp.**
Adult male. Australia, Qld. 16°49′S, 145°40′E (GE) 151, Upper Stanton Rd (Smithfield), 104 m., 5 Feb. 2012, coll. DCF Rentz & O Béthoux, stop 12-7	Gryllacri 1	Originally preserved dry. Thoroughly dissected, all body cavities apart from digestive system checked for mites. Mites found on thoracic surfaces, wings and in sternal apodemata, the latter mites heavily damaged by decomposition	9 specimens: 7 adult females, 1 teneral female and 1 deuto-nymph on wings and membrane between thoracic sclerites; being described separately	on soft cuticle at wing bases: ca 50 larval females, ca 10 of which with stylets embedded in host's cuticle, easily detachable; ca 10 adult males; ca 10 adult females in sternal apophysae, heavily decomposed; 26 larval females on 8 katydiseiine females, with stylets embedded in leg or opisthosoma soft cuticle, broken if detached
Adult female. Australia, Qld. 16°06′10.1″S 145°26′56.24″E. James Cook University, Rainforest Site, 46 m. 3–6 Feb 2016. DSF Rentz, B. Richardson. Rainforest.	Gryllacri 3–6Feb2016	Originally preserved in alcohol. Thoroughly dissected, all body cavities apart from digestive system and ovaria checked for mites. Mites found on the surface of thorax posteriorly, abdomen near spiracles, on wings, and in sternal apodemata. Preservation of mites generally good. Two Parasitengona larvae found on hind wing		around 1st abdominal spiracle—ca. 75 larval females, few males, females loosely attached (with legs only), a few with stylets penetrating host′s cuticle, and a few males, stylets free; around 2nd abdominal spiracle—11 larval females; on hind wings, 5 larval females, stylets free; in sternal apodemata (apophysae auct.)—ca 15 adult females, attached, physogastric, each with 40–100 progeny from oocites to fully formed larval females and males; 3 engorged larval females, 2—with adult females fully formed, no small males found; few decomposed and few attached, intact larval females
Adult male. Australia, Qld. 16°57.734′S, 145°40.781′E (car), Crystal Cascades (Redlynch Intake Rd) nr Cairns Qld. 67 m. 6 Feb. 2017, coll. DCF Rentz & O Béthoux, stop 7	Gryllacri 6Feb2017m1	Originally preserved dry. Thoracic ventrum dissected. Mites found on thoracic surfaces, wings and in sternal apodemata, the latter mites heavily damaged by decomposition	6 adult females on soft thoracic membranes and on hind wings	ca 40 larval females and few males on downside of both hind wings close to base and on soft cuticle under hind wings; in sternal apodemata- >10 adult females, all severely decomposed, and >5 difficult-to-identify cast skins or decomposing carcasses of engorged larval females; 1 well-preserved engorged larval female with adult fully formed; no small male found; 35 larval females collectively on 6 katydiseiine mites, with stylets embedded in their soft cuticles

Type deposition. The holotype and some of the paratypes of the new species are deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra; additional paratypes are deposited in the Canadian National Collection of Insects and Arachnids (CNCI), Science & Technology Branch, Agriculture & Agri-Food Canada, Ottawa, and the Zoological Institute, Russian Academy of Sciences, St.-Petersburg (ZISP—Zhang 2018). Details are provided with the description.

SYSTEMATICS

Hyporder (Cohort) Heterostigmata Berlese, 1899, *sensu* Lindquist, 1976
Family Podapolipidae Ewing, 1922
Genus *Podapolipus* Rovelli & Grassi, 1888, *sensu* Regenfuss, 1968
Type species: *Podapolipus reconditus* Rovelli & Grassi, 1888, by original designation

Podapolipus gryllacridi new species
(Figures 1–7)

Diagnosis. Larval female: distinctive from all other described species of *Podapolipus* in having all dorsal and ventral idiosomatic setae, except the greatly elongated pairs of scapular setae sc_2 and caudal setae h_1, reduced to the size of microsetae, similar in size to pair *e* on tergite EF; in addition, prodorsal setae v_2 inserted slightly posterolaterad level of v_1, and tergite C separate from D. Adult male: distinctive from all other described species in having all dorsal idiosomatic setae, other than elongated scapulars sc_2, reduced to microsetae; in addition, prodorsal shield entire, with apex of aedeagus between bases of setae v_1, slightly behind shield's anterior margin. On both larval female and adult male, legs II and III without claws; tibiae II and III with seta l' setiform, and, femur II with one seta (v'' absent). Adult female: idiosoma lacking scaly or other ornamentation; leg I with a single seta, l', located on dorsal face of femur; gnathosoma lacking setae; cheliceral stylets smooth.

Description.

Larval female (n=7). Figs 1, 2, 4. Gnathosomatic capsule (Figs 1A, B, 4A) greatest width (45–54) slightly greater than middorsal length (43–53); dorsomedian apodeme evident along proximal half of capsule; dorsally, cheliceral seta *ch* (30–40) about 3X longer than ventral subcapitular seta *su* (12–17); cheliceral stylets (length 35–43) with three or four retrorse teeth along apical third of shaft; cheliceral levers slightly wider (13–15) than long (7–9); palpus with subapical cluster of four setal vestiges; palpal setae *dFe* (10–17) and *dGe* (6–10) strongly developed, *dFe* about as long as *su*; transverse distances between bases of setae: *ch–ch* 36–44, *su–su* 17–22, *dFe–dFe* 15–21, *dGe–dGe* 8–9; pharynx length 16–18, width 11–13.

Idiosomatic dorsum (Figs 1A, 2A), length 100–125, width at level of setae c_2 85–110. Prodorsal shield subtrapezoidal, greatest width (79–108) at level of setae sc_2 about 2.4X mid-line length (38–43), with three pairs of setae, of which v_1 and v_2 microsetae (0.5–1.5), sc_2 greatly elongated, attenuated (63–80); v_2 inserted at level slightly posterolaterad v_1. Tergite C with posterior margin somewhat concave but not surrounding lateral margins of tergite D; greatest width (85–110) at level near its anterior margin about 3X mid-line length (29–33), with setae c_1 and c_2 microsetae (1.5–3.0), c_2 inserted at level slightly posterolaterad c_1; tergite D somewhat inversely subtrapezoidal, greatest anterior width (50–68) about 2.3X mid-line length (16–31), with microsetae *d* (2–3); tergite EF inversely subtrapezoidal, basally overlapped by tergite D, greatest anterior width (32–48) nearly 3X mid-line length (11–21), with microsetae *e* (1.0–2.0); tergite H, fully covered by tergite EF, greatest width (13–18) about 1.8X length (3–10), with greatly elongated, attenuated setae h_1 (142–190), lacking any vestige of setae h_2; transverse distances between bases of idiosomatic setae: v_1–v_1 28–36, v_2–v_2 55–62, sc_2–sc_2 60–64, c_1–c_1 59–65; c_2–c_2 82–98, *d–d* 25–27, *e–e* 20–24, h_1–h_1 contiguous. Tergites without discernible vestiges of cupules *ia*, *im*, *ip*.

Idiosomatic venter (Figs 1B, 2B). Prosternal region with apodemes 1 reaching to prosternal apodeme; apodemes 2 slightly short of reaching prosternal apodeme; prosternal apodeme reaches to posterior margin of coxisternal plates II; sejugal apodeme reduced, with short lateral remnant on either side; coxisternal plates I and II each with one pair of microsetae, *1a* and *2a*, well removed from apodemes 1 and 2, respectively; alveolar vestiges of setae *1b* and *2b* absent. Metasternal region with coxisternal plates III separated by wide strip of soft cuticle from prosternal region (this strip partly covers plates III on unengorged, specimens); coxisternal plates III with anterior margin strongly arched anteriorly, but lacking clearly formed apodemes; plates III with poststernal apodeme narrowly delineated medially, and with remnants of apodemes 3 and 4 flanking bases of legs III; plates III each with one pair of microsetae *3b*, lacking alveolar vestiges of *3a*; all ventral microsetae of idiosoma subequal (1.5–3.0).

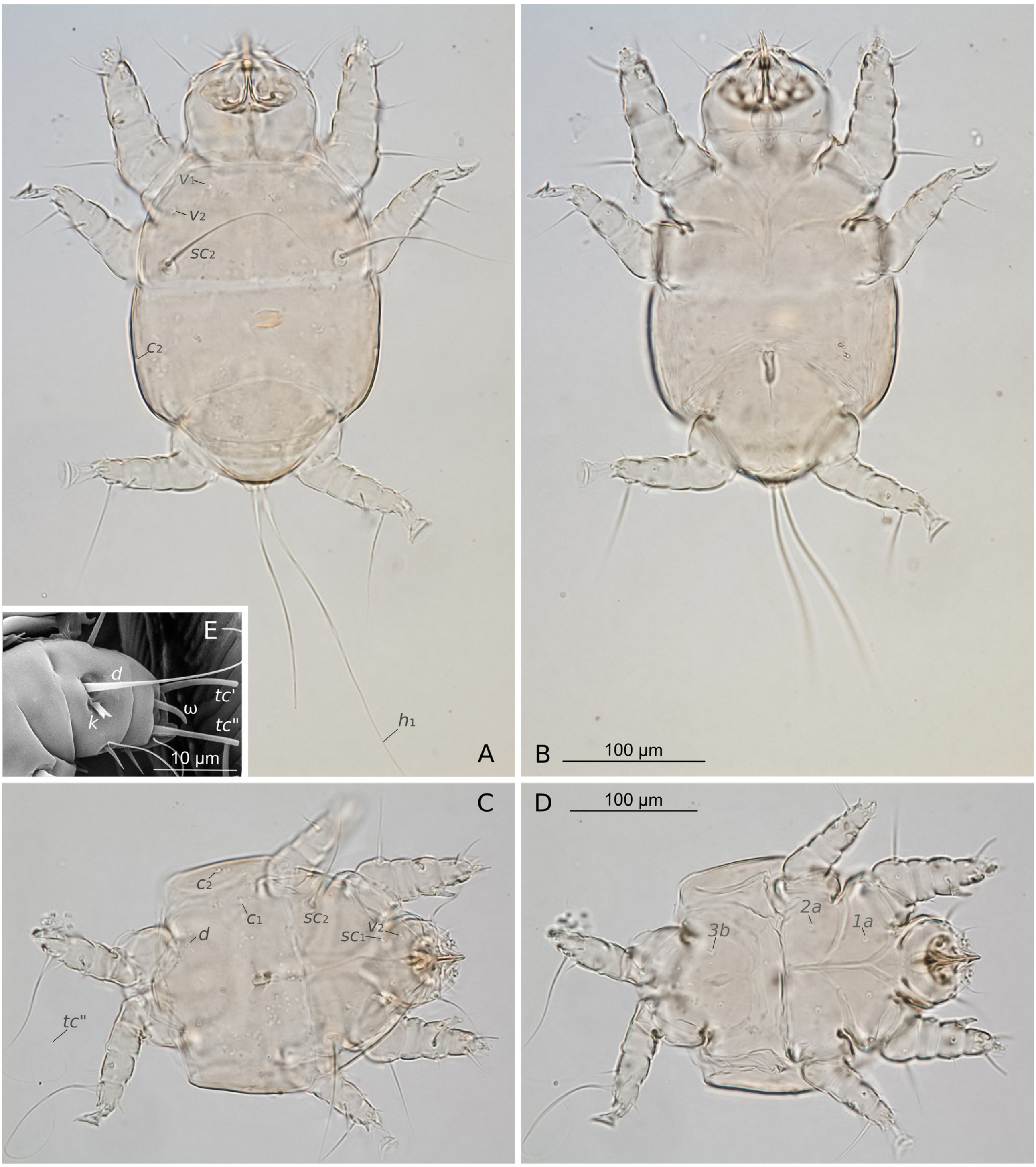

FIGURE 1. *Podapolipus gryllacridi* **n. sp.**, layered brightfield micrographs and SEM. A, B, larval female, anterior to top: A, dorsal aspect; B, ventral aspect; C, D, male, anterior to right: C, dorsal aspect, D, ventral aspect. Note length of leg III setae *tc″* in male (fine curved distal half); E, larval female, detail of leg I, SEM. Note apically forked tibial seta *k*.

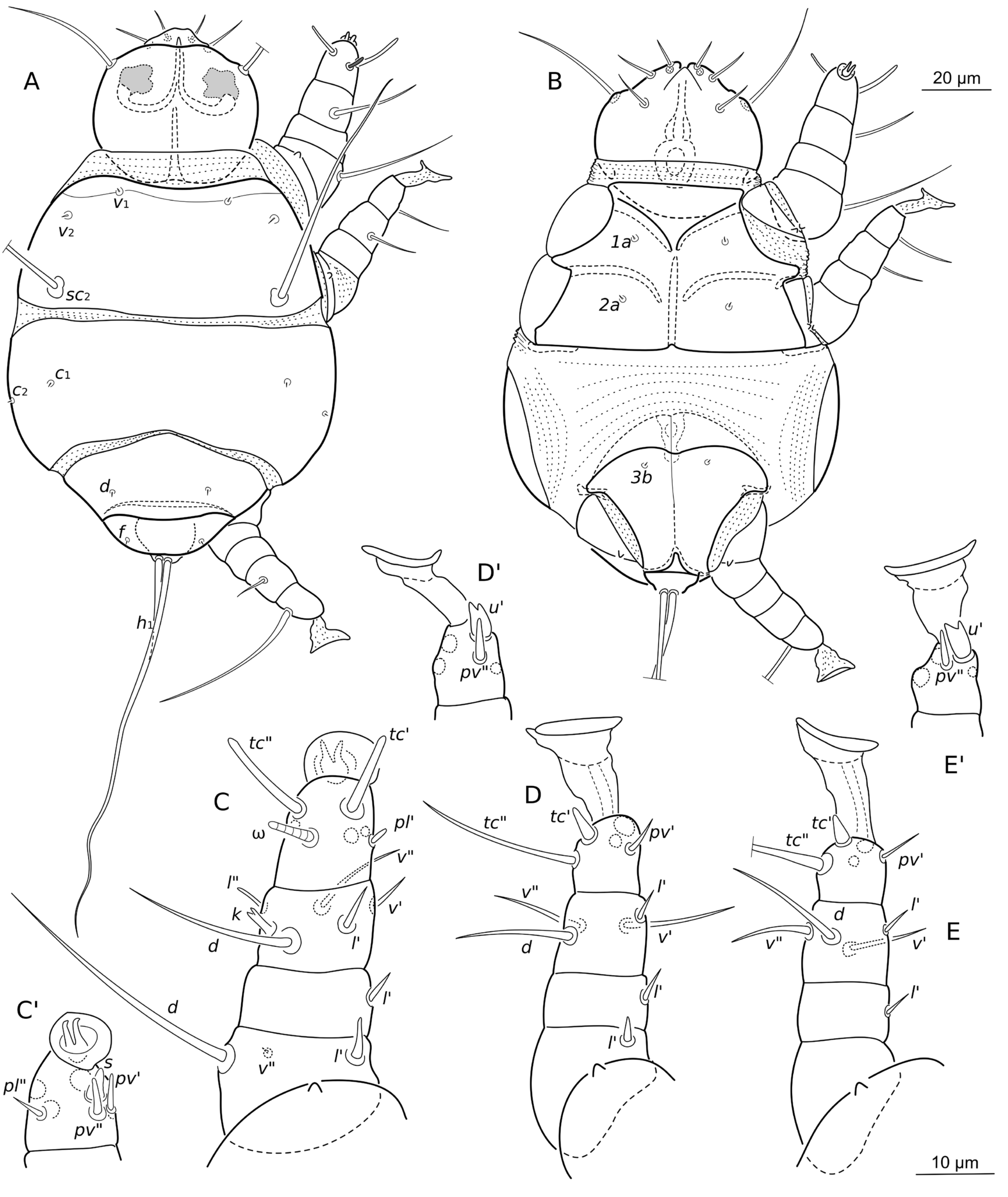

FIGURE 2. *Podapolipus gryllacridi* **n. sp.**, larval female. A, dorsal, legs and leg setae partly omitted; B, ventral, legs and leg setae partly omitted; C, leg I dorsally; C′, tarsus I ventrally; D, leg II dorsally; D′, tarsus II ventrally; E, leg III dorsally; E′, tarsus III ventrally. On leg tarsi, dotted circles mark positions of setae rooted on hidden surface.

Legs (Figs 1E, 2C–E). Legs I thicker but similar in length to other legs, their lengths from trochanter bases to tarsal apices excluding apoteles: I 46–52, II 42–46, III 40–45; lengths of segments similar to one another on each, and between, leg pairs. Number of setae (and solenidia in parentheses) on segments of legs I-II-III, respectively, trochanters 0-0-0; femora 3-1-0; genua 1-1-1; tibiae 6-4-4; tarsi 7(1)-5-5; homologies of leg setae denoted in Figs 2C–E, noting that the sixth seta on tibia I represents birefringent seta *k*, not solenidion ϕ. Leg I (Figs 2C, C′): femur with seta *l′* slightly spinelike (6–8), *d* (inserted in nearly *l″* position) greatly elongated, attenuated (30–42), *v″* minute (2.0–2.5); tibial setae *l′*, *l″*, *v′* disparately short (*l′* 6–15, *l″* 3–7, *v′* 4–8), *v″* longer (12–20), *d* longest (25–32) but shorter than Fe *d*, *k* (3–5) untapered, bifid apically (Fig. 1E); tarsus with solenidion ω (4–7) about half as long as tectals (*tc′* 10–13 slightly shorter than *tc″* 14–15), *pl′* peg-like, very short (2), *pl″* slender, short (4–7), (*pv*) slightly spinelike, short (3–6), proximally flanking more strongly spinelike *s* (5); pretarsus with small bifid claw in adhesive pad (Figs 1B, 2C′). Leg II (Figs. 2D, D′): femur with seta *l′* short (4–5), slightly spinelike, seta *v″* absent; genual seta *l′* short, as on legs I, III (3–5), tibial setae slender, *l′* short (2–4), (*v*) moderately long (11–15), *d* longest (18–23); tarsus with *tc′* bluntly spinelike, short (2–4), *tc″* elongated, attenuated (20–26), *pv′* short (3–6), slender, *pv″* similarly short but slightly spinelike and flanking strongly spinelike, apically bifid *u′* (3–6); pretarsus elongate (13–18), with adhesive pad apically, lacking rudiments of claws. Leg III (Figs 2E, E′) with genual, tibial, tarsal setae similar in form and size to those of leg II, but tarsal *tc″* much more elongated (45–65); pretarsus formed as on leg II.

Adult male (n=5). Figs 1, 3, 4. Gnathosomatic capsule (Fig. 4B) greatest width (33–34) ca1.2 greater than mid-dorsal length (29–31); dorsomedian apodeme evident along proximal half of capsule; dorsally, cheliceral seta *ch* (35–40) about 2X longer than ventral subcapitular seta *su* (17–20); palpal setae *dFe* (3–4) and *dGe* (2) minute, much shorter than *su*; transverse distances between bases of setae: *ch*–*ch* 26–29, *su*–*su* 17–19, *dFe*–*dFe* 17–18, *dGe*–*dGe* 9–11; palpus with subapical cluster of four setal vestiges; cheliceral stylets (length 20–22) with two or three retrorse teeth along apical half of shaft; cheliceral levers clearly wider (10–11) than long (5–6); pharynx length 14–15, width 10–11.

Idiosomatic dorsum (Figs 1C, 3A), length 125–135, width at level of setae c_2 91–104. Prodorsal shield subtriangular, greatest width (80–95) at level of setae sc_2 about 1.6X mid-line length (54–63), with four pairs of setae, of which v_1, v_2 and sc_1 microsetae (1.0–1.5), sc_2 greatly elongated, attenuated (70–75); v_1 inserted at level on either side of aedeagal apex; genital capsule not extending beyond anterior margin of prodorsal shield (Fig. 4C). Fused plate CD with posterior margin vaguely delineated, blending into extension of soft cuticle covering bases of legs III, with three pairs of microsetae of similar size (1.5–3.0); greatest width at level of setae c_2 (90–104) exceeds mid-line length including extension over bases of legs III (60–75); transverse distances between bases of idiosomatic setae: v_1–v_1 15–19, v_2–v_2 17–23, sc_1–sc_1 15–22, sc_2–sc_2 54–57, c_1–c_1 61–67; c_2–c_2 85–93, *d*–*d* 30–32. Tergites without discernible vestiges of cupules *ia*, *im*.

Idiosomatic venter (Figs 1D, 3B). Prosternal region with apodemes 1 united with prosternal apodeme; apodemes 2 slightly short of, or barely reaching prosternal apodeme; prosternal apodeme reaches to posterior margin of coxisternal plates II; sejugal apodeme reduced, with short lateral remnant on either side; coxisternal plates I and II each with one pair of microsetae, *1a* and *2a*, well removed from apodemes 1 and 2, respectively; alveolar vestiges of setae *1b* and *2b* absent. Metasternal region with weakly defined margins of coxisternal plates III separated by narrow strip of soft cuticle from prosternal region; coxisternal plates III with anterior margin strongly arched anteriorly and laterally, outward from weakly formed apodemes; plates III with poststernal apodeme united anteriorly with arch of apodemes 3, and extending posteromedially to level of setae *3b*; separate remnants of apodemes 3 flank anterior bases of legs III; all ventral microsetae of idiosoma subequal (2.0–3.5). Transverse interval between bases of legs III 15–19.

Legs (Figs 3C–E). Legs I thicker but similar in length to other legs, their lengths from trochanter bases to tarsal apices excluding apoteles: I 45–50, II 46–50, III 50–56; lengths of segments similar to one another on each, and between, leg pairs. Number of setae and solenidia on segments of legs I-II-III as in larval female, including presence of seta *l′* on femur II, and apically bifid seta *k* on tibia I; homologies of leg setae denoted in Figs 3C–E. Leg I (Figs 3C, C′): femur with seta *l ′* slightly spinelike (7), *d* greatly elongated, attenuated (35–47), *v″* minute (2–3); tibial setae *l′* (10–14), *l″* (5), *v′* (8–10) of disparate lengths, *v′* strongly spinelike, incurved, *v″* longer (15–18), *d* longest (30–40) but slightly shorter than Fe *d*, *k* untapered (4–5); tarsus with solenidion ω (6–7) about half as long as tectals (*tc′* 11 and *tc″* 13), *pl′* peg-like, very short (2), *pl″* slender, short (5), (*pv*) slender, short (3–5), *pv′* proximally flanking spinelike *s* (5–6); pretarsus with vestigial lobe of single, blunt claw (ca 5) in adhesive pad. Leg II (Figs 3D, D′): femur with seta *l′* short (4–5), slightly spinelike; genual seta *l′* short, as on legs I, III (4–5), tibial setae slender, *l′* short (3–4), (*v*) moderately long (14–17), *d* longest (17–28); tarsus with *tc′* short (4–5), bluntly spinelike, *tc″* elongated, attenuated (32–40), *pv′* short (7), slender, *pv″* similarly short (5–6) but slightly spinelike and flanking strongly spinelike, apically bifid *u′* (4–6); pretarsus elongate (16–18), with adhesive pad apically, lacking rudiments of claws. Leg III (Figs 3E, E′) with genual, tibial, tarsal setae similar in form and size to those of leg II, but tarsal *tc″* much more elongated (85–105); pretarsus formed as on leg II, and lacking rudiments of claws.

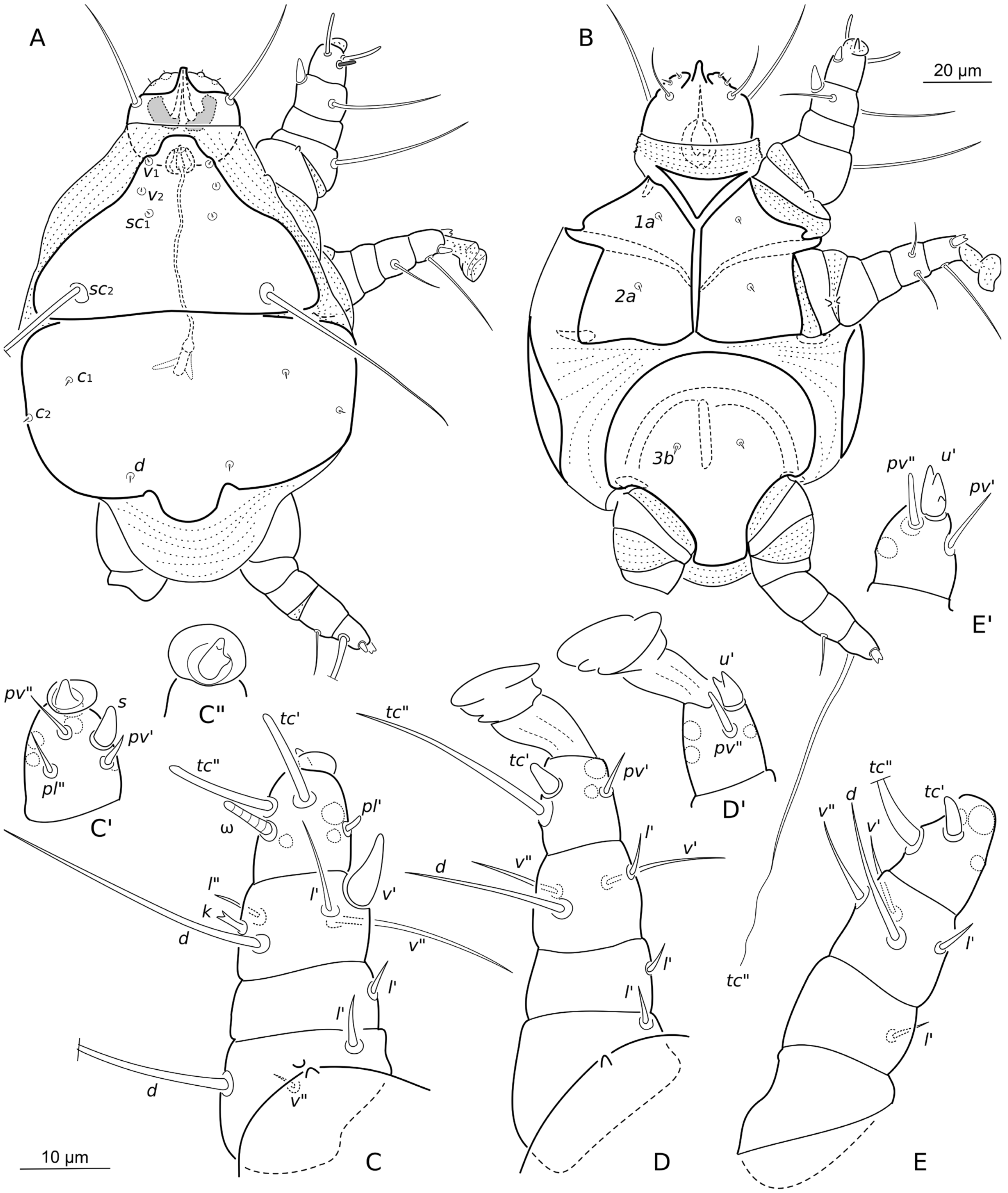

FIGURE 3. *Podapolipus gryllacridi* **n. sp.**, adult male. A, dorsal, legs and leg setae partly omitted; B, ventral, legs and leg setae partly omitted; C, leg I dorsally; C′, tarsus I ventrally; C″, variation of ambulacrum I in male; D, leg II dorsally; D′, tarsus II ventrally; E, leg III dorsally; E′, tarsus III ventrally. On leg tarsi, dotted circles indicate positions of setae rooted on hidden surface.

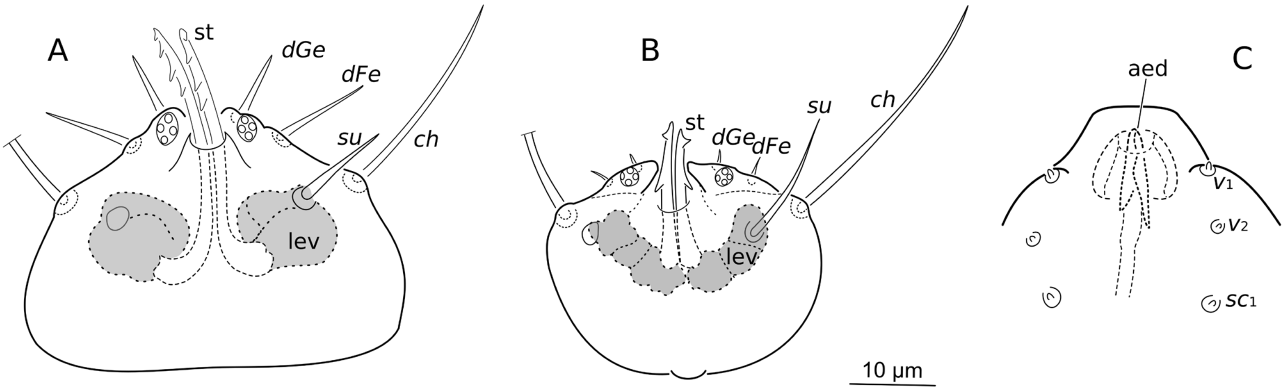

FIGURE 4. *Podapolipus gryllacridi* **n. sp.**, details. A, B, gnathosoma, ventral aspect (pharynx not shown): A, larval female; B, male; C, male anterior extent of prodorsal plate covering aedeagal capsule. Abbreviations: **aed**, aedeagus; **lev**, lever of cheliceral stylet; **st**, cheliceral stylet.

Engorged larva with pharate adult female (n=1; second, partly decomposed, specimen not measured). Figs 5D, 7A, A′. Almost globular (length of folded adult female 135, width 165, height 160, equal to idiosomal dimensions of larva), with larval cheliceral stylets splayed laterally in one specimen, contiguous in second; female inside with gnathosoma, stigmata, tracheae and legs as in adult (see below); idiosoma telescopically folded, showing 3 dorsal shields, all anteriorly: oval prodorsal (*prod*, 45x70), horseshoe-shaped (*sh2*, 13x88) encompassing it and smaller oval shield posterior to second (*sh3*, 13x88); weak lateral sclerites seem present laterally from *sh2* and *sh3*; no branching ducts (see below) visible; no small male or eggs found.

Physogastric adult female (n=5). Figs 5–7. Whitish with light-brown gnathosomatic capsule in alcohol. Gnathosomatic capsule (Figs 5B–D, F–K; 6D–H; 7C, D) slightly longer than wide (55–65 per 50–55); no setae or respiratory apertures found; minute notch (*n*) present in some specimens between fused cheliceral bases; dorsomedian apodeme evident along proximal half of capsule, widened posteriorly, hollow, with paired tubules (*tu*) extending lateroposteriorly; palps (*plp*) visible at most as weakly circumscribed protrusions; cheliceral stylets (*st*), length 35–40, smooth, trough-shaped, with salivary ducts visible at SEM in cross-section (arrow in Fig. 6E); in natural position stylets contiguous, one specimen had remnants of stylostome (*sst*) attached to them; levers (*lev*) about as wide as long, about half length of stylets; pharynx (*pha*) slightly longer than wide (30–40 per 30–35).

Idiosoma (Figs 5A, F–K; 6A–D; 7B–D) sacciform, elongate (length 1215–2150, maximal width 260–510), shallowly bilobate caudally where genital opening situated; without discernible ornamentation, setae or cupules; prodorsal shield (*prod*) oval, considerably shorter (30–45, length may be underestimated due to foreshortening) than wide (50–70); horseshoe-shaped second shield (*sh2*, 11–12x70–130), SEM shows its whole extent, while well-visible under light microscope only laterally, where multiple branching tubes (*bd*, possibly ducts of podocephalic canal system) originate; third shield indistinguishable; ovary with progeny staging from disk-shaped oocytes to fully formed larval females and adult males occupies ca 85% of idiosomatic volume; anterior and posterior compartments harbor granulate, possibly fat and/or glandular tissues. Idiosomatic venter (Figs 5G, J–K; 6C, D; 7C) shows glabrous coxisterna of single leg pair just posteriad, and pair of club-shaped stigmata (*stg*) ventrolaterad gnathosoma; one trachea (*tr*) extends from each stigma posteriorly.

Legs (Figs 5E, J–K; 6D; 7C) four-segmented (Tr, Fe, Ge, Ti-Ta), with single femoral seta (*l*′Fe, 12–16) and blunt, strongly hooked, claw-like tarsal seta *s* (cl, 12–16).

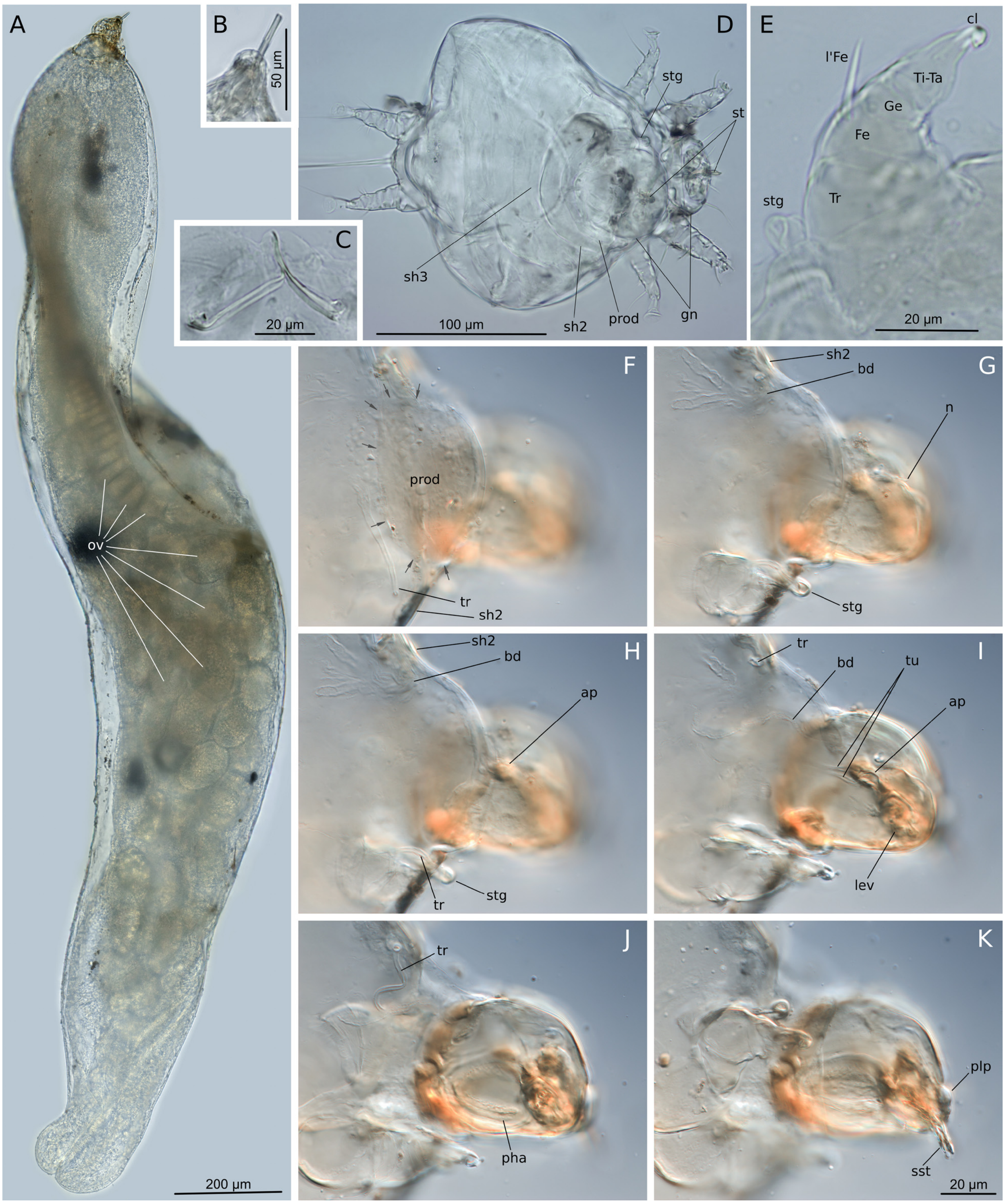

FIGURE 5. *Podapolipus gryllacridi* **n. sp.**, female. Layered polarized (A–E) and DIC (F–K) micrographs. A, freshly mounted adult female (glycerol)-note ovary with ca 100 progeny; B, detail of cheliceral stylets in normal position (tips broken); C–D, engorged larval female with pharate adult female: C, detail of cheliceral stylets after artificial splaying, note glabrous tips; D, position of adult female in her larval skin and her dorsal sclerites; E, adult female leg I; F–K, details of adult female prosoma at subsequent groups of focal planes. Abbreviations: **ap**, dorsomedian apodeme; **bd**, branching ducts of podocephalic canal system; **cl**, claw, modified from subunguinal seta *s* into terminal hook-like spine; **Fe**, femur; **Ge**, genu; **gn**, gnathosoma; **l′Fe**, dorsal seta of leg femur, homologous to *l′* of larva; **lev**, lever of cheliceral stylet; **n**, notch; **ov**, ovary with developing progeny; **pha**, pharynx; **plp**, palp; **prod**, prodorsal shield; **sh2**, **sh3**, dorsal shields; **sst**, stylostome fragments; **st**, cheliceral stylet; **stg**, stigma; **Ti-Ta**, tibiotarsus; **Tr**, trochanter; **tra**, trachea; **tu**, tubules connected to dorsomedial apodeme.

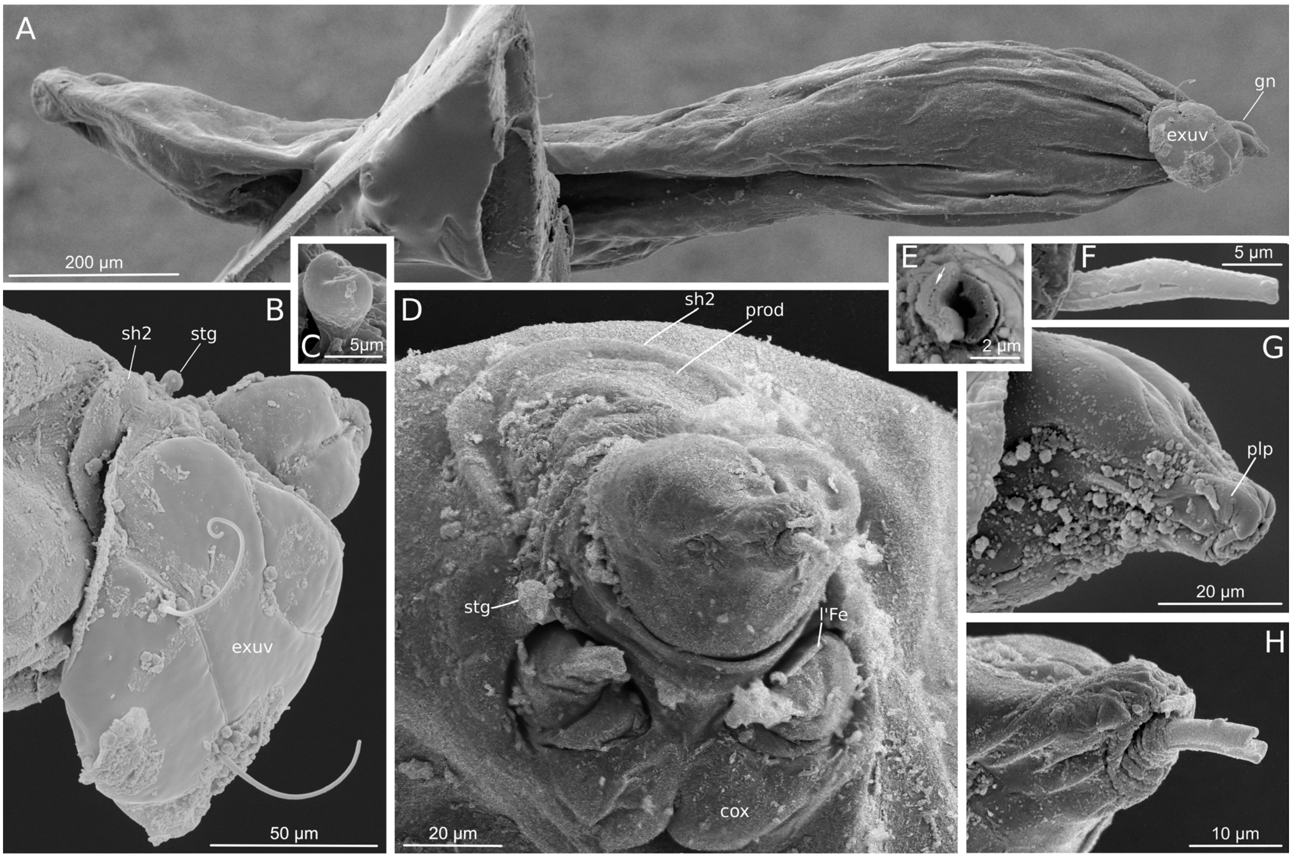

FIGURE 6. *Podapolipus gryllacridi* **n. sp.**, SEM images. All specimens but D, H, dehydrated with hexamethyldisilazane; D, H, critical point-dried specimen. A, entire specimen dorso-laterally, note larval exuvium attached to prodorsum; B, detail of A dorsally; C, stigma; D, frontal view of another specimen; E, cross-section of broken cheliceral stylets, note salivary ducts (arrow); F, cheliceral stylets in natural position, tips broken off; G, lateral view of gnathosoma, note possible palp outline; H, anterior part of gnathosoma, fronto-ventrolateral view, note soft cuticle around cheliceral stylets; stylets broken, artificially splayed. Abbreviations: **cox**, coxisternal plate; **exuv**, larval exuvium; **gn**, gnathosoma; **l′Fe**, dorsal seta of leg femur, homologous to *l′* of larva; **plp**, palp; **prod**, prodorsal sclerite; **sh2**, second dorsal shield; **stg**, stigma.

Type material

All male and larval female specimens were collected from various locations on three raspy ("Gryllacri") crickets, identified as "*Chauliogryllacris* sp." by David Rentz and Olivier Béthoux (subsequently described as *Chauliogryllacris acaropenates* Rentz, Su & Béthoux, 2018), collected from the subtropical northern peninsula of Australia: QLD (Table 1): (1) Adult male (Gryllacri 1). 16°49′S, 145°40′E (GE) 151, Upper Stanton Rd (Smithfield), 104 m., 5 Feb. 2012, coll. DCF Rentz & O Béthoux, stop 12-7. (2) Adult female (Gryllacri 3–6 Feb). 16°06′10.1″S, 145°26′56.24″E, James Cook University, Rainforest Site, 46 m. 3–6 Feb 2016, coll. DCF Rentz & B. Richardson. (3) Adult male (Gryllacri 6 Feb m1). 16°57.734′S, 145°40.781′E (car), Crystal Cascades (Redlynch Intake Rd) nr Cairns, 67 m. 6 Feb. 2017, coll. DCF Rentz & O Béthoux, stop 7. HOLOTYPE: larval female, ex wing base of Gryllacri 1, deposited in ANIC. PARATYPES: 6 larval females, 4 males, ex wing bases; 2 larval females, 2 males, ex thorax; 2 larval females, ex metathorax of Gryllacri 1; 3 larval females, detached ex female mesostigmatid gamasine mite #1 ex hind wing of Gryllacri 1; 1 physogastric adult female and 1 engorged larva with pharate adult female, ex sternal apodemes of Gryllacri 3–6 Feb 2016. DEPOSITION: 4 larval females, 2 males, 1 physogastric adult female and 1 engorged larval female with dissected parts of adult female deposited in ANIC; 4 larval females and 2 males deposited in CNCI; 3 larval females, 2 males deposited in ZISP.

Additional material

About one hundred larval females, about a dozen adult males and about 30 adult females from the same specimens, removed and placed in alcohol or left on hosts, along with the dissected remnants of the hosts, deposited in the Australian Natural Insect Collection, CSIRO, Canberra. One physogastric female on SEM stub remains at Tyumen State University, Russia. Larval females, but no males, were also found attached to adult female gamasine mites attached to the wings and thoracic surfaces of Gryllacri 1 and Gryllacri 6 Feb m1 (see Table 1) and identified by us as a new species of the gamasine genus *Berlesia* Canestrini 1884, to be described separately. These *P. gryllacridi* specimens will be distributed along with type specimens of the gamasine mite species.

Etymology

The new species name is based on 'gryllacris', a compound word meaning 'chirping cricket' and forming the name of a genus of crickets, with 'gryllacrid-' as the stem. It is meant in reminiscence of the orthopteran family name Gryllacrididae, which includes crickets of the genus *Chauliogryllacris*, upon which these mites were found.

Differential diagnosis

Larval females and males of the new species are most similar to those of *P. libratus* Naudo, 1967 and *P. transversus* Lo, 1992, in that larval females have tergital plates C and D separate, prodorsal setae v_1 inserted at least slightly anterior to the level of setae v_2, and males have the prodorsal plate entire, covering the aedeagal extension which opens near or slightly beyond that plate's anterior margin. Larval females and males of the latter two species differ from those of *P. gryllacridi* in having tergital setae c_1, c_2 much longer (4–5X) than their alveolar diameters, and the larval females also having tergital setae *d* much longer (ca 3X) than tergital microsetae *e*. Males of *P. libratus* further differ from those of *P. gryllacridi* in having setae *d* not reduced to microsetae; those of *P. transversus* differ in having the aedeagal apex opening anterior to, rather than between, the bases of vertical setae v_1. Adult females are not readily distinguishable from those of *P. libratus* and *P. transversus*, based on their descriptions.

Remarks

Among the some thirty genera of Podapolipidae, *Podapolipus* is exceptional in including species parasitic on hosts of three different orders of insects (Husband 1986, Walter *et al.* 2009). Attempts to recognize subgroups of *Podapolipus*, reflecting parasitic specialization and adaptation to different orders of insects, have been problematical (Feldman-Muhsam & Havivi 1972, Husband 1989). The species from coleopterans form a group which is characterized by some attributes that may be apomorphic, though not exclusively so: larval females and males lack the posterior seta v'' on femur II, and males have tibial seta l' modified, spinelike, on legs II and III. The two known species from Blattodea are characterized also by non-exclusive apomorphies: larval females and males have exceedingly small idiosomatic setae, other than scapular sc_2, and males have an aedeagus projecting beyond the anterior margin of the prodorsum. The species associated with orthopterans are more diverse, not readily defined as a group; however, as indicated by Husband (1986, 1989), they fall into two or three subgroups, which are somewhat indicated by attributes in our following keys. These keys are limited to descriptive or illustrative data indicated in available descriptions which are often inadequate and otherwise inconsistent in what attributes are presented.

Key to larval females of species of *Podapolipus* parasitizing orthopterans (those of *P. pseudoichthys* Mohanasundaram, 1993, and *P. pteronicheus* Mohanasundaram, 1993 are undescribed)

1. Dorsal idiosoma with plate D free from plate C. 2

\- Dorsal idiosoma with plate D at least partially fused with plate C 10

2. Prodorsal setae v_2 inserted clearly anterolaterad v_1 3

\- Prodorsal setae v_2 inserted laterad or posterolaterad v_1 6

3. Prodorsal setae v_2 4X longer than v_1, and about half as long as sc_2 . . . .*berlesei* Lahille, 1906, *sensu* Husband *et al.* 2008

\- Prodorsal setae v_2 similar in short length to v_1, and not more than 0.3 as long as sc_2 4

4. Leg II femur with two setae, l' and v'' . . . . *monistriae* Husband, 1986

\- Leg II femur with no or one seta, l' usually present, v'' absent 5

5. Tergital setae c_1, c_2 and *d* subequally very short (5–8), about twice length of microsetae *e* (3) . . . .*kurosai* Husband, 2011

- Tergital setae c_1 and d subequally short, illustrated as about thrice length of microsetae c_2 and e . . . . *lahillei* Naudo, 1967
6. Prodorsal setae v_1, v_2 and tergital setae c_1, c_2 very short (<4), as microsetae no more than twice their alveolar diameters. . . . . *gryllacridi* **n. sp.**
- Prodorsal setae v_1, v_2 and tergital setae c_1, c_2 moderately long (>5), much longer than their alveolar diameters 7
7. Prodorsal setae v_1, v_2 and tergital setae c_2, d relatively long (20–30), such that v_2 and c_2 as long as intervals v_2–sc_2 and c_1–c_2, respectively. *sundarababui* Ramaraju and Mohanasundaram, 1999
- Prodorsal setae v_1, v_2 and tergital setae c_2, d shorter (6–17), such that v_2 and c_2 clearly shorter than intervals v_2-sc_2 and c_1–c_2, respectively. 8
8. Tergites C, D, EF reticulated with cell-like pattern; leg III with tarsal seta *tc″* exceedingly attenuated (190–210), at least 0.8X as long as entire idiosoma or caudal setae h_1 . . . . *nitidulae* Ramaraju and Mohanasundaram, 1996 and *husbandi* Sarangi, Biswas, Gupta, Saha, 2012, collected from same host species and doubtfully distinguishable based on inadequate descriptions
- Tergites C, D, EF unornamented; leg III with tarsal seta *tc″* less strongly attenuated (60–170), 0.4 to 0.6X as long as entire idiosoma or caudal setae h_1. 9
9. Prodorsal setae v_2 slightly shorter than v_1; tergital setae c_1 and c_2 subequal in size . . . . *transversus* Lo, 1992
- Prodorsal setae v_1 and v_2 subequal in size; tergital setae c_2 slightly shorter than c_1 . . . . *libratus* Naudo, 1967 and *ichthyus* Mohanasundaram, 1993, doubtfully distinguishable based on inadequate descriptions
10. Prodorsal setae v_2 5X longer than v_1, as long as interval v_2–sc_2 . . . . *welbourni* Husband, 1987
- Prodorsal setae v_2 similar in short length to v_1, much shorter than interval v_2–sc_2. 11
11. Prodorsum with setae v_2 longer (6) than, and inserted clearly anterior to level of microsetae v_1 (1); femur II with two setae . . . . *naudoi* Husband, 1986
- Prodorsum with setae v_1 and v_2 similarly short or minute (1–5), v_2 inserted laterad or posterolaterad setae v_1; femur II with one seta 12
12. Coxisternal setae *1a*, *2a*, *3b* very short (5–6), similar in length to tergital setae c_1, c_2 . . *klompeni* Husband and Husband, 2006
- Coxisternal setae *1a*, *2a*, *3b* moderately short (10–25), about twice longer than setae c_1, c_2 13
13. Prodorsum with setae v_1 and v_2 minute (1–2), much shorter than tergital setae c_1, d (5–11); v_2 inserted posterolaterad setae v_1. . . . . *aharonii* Hirst, 1921, *sensu* Feldman-Musham and Havivi, 1972
- Prodorsum with setae v_1 and v_2 similarly short (5–7), similar in size to tergital setae c_1, d (7–8); v_2 inserted laterad or slightly anterolaterad v_1 . . . . *elongatus* Naudo, 1967, *sensu* Husband and Husband 2006

Key to males of species of *Podapolipus* parasitizing orthopterans (those of *P. ichthyus* Mohanasundaram, 1993, *P. pteronicheus* Mohanasundaram, 1993, *P. nitidulae* Ramaraju and Mohanasundaram, 1996, and *P. husbandi* Sarangi, Biswas, Gupta, Saha, 2012 are undescribed; that of *P. pseudoichthyus* Mohanasundarum, 1993 is inadequately described)

1. Tibia of all legs without spinelike setae . . . . *aharonii* Hirst, 1921, *sensu* Feldman-Musham and Havivi 1973
- Tibia of leg I with seta *v′* spinelike; tibia of legs II–III with seta *l′* commonly spinelike 2
2. Prodorsal plate divided longitudinally by extension of aedeagus 3
- Prodorsal plate entire, covering extension of aedeagus 5
3. Metapodosomal plate CD entire. . . . . *welbourni* Husband, 1987
- Metapodosomal plate CD divided longitudinally by extension of aedeagus 4
4. Coxisternal setae *1a*, *2a*, *3b* very short (3), similar in length to tergital setae c_1, c_2 . . . . *klompeni* Husband and Husband, 2006
- Coxisternal setae *1a*, *2a*, *3b* short (6–10), about twice longer than setae c_1, c_2 . . . . *elongatus* Naudo, 1967
5. Prodorsum with aedeagus opening between level of vertical setae v_1 6
- Prodorsum with aedeagus opening clearly anterad level of vertical setae v_1 7
6. Metapodosomal plate setae c_1, c_2, d and coxisternal setae *1a*, *2a* very short (2–3), scarcely longer than prodorsal microsetae v_1, v_2, sc_1; tibia II and III with seta *l′* setiform . . . . *gryllacridi* **n. sp.**
- Metapodosomal plate setae c_1, c_2, d and coxisternal setae *1a*, *2a* short (ca 6–10), about twice longer than prodorsal setae v_1, v_2, sc_1; tibia II and III with seta *l′* spinelike . . . . *libratus* Naudo, 1967
7. Coxisternal setae *3b* short (9), about 4X as long as microsetae *1a*, *2a* (2) . . . . *naudoi* Husband, 1986
- Coxisternal setae *1a*, *2a*, *3b* subequal in minute to short size (4–12) 8
8. Metapodosomal plate with setae c_2 only half as long as c_1, and transverse interval c_2–c_2 similar to c_1–c_1 . . . . *lahillei* Naudo, 1967
- Metapodosomal plate with setae c_2 subequally as long as c_1, and transverse interval c_2–c_2 much greater than c_1–c_1 9
9. Metapodosomal plate setae c_1, c_2, d and coxisternal setae *1a*, *2a*, *3b* very short (ca 3), scarcely longer than prodorsal microsetae v_1, v_2, sc_1 . . . . *sundarababui* Ramaraju and Mohanasundaram, 1999
- Metapodosomal plate setae c_1, c_2, d and coxisternal setae *1a*, *2a*, *3b* short (ca 4–12), at least twice longer than prodorsal microseta/setae v_1, v_2, sc_1 10
10. Tibiae II and III with seta *l′* setiform 11
- Tibiae II and III with seta *l′* spinelike. 12
11. Tibia I with spinelike seta *v′* curved, ridged. . . . . *berlesei* Lahille, 1906, *sensu* Husband 1986, 2008 *et al.*
- Tibia I with spinelike seta *v′* tapered, smooth . . . . *transversus* Lo, 1992

12. Apex of aedeagus on conspicuous neck-like extension anterad prodorsal shield; pretarsus of leg I with pair of small claws . . . .*kurosai* Husband, 2011

\- Apex of aedeagus a short lobular projection anterior to prodorsal shield; pretarsus of leg I with a single claw. . . . . *monistriae* Husband, 1986

Discussion

Genus-group taxonomic considerations

Of the five genera of Podapolipidae with species parasitic on Orthoptera, all species of three, *Podapolipoides* Regenfuss, 1968 (including *Locustipolipus* Lo, 1990), *Wetapolipus* Husband and Zhang, 2002, and *Orthapolipus* Husband and Li, 1993, are restricted to insects of that order (a record of a species of *Orthapolipus* on cockroaches, Blattodea, is considered doubtful by Husband *et al.* 2005). *Locustacarus* Ewing, 1924 includes a species parasitic on bees; and *Podapolipus* includes four species groups, of which two are parasitic on cockroaches and beetles, respectively (Husband 1986). Based on a phylogenetic analysis among all of the then-known taxa of Podapolipidae, Regenfuss (1973) found *Podapolipus*, *Locustacarus*, and *Podapolipoides* together to form the most highly derived group of genera. Since that analysis, the more recently described genera *Panesthipolipus* Husband, 1984 and *Peripolipus* Husband, 1984, both associated with Blattodea, have been listed with the number of apomorphic attributes similar to *Podapolipus* by Husband (1984, 1990). However, numbers of apomorphies do not necessarily indicate whether genera are more early or recently derived from ancestral stocks (Regenfuss 1973), so it is possible that various taxa have adapted to Orthoptera and Blattodea independently and at different times during evolutionary history. In this regard, there are few apomorphic attributes that distinguish the genus *Podapolipus* from *Podapolipoides*: primarily, apomorphically in the former, larval females lack setae h_2, and male aedeagi extend anteriorly beyond mid-level of the prodorsum. After Regenfuss' analysis, *Podapolipoides* was left unclearly defined apomorphically. However, subsequent studies by Husband (1990), Husband *et al.* (2008) and Hajiqanbar and Joharchi (2011) have indicated apomorphic distinctions for *Podapolipoides*, with larval females and males lacking tergital setae c_1 and lacking tarsal seta *pv′* on legs II–III, and males having prodorsal setae sc_1 vestigial or absent and lacking genual seta *l′* on all legs. Husband (1980, 1986) noted that the species of *Podapolipus* associated with beetles have more attributes (whether apomorphic or plesiomorphic) in common with each other than with those species associated with orthopterans and blattodeans. This may support the hypothesis of Regenfuss (1973) of a secondary and repeated transition among some species of *Podapolipus* back to beetles, from an evolutionary line of highly derived genera otherwise predominantly associated with orthopterans. On the other hand, we do not exclude the possibility that the species groups of *Podapolipus* adapted to living with orthopterans and blattodeans may be derived from (and more closely related to) the stem comprising *Podapolipoides* (rather than linked with the species group of *Podapolipus* associated with coleopterans). For example, the apomorphic attribute of male *Podapolipoides* having tergite CD divided by incursion of tergite EF is somewhat similar to the divided tergite CD found in males of a few species of *Podapolipus* on orthopterans (e.g., *P. madagascariensis* Naudo, 1967, *P. aharonii* Hirst *sensu* Feldman-Musham & Havivi, 1973). This may be an example of homoplasy or convergence, to be tested by molecular analyses.

Host and life cycle peculiarities of *Podapolipus gryllacridi*

Orthopteran host records for described and undescribed species of *Podapolipus* include the families Acrididae and Tetrigidae (Husband 1984, 2011). Hosts among other podapolipid genera parasitic on orthopterans include Tettigoniidae for *Orthapolipus* (Husband *et al.* 2005) and Anostostomatidae for *Wetapolipus* (Husband and Zhang 2002). Our host records are the first for any podapolipid on a member of the family Gryllacrididae, and only the third described species collected from hosts of the orthopteran suborder Ensifera.

Numerous larval females and adult males of *Podapolipus gryllacridi* were observed on various surfaces of the crickets' thoraces and proximal abdomens, particularly along pleural fissures, near spiracles, and clustered under the wing bases; a few were found on the wings, and a considerable proportion of larval females were found attached to the gamasine mite parasites when also present on their host (see below). No specimens were found in the host's spiracular atria or tracheal trunks, or caudally on the genitalia (see Table 1). Most of the larval female and male mites were not apparently feeding on the crickets—they were readily lifted off, their feeding stylets intact. This contrasted to the firm attachment of the larval females to their gamasine carriers: cheliceral stylets of these larvae were broken in attempts at their removal. Perhaps larval females adhering to mobile gamasine mites need a stronger attachment, where not being dislodged becomes crucial. Some of them as viewed attached had most of their body and some legs freely suspended from the gamasine carrier, such that their ambulacrae seemed to play less of a role in attachment. The engorged larval and adult physogastric females were only found in the cavities of the crickets' sternal apodemata, the cuticular ingrowths that provide attachment to the host's leg musculature. This is the first stated instance of a mite being found in this kind of a body cavity. Adult females are apparently well protected within these microhabitats: their cheliceral stylets do not even have retrose teeth that would preclude their displacement upon a physical disturbance. The possible tradeoff of using such habitat is the space restriction: each host specimen harbored only a dozen adult females, although this cricket species has an impressive body length of 4.5 to 6 cm. In contrast, *Podapolipoides diander* (Volkonsky, 1940) develops several dozens of adult females under its similarly sized host's elytra (cf. Table XXXVI in Volkonsky 1940). While becoming physogastric, the soft, pliable and expansive idiosomas of adult females may take on the form of the surrounding microhabitats in which they are confined. In the case of four specimens at hand, physogastric females were symmetrically elongated, about three to six times longer than wide, within narrowly linear apodemata. Although their microhabitats were not indicated, the forms of physogastric females of certain other species of *Podapolipus* suggest similar confinements on their orthopteran hosts, whether much (thrice) wider than long, symmetrically (e.g. *P. libratus* Naudo, 1967, *P. transversus* Lo, 1992) or asymmetrically (*P. elongatus* Naudo, 1967, *P. klompeni* Husband, 2006), or much (3X–4X) longer than wide (e.g. *P. aharonii* Hirst, 1921). Possibly, the physogastric form may be highly variable among individuals of the same species, even on the same host, depending on the dimensions of the microhabitats invaded, and on where the mite initiates its feeding probe, near the middle or extremity of dimensions of a confinement.

Some interesting observations were made from the two physogastric adult females, cleared and slide-mounted for transmitted light microscopic study and imaging. Although the smaller one used for drawing (Fig. 7B) was greatly elongated (idiosomal length ca 1535 um, nearly 4X its greatest width 410 µm), it was still in the process of probably fuller elongation and many more progeny, based on the sequential string of many disc-shaped embryos forming anteriorly in the ovarian tract, and on greater length of the other female (length ca 2150 um, nearly 6X its greatest width 360 µm). The ovary of the larger female (used for micrographic imaging, Fig. 5A), contained ca 100 progeny, indistinguishable in sex, leading posteriorly from a string of many disc-shaped embryos forming anteriorly in the ovarian tract. In the smaller female, about forty well-formed eggs and immatures were visible posterad the string of embryos; most posteriorly among them were nine distinguishable female larvae (7 arrowed in Fig. 7B), some of them within their egg chorions, and a single male. The presence of just one male among the few earliest formed specimens among the progeny may indicate that a pattern of only one male suffices for adequate mating of some of the larval females. Unmated larval females would probably still produce all-male offspring (Kaliszewski *et al.*, 1995), which would account for their abundance in aggregations of larval females and males on the above-noted areas of the crickets' thoraces and proximal abdomens.

We observed no instances of copulation in *P. gryllacridi*, but the absence of small males (cf plates XXXVIII–XXXIX in Volkonsky 1940) suggests that both of the pharate females we found were fertilized prior to their engorgement. No males were, however, found inside the sternal apodemata. Probably, fertilization occurs in the aggregations of larval females and males on the above-noted areas of the crickets' thoraces and proximal abdomens, which were the only places where males were found. Fertilization by males of the young, non-fed larval females prior to their migration to another host, or to feeding on the primary host, has been observed in, *i.e.* the weevil parasite *Tetrapolipus rhynchophori* Ewing, 1924 (cf Fig. 7 in Regenfuss 1973), and appears common in the genus *Podapolipus* (Regenfuss 1973). Notably, Husband and Sinha (1970), in citation of Wehrle and Welch (1925), indicated a similar pattern for *Locustacarus trachealis* Ewing, 1924, a tracheal parasite of various orthopterans. However, we find no indication of such observations as those by Wehrle and Welch (1925), who did not even distinguish between larval and adult females and a molting between the two instars. Separate observations by Husband and Sinha (1970) on *Locustacarus buchneri* (Stammer, 1951), a tracheal parasite of bumblebees, indicated that after copulation, larval females migrate to the tracheae of other bees in the nest, where they molt to adult females and begin to enlarge (Husband & Sinha 1970). Our assumption, thus, looks plausible.

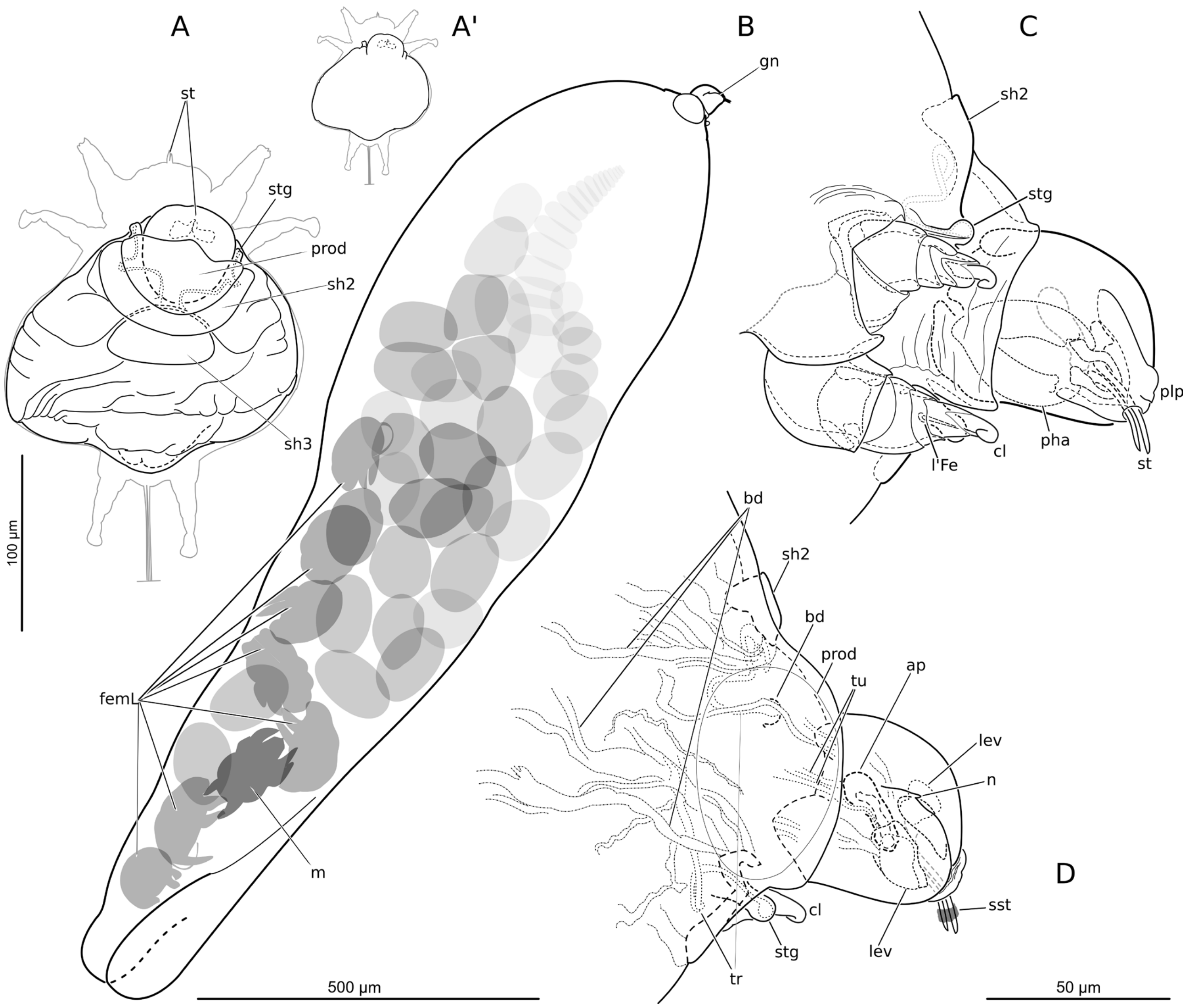

FIGURE 7. *Podapolipus gryllacridi* **n. sp.**, female. A, adult female in her larval skin, showing sclerites; A′, same as A, to scale with B; B, adult female with her progeny; C, prosoma ventrally; D, prosoma dorsally. Abbreviations: **ap**, dorsomedian apodeme; **bd**, branching ducts of podocephalic canal system; **cl**, claw, modified from subunguinal seta *s*; **femL**, female larvae; **gn**, gnathosoma; **l′Fe**, dorsal seta of leg femur, homologous to *l′* of larva; **lev**, lever of cheliceral stylet; **m**, male; **n**, notch, variably present; **pha**, pharynx; **plp**, palp; **prod**, prodorsal shield; **sh2**, **sh3**, dorsal shields; **sst**, stylostome fragments; **st**, stylets; **stg**, stigma; **tr**, trachea; **tu**, tubules connected to dorsomedial apodeme.

Dispersal of *P. gryllacridi* to a new host remains to large extent unknown. One extraordinary aspect of it, however, is evident: such dispersal may involve another parasitic mite species, when available (Lindquist *et al.* 2016). The second mite parasite of the *P. gryllacridi*'s host is an undescribed species of the poorly known genus *Berlesia* Canestrini, 1884 (Gamasina: Dermanyssoidea). On the two cricket specimens that were co-parasitized by the two mite species, from one-third to half of the larval podapolipid females were firmly attached to the adult gamasine females—apparently, they were not only phoretic, but also feeding. This represents the first known, facultative instance of interspecific mite-on-mite hyperparasitism, which is a subject of a separate contribution.

Acknowledgements

We cordially acknowledge Olivier Béthoux (Muséum national d'Histoire naturelle, Paris) and David Rentz (19 Butler Dr, Kuranda, Qld. 4881 Australia) for collecting and identifying the host gryllacridid crickets, Ninon Robin

(Muséum national d'Histoire naturelle, Paris) and Olivier Béthoux for bringing our attention to the mites on the first host and allowing us to study them. We gratefully acknowledge the help of Dmitry Vorontsov (Institute of Developmental Biology, RAS, Moscow) in searching for mites in the cricket's structural systems, photomicrography, and some final manuscript preparation, and of Roman Rakitov (Palaeontological Institute RAS, Moscow) and Alexander Khaustov (Tyumen State University, Tyumen, Russia) in obtaining the SEM images. A search for more specimens of *Cauliogryllacris* in Australian National Collection holdings by You Ning Su (CSIRO, Canberra) and his help in arranging loans are deeply appreciated. Fred Beaulieu (Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa) organized EAS′s visit to CNC in winter of 2016, which expedited our work on this and other projects. Victoria Nowell (CNCI, Ottawa) assisted EEL with graphic presentation of the tabular data. Final aspects of this paper were completed after the tragic passing of coauthor Katya Sidorchuk (Rasnitsyn 2019; Lindquist & Norton 2019). Katya was instrumental in initiating this study as well as later discovering, illustrating and measuring adult females of the new species. Thoughtful reviews of this manuscript by Owen Seeman and an anonymous reviewer are deeply appreciated.

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