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# *Anderemaeus* (Acari, Oribatida)—overview, three new species from South America and reassessment of Anderemaeidae supported by ontogeny

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## Abstract

*Anderemaeus* is a genus of Gondwanan soil-dwelling oribatid mites with seven of the eight previously known species being South American. We propose two new species from Chile— *A. sidorchukae* **sp. nov.** and *A. dentatus* **sp. nov**.—and a third from Ecuador, *A. mataderoensis* **sp. nov.** Juveniles of the former two species are described, comprising the first such data for Anderemaeidae: nymphs notably lack both exuvial scalps and centrodorsal gastronotic setae, and the opisthonotal gland opens on a distinct stalk. The generic description is revised and expanded and a key to known species of *Anderemaeus* is presented, including *A. tridactylus* **comb. nov.** We reject the inclusion of *Anderemaeus* in a broad concept of Caleremaeidae and the implied subsumption of Anderemaeidae, as there are no synapomorphies linking the taxa. *Anderemaeus* species possess derived traits—e.g. adult with circumpedal carina and nymphs with smooth cuticle and no scalp retention—that are absent from *Caleremaeus* but are shared with more derived brachypyline taxa. The higher classification of *Anderemaeus* is reviewed: an analysis of known traits is inconclusive regarding both the generic composition of Anderemaeidae and its superfamilial relationships. However, on the strength of juvenile morphology, we propose the transfer of Anderemaeidae to Gustavioidea.

**Key words**: oribatid mites, Gondwanan soil fauna, Caleremaeidae, Gustavioidea, Cepheoidea, identification key

## Introduction

The oribatid mite genus *Anderemaeus* was proposed by Hammer (1958) with *Anderemaeus monticola* Hammer, 1958 as type species. Overall, its members seem part of the Gondwanan soil mite fauna and are best known from (but not restricted to) mountainous regions of South America, where their distribution 'largely coincides with the upper limit of the *Nothofagus* region and with the páramo vegetation' (Balogh & Balogh 1985, p. 42). In its current context, *Anderemaeus* comprises eight species (Subías 2004), of which seven are found in South America; here, the genus has been reported from all countries except Paraguay, Uruguay, Venezuela, Guyana and Suriname, and these gaps may result simply from insufficient sampling.

To our knowledge, there are only three records of *Anderemaeus* from outside South America. (1) Vázquez González *et al.* (2015) reported the Andean species *Anderemaeus chilensis* Hammer, 1962 from tropical Mexico (Quintana Roo). (2) An unusually small species, *Anderemaeus australiensis* Balogh & Balogh, 1983, appears to be endemic to Australia. (3) *Anderemaeus monticola* (as 'moticola') was included in a list of oribatid mites from Huangshan Mountain (Anhui Province) in eastern China (Chen *et al.* 1992), based on a single specimen and without comment about the unusual distribution. This latter species was not found by Wang *et al.* (1996), who more comprehensively surveyed the oribatid mite fauna of the adjacent Jiuhua Mountain in a multiyear study, and there has been no subsequent confirmation or further record of this or any other *Anderemaeus* species from China. Since *A. monticola* is otherwise known only from the Andes Mountains—Bolivia (Hammer 1958), Peru (Beck 1963) and Argentina (Balogh & Csiszár 1963)—we consider the Chinese record doubtful.

Argentina has been richest in known *Anderemaeus* species, with five reported: *Anderemaeus hammerae* Mahunka, 1980, *Anderemaeus magellanis* Hammer, 1962, *A. monticola* and *A. chilensis*, (see Fredes 2018), as well

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as *A. tridactylus* (Trägårdh, 1907) **comb. nov.** (see below). But Chile has similar richness, including the first three noted above (Hammer 1962; Ermilov 2016) and two newly discovered species from the central region. Several juveniles of these new species are available for study, which is significant since Anderemaeidae is one of 45 families of Brachypylina for which juveniles have remained unknown (Norton & Ermilov 2014).

Below, we describe and illustrate the two new Chilean species, including the available juveniles. We also describe a new species from Ecuador, based only on adults; the genus has been reported from Ecuador previously, but only regarding unidentified specimens (Marian *et al.* 2018). Based in part on new information, we first offer a revised diagnosis and an expanded description of the genus, then a key to known species. Finally, we assess current views of the family-level classification of *Anderemaeus*, incorporating the new information on juveniles.

## Materials and methods

### *Specimens*

Specimens of the three new species were sorted from Berlese-funnel samples having been stored in ~70% ethanol since their collection; provenance data are given with the respective descriptions. As detailed below, type specimens are distributed among four institutions: the Senckenberg Museum of Natural History, Görlitz, Germany (SMNH); the Tyumen State University Museum of Zoology, Tyumen, Russia (TSUMZ); the University of Concepción, Museum of Zoology, Concepción, Chile (UCMZ) and the Canadian National Collection, Ottawa, Canada (CNC). Other material is retained in the personal collection of author RAN.

Juvenile specimens of *Anderemaeus sidorchukae* **sp. nov.** and *A. dentatus* **sp. nov.** were removed from the same respective Berlese sample as the adults. Since no juveniles of Anderemaeidae had been described previously, in each instance we made the association with adults using criteria outlined by Norton & Ermilov (2014). (1) Size and proportions are appropriate for the respective adult. (2) Adults of other species in the samples were either too large or small, had clearly disproportionate body-leg relationships, or were in taxa with juveniles well known to have different characteristics. (3) Gnathosomal characters are similar, including the independent, prone palp solenidion (see below). (4) Leg and body setations are entirely consistent, considering the normal ontogenetic changes.

For comparisons and generic redescription, we also studied specimens of *Anderemaeus chilensi*s and *A. hammerae*. The holotype adult of *A. chilensis* was borrowed from the Zoological Museum, University of Copenhagen; the specimen is somewhat damaged (flattened and broken), having been removed from a prepared slide in the past. Eighty-four adult *A. chilensis* from the following locations (habitat unknown unless given) also were examined: Región de Ñuble, Provincia de Diguillin, Chillán, Cueva de las Pincheros, 19-IX-1986, T. Cekalovic, col. (3 adults); same, but Los Lingues (31 adults); Región del Maule, Provincia de Linares, Linares, 1-IV-2005, M. Casanueva, col. (3 adults); Región del Biobío, Provincia de Concepción, Tome, 19-IX-1986, T. Cekalovic col. (14 adults); same, but Penco (18 adults); same, but 8 km south of Florida (8 adults); same, but 7 km west of Concepción, 19-X-1994, R.A. Norton, col. (7 adults from general litter under olivillo and peumo trees). Approximately 100 adults of *A. hammerae* were available for study, originating from Región de Magallanes y de la Antártica Chilena; Reserva Nacional Magallanes, 8 km west of Punta Arenas, 485 m a.s.l., 11-II-1985, N. Platnick and O. Francke, col., from disturbed forest litter.

For the analysis of Anderemaeidae, we studied adults of *Cristeremaeus humeratus* Balogh & Csiszár, 1963 from Chile, as well as the type-species of *Epieremulus—E. geometricus* (Berlese, 1916)—and *E. apicalis* (Banks, 1895) from the U.S.A., all in the personal collection of RAN. Discussions of superfamily placement include previously unpublished details of adult and juvenile *Hauseroceratoppia horaki* Mahunka, 1980, based on specimens from the same location as *A. hammerae* (above).

### *Observation and documentation*

Specimens of adults and juveniles were mounted in lactic acid on temporary cavity slides for measurement and illustration. All body measurements are presented in micrometers. Body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the notogaster (adult) or hysterosoma (juveniles). Notogastral width refers to the maximum width seen in dorsal aspect; width of juveniles relates to maximum hysterosomal width. Body setae were measured in lateral aspect. Formulas for leg and palp setal counts are given in parentheses according to the sequence trochanter–femur–genu–tibia–tarsus (famulus included); formulas for leg solenidia are given in square brackets according to the sequence genu–tibia–tarsus.

Drawings were made with a camera lucida using a Leica DM 2500 compound light microscope. Photographs were obtained, usually as image stacks, using an AxioCam ICc5 or AmScope MU800 digital camera mounted on the above-mentioned Leica or a Nikon Eclipse E-800 compound microscope with DIC illumination, respectively. Image stacks were combined using the Helicon Focus Pro (v. 5.0) suite; the stacks varied widely in number of individual images, usually only several for highly magnified (1000 x) images and 15-30 for lower magnifications. As needed, images were adjusted with Adobe Photoshop (CS3) for contrast and color balance.

### *Terminology and conventions*

General morphological terminology used in this paper mostly follows that of F. Grandjean: see Travé & Vachon (1975) for references, Norton (1977) for leg setal nomenclature, and Norton & Behan-Pelletier (2009) for overview. Parentheses around a leg seta indicates a pseudosymmetrical pair, unless indicated otherwise; when denoted separately, prime and second (′, ″) distinguish the seta on the anterior and posterior face, respectively.

Surface-sculpture terminology is from Harris (1979). Paired structures are described in the singular unless noted. Authorities for supraspecific names can be found in Subías (2004).

The generic redescription and discussion of classification include references to numbered 'Remarks' that are appended at the end. Each reference is parenthetic, in the form 'see R1', R2, etc.

### *Abbreviations and notations*

*Prodorsum*. Setae: *ro*, *le*, *in*, *bs*, *ex*—rostral, lamellar, interlamellar, bothridial and exobothridial setae, respectively. Other structures: *bo*—bothridium; *ea*—prodorsal enantiophysis; *exv*—alveolar vestige of second exobothridial seta; *lam*—lamella; *lr*—laterorostral carina; *lt*—lateral tooth; *mu.gn*—gnathosomal muscles; *PD*—prodorsum; *plr*—prelamellar; *prl*—prelamella; *sej*—dorsosejugal groove; *t.inc*—internal transverse incision between prodorsum and notogaster; *tu*—tutorium; *rb*—rostral bulge; *rex*—rostral excavation.

*Notogaster*. Setae: *c* (or *c*-row, $c_1$, $c_2$, $c_3$ in juveniles); *da*, *dm*, *dp* (centrodorsal setae); *la*, *lm*, *lp* (laterodorsal setae); *h*-row ($h_1$, $h_2$, $h_3$); *p*-row ($p_1$, $p_2$, $p_3$). Other structures: *cgs* – circumgastric scissure; *cr*—crista; *gla*—opening of opisthonotal gland; *hpr*—humeral process; *ia*, *im*, *ip*—anterior, middle, posterior lyrifissures (or cupules in juveniles), respectively; *ih*, *ips*—same, associated with setal rows, *h* and *p*, respectively; *mu.dv*—dorsoventral muscles between notogaster and ventral plate; *NG*—notogaster.

*Coxisternum and lateral podosoma.* Setae: *1a*, *1b*, *1c*, *2a*, *3a*, *3b*, *3c*, *4a*, *4b*, *4c*—setae of epimeres I–IV. Structures: *bo.1, bo.*2, *bo.3*, *bo.4*—internally-defined borders of epimeres I–IV, respectively; *bo.sj*—sejugal border; *cir*—circumpedal carina; *Cl*—Claparède's organ; *dis*—discidium; *e3* enantiophysis across *bo.3*; *e4*—aggenital enantiophysis, across *bo.4*; *PdI*, *PdII*—pedotectum I, II respectively; *tr.1*—trachea of acetabulum I; *tr.sj*—sejugal trachea; *vpr*—vertical pleural ridge.

*Anogenital region*. Setae: *ag*—aggenital seta; $ad_1$, $ad_2$, $ad_3$—adanal setae; $an_1$, $an_2$—anal setae. Structures: *AN*—anal plate; *GEN*—genital plate (or aperture); *iad*, *ian*—adanal, anal lyrifissure (or cupules in juveniles), respectively; *mu.gen* – genital plate muscle; *mu.ps*—postanal suspensor muscle; *ovp*—ovipositor; *po.st*—postanal strut; *pr.o*—preanal organ; *sp* – spermatopositor; *VP*—ventral plate.

*Gnathosoma*. Setae: *a*, *m*—anterior, middle seta of gena; *h*—hypostomal seta of mentum; $or_1$, $or_2$—adoral setae; *v*, *l*, *d*, *cm*, *acm*, *ul*, *sul*, *vt*, *lt, sup, inf*—palp setae; *ω*—palp tarsal solenidion; *ep*—postpalpal seta; *cha*, *chb*—cheliceral setae; Structures: *rbr*—rutellar brush; *ru*—rutellum; *Tg*—Trägårdh's organ.

*Legs*. Setiform organs: *σ*, *φ ω* – solenidia of genu, tibia and tarsus, respectively; *e*—famulus of tarsus I; *d*, *l*, *v*—dorsal, lateral, ventral setae, respectively; *ev*, *bv*—basal trochanteral setae; *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl*—tarsal setae. Structures: *bpr*—basal process; *p.a*—porose area; *t*—tooth; *vk*—ventral keel.

## Genus *Anderemaeus* Hammer, 1958

*Type species*: *Anderemaeus monticola* Hammer, 1958, p. 62

### *Diagnosis*

Anderemaeidae (see Balogh 1972; Balogh & Balogh 1985) with adults of medium size, length ca. 350–830. Cuticle conspicuously foveate on projecting structures of prodorsum and podosoma; cerotegument (cuticular secretion layer) abundant, with spherical to columnar excrescences. Prodorsum with paired blade-like tutoria and converging lamellae; each lamella with or without small cusp bearing seta *le*, each tutorium proximally forming part of prodorsal enantiophysis. Bothridium strongly projecting, seta baculiform to clavate. Dorso- and pleurophragmata absent. Lateral podosoma with pedotecta I and II and large discidium. Circumpedal carina and aggenital enantiophysis present; preanal organ hollow, tubular to distinctly expanded internally. Notogaster with rectangular humeral process and relatively straight anterior margin, but immovably fused with prodorsum within distinct dorsosejugal furrow; with 10 pairs of setae, *lm* positioned medially; without porose organs. Coronal setae absent from ovipositor. Chelicera chelate-dentate; rutellum pantelobasic; palp solenidion independent, prone. Legs relatively short, thin; pretarsi heterotridactylous; seta *d* lost from all tarsi and genua I–III; iteral setae present on tarsi I–III. Juveniles without exuvial scalps; nymphs lacking centrodorsal setae, $c_1$, $c_3$, *l*- and *h*-series flagellate; opisthonotal gland of nymphs opening on long stalk.

### *Adult*

(Figs 1–6, 10–15, 17–24)

Modified and expanded from Hammer 1958.

Length ca. 350–830, mostly greater than 550. Color in preserved, mature specimens dark reddish-brown to light tan (Fig. 12A–C; except for teneral specimens, lighter colors probably due to gradual bleaching). Cuticle partly with distinct sculpturing, microtuberculate locally (e.g. Fig. 3E): projecting structures of prodorsum and podosoma (lamella, tutorium, pedotecta, parietal walls of acetabula, various carinae) conspicuously foveate (Figs 3J; 12D, G); notogaster unsculptured or shallowly, inconspicuously foveolate (i.e., with smaller, well-spaced circular depressions); venter mostly without foveation. Cerotegument encrusting body and basal parts of legs; excrescences spherically granular in some areas, but mostly columnar, from simple to variously ornamented (Figs 4, 13, 21, 23); with (Figs 12A, 22J) or without particles of exogenous organic and mineral debris.

Rostrum subtriangular in dorsal view, with (Fig. 1A) or without (Fig. 17) small terminal mucro; with medial bulge (*rb*) in rostral limb between rostral setae, bulge strongly excavated on ventral ('internal') face (Figs 2A, 11A, 20F; see R1); some species with margin of limb extended posteriorly as laterorostral carina (*lr*; Figs 2A, 3J ), reaching parietal wall of acetabulum I and forming prodorsal contour in dorsal view; border of camerostome below carina smooth, irregularly scalloped or toothed. Lamella about two-thirds length of prodorsum, pair convergent but separated anteriorly; each formed as thin, near-vertical blade starting at bothridium and ending at insertion of lamellar seta, usually on small, tubular cusp, hardly longer than wide (Fig. 2A, 3J insert); lamella continuing, or not, short distance past cusp as low, narrow prolamella (*prl*; Fig. 19D, G). Transverse prelamellar ridge (*plr*; Figs 10A, 11A) present or absent. Tutorium thin, blade-like (*tu*; Figs 2A, 3J); height decreasing anteriorly to efface without cusp, usually between levels of lamellar and rostral setae; with abrupt posterior end, opposing separate tubercle to form prodorsal enantiophysis (*ea*). Posterodorsal tubercles present in various configurations or absent. Without dorso- or pleurophragma; cheliceral retractor and subcapitular levator muscles inserting directly on external prodorsal cuticle (Fig. 21B). Bothridium strongly projecting (Fig. 23G), emarginate laterally; bothridial seta (*bs*) of various form, baculiform to clavate (Figs 3C, D, 23G); usually with minute, inconspicuous barbs or scalloping, restricted to clear, isotropic outer cuticle layer. Interlamellar seta (*in*) long, erect, inserted on small or conspicuous tubercle; exobothridial seta (*ex*) shortest, inserted posterior to prodorsal enantiophysis and dorsal to alveolar vestige (*exv*) of second exobothridial seta (Fig. 2A); lamellar (*le*) and rostral (*ro*) setae intermediate in size.

Circumgastric scissure (*cgs*; Fig. 2A) incomplete: fully developed posteriorly, but gradually narrowing anteriorly to efface in humeral region. Notogaster without posterior tectum (Fig. 20C); with discrete, straight anterior margin but fused to prodorsum across distinct dorsosejugal groove; line of fusion indicated by internal transverse incision (*t.inc*; Figs 12I, 21A; see R2). With projecting, rectangular humeral process (*hpr*; Figs 1A, 2A) aligned with bothridium across sejugal groove, and weak to well-defined ridge ('crista') running posteriorly from process, best seen in lateral view (*cr*; Figs 2A, 11A). Ten pairs of notogastral setae, *lm* with central position; usually with conspicuous barbs extending from birefringent core. Opisthonotal gland opening (*gla*) and normal complement of five lyrifissures (*ia*., *im*, *ip*, *ih*, *ips*) present, in typical positions (Figs 2A, 11A, B).

Podosoma with pedotectum I (*PdI*; Figs 1B, 12G) of medium size, uniformly curved; with vertical pleural ridge (*vpr*; Fig. 2A, 3J) running from its dorsal end to near insertion of exobothridial seta, usually as distinct carina; pedotectum II (*PdII*) smaller, scaliform. Circumpedal carina (*cir*; Figs 2A, 3I) sharply defined, originating near posterior margin of acetabulum IV, then curving to approach circumgastric scissure asymptotically, ending below humeral process; lateral portion foveate. Coxisternum with epimeral borders mostly well-delineated (Figs 1B, 3B, G, 20B): *bo.1* complete medially; *bo.2* indistinct, incomplete or irregular medially; *bo.sj* and *bo.3* complete, transverse; *bo.4* slightly oblique, merging with genital rim to meet with *bo.3* in vague X-pattern; sternal borders (midline) often variable, absent to weakly defined. Surface distinctly grooved at posterior three borders (Fig. 21G); *bo.4* spanned by large aggenital enantiophysis (*e4*), *bo.3* with or without enantiophysis *e3*; seta *3b*, on or near tubercle posterior to groove of *bo.sj*. Apodemes differing in form: *ap.1* (Fig. 21H) large, with thickened, sloping medial edge, pair forming approximate V-shape when viewed face-on; *ap2* (Fig. 23H) also large, with near-vertical thickened edge, pair well separated; *ap.sj* (Fig. 23I) small, oblique, penetrated by trunk of sejugal trachea; *ap.3* (Fig. 23J) small, indistinct, merging with thick *bo.3* to form apparent wall-like band across coxisternum; *ap.4* essentially absent (Figs 21I, 23K). Tracheal system normal, with *tr1* and *tr.sj* double-branched (Fig. 23D, I), *tr3* single. Epimeral setal formula (I–IV) 3–1–3–3 (Figs 1B, 10B; see R3).

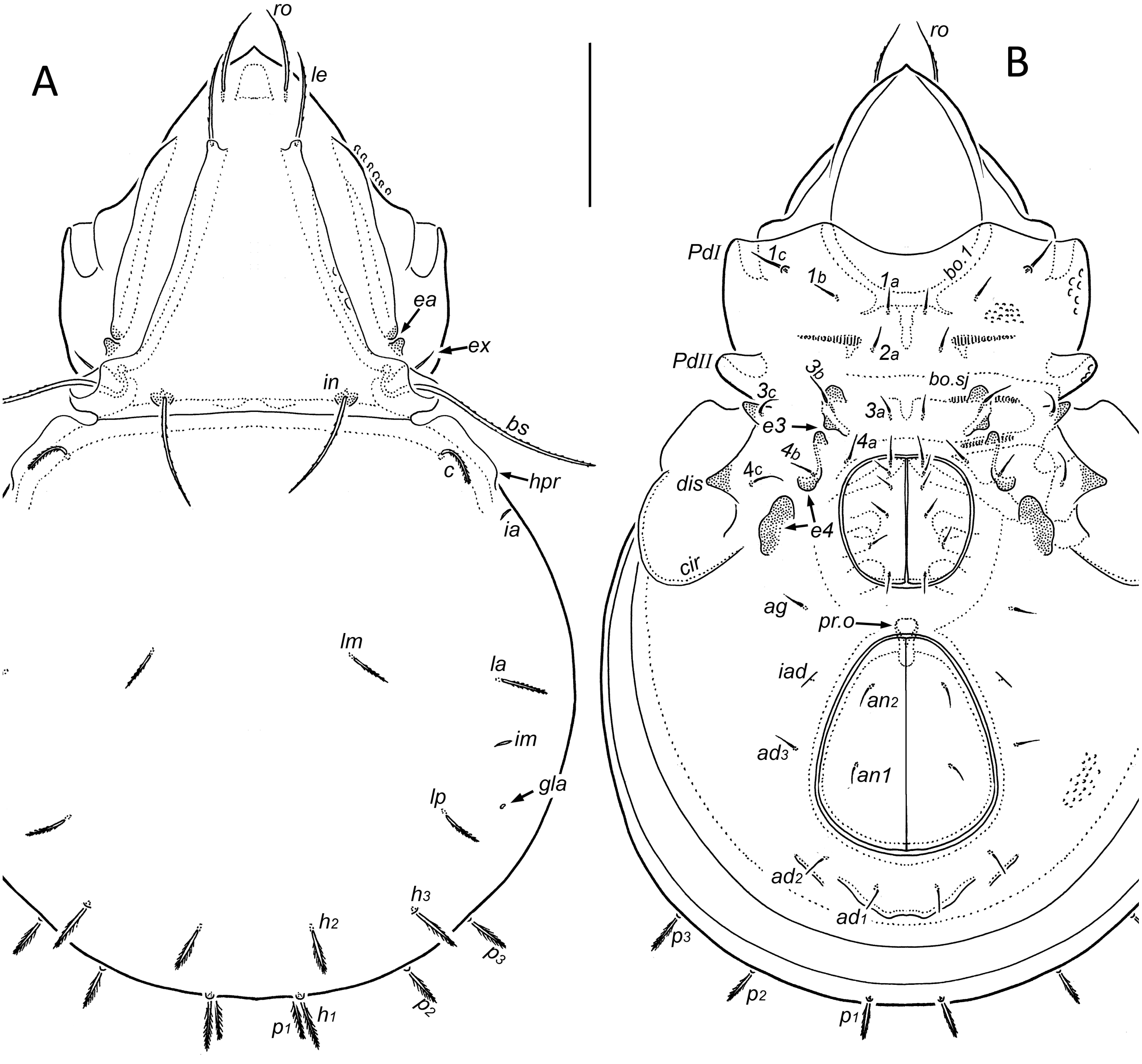

**FIGURE 1.** *Anderemaeus sidorchukae* **sp. nov.**, adult (gnathosoma and legs omitted): A, dorsal view; B, ventral view. Scale bar 100 µm.

Anogenital region with six pairs of genital (see R4), one pair of aggenital, two pairs of anal and three pairs of adanal setae; *ad*$_1$ and *ad*$_2$ posterior to, *ad*$_3$ lateral to anal aperture. Lyrifissure *ian* absent; *iad* oblique, removed from anal plate at level near that of *an*$_2$. Preanal organ (*pr.o*; Figs 1B, 21C, D) hollow, caecum-like, tubular or expanded internally. Posteromedial corner of each anal plate with long, narrow strut (*po.st*; Fig. 21E, F) serving for attachment of postanal suspensor muscle (*mu.ps*); pair approximate, but not merging. Ovipositor (*ovp*; Fig. 21D) with lobes occupying about half length of distal section; with normal complement of 12 setae, four on each lobe, all similar in size; coronal setae absent. Spermatopositor (*sp*; Fig. 23K) small, typical of Brachypylina.

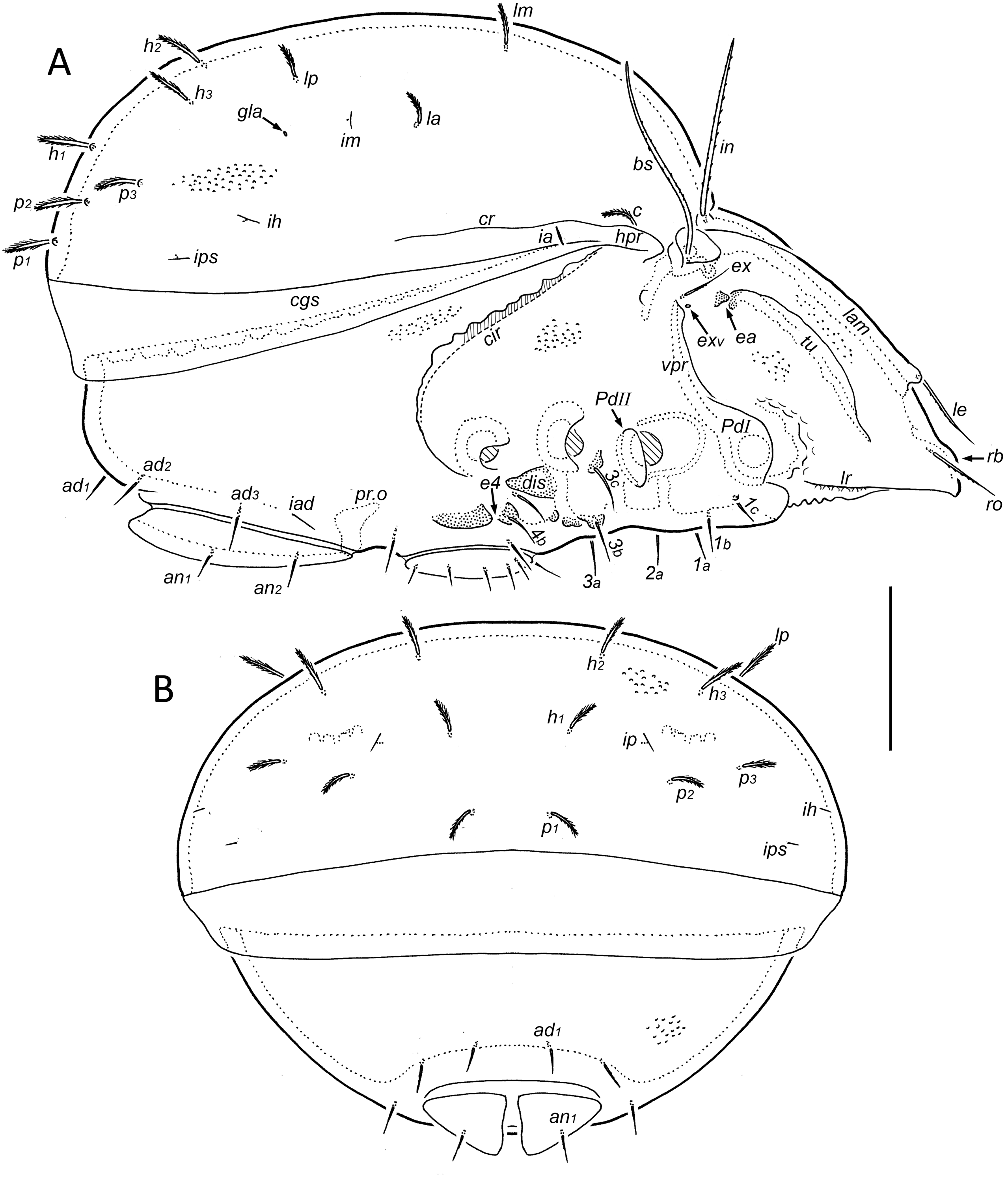

**FIGURE 2.** *Anderemaeus sidorchukae* **sp. nov.**, adult (gnathosoma and legs omitted): A, lateral view; B, posterior view. Scale bar 100 μm.

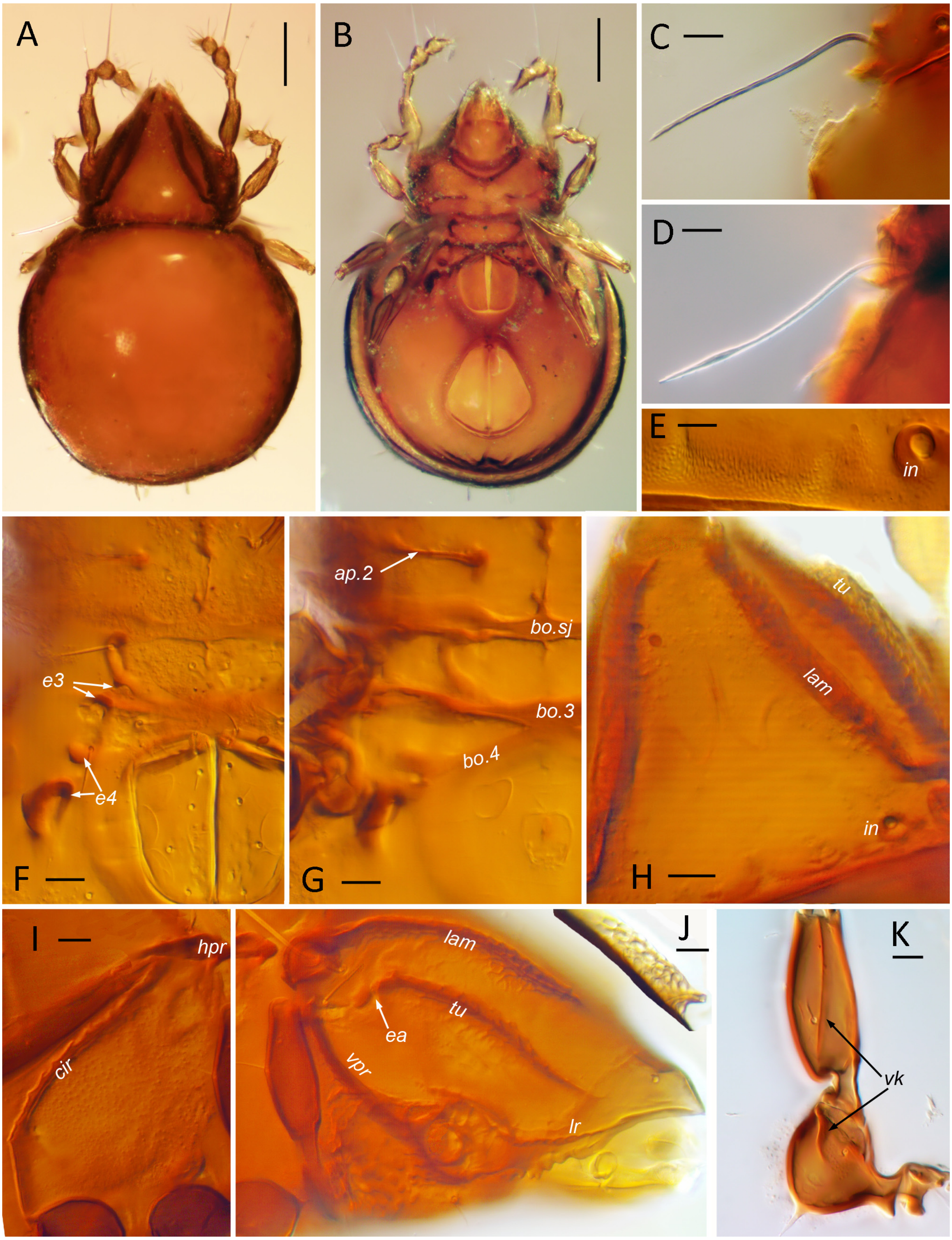

**FIGURE 3.** *Anderemaeus sidorchukae* **sp. nov.**, adult: A, dorsal view; B, ventral view, C, bothridial seta of paratype; D, same, non-type specimen from Concepción; E, region of right interlamellar seta, showing cuticular microtubercles; F, coxisternal and genital region, surface focus; G, same, deeper focus; H, prodorsum, dorsal view; I, lateral view above legs III, IV; J, proterosoma, lateral view (insert: deeper focus to show opposite lamella); K, trochanter and femur III, ventral view. Photomicrographs in transmitted light, except A, B reflected light. Scale bars: 100 µm (A, B); 20 µm (C, D, F–I); 10 µm (E).

Subcapitulum diarthric, without axillary saccule; rutellum (*ru*; Fig. 5A) pantelobasic, with typical dentition and rutellar brush (*rbr*). Chelicera (Figs. 5D, 14D) chelate-dentate, slightly elongated (~3 times longer than deep), with relatively small chela occupying about one-quarter of cheliceral length; usually with 1–2 minute denticles proximal to seta *cha*; Trägårdh's organ (*Tg*) relatively narrow. Palp (Figs 5C, 14C) with usual setal formula: 0–2–1–3–9(+$\omega$); setae of trochanter to tibia long, attenuate, barbed. Tarsus with four short, blunt distal eupathidia—*acm*, *sul*, (*ul*); other tarsal setae smooth or with sparse, inconspicuous barbs; solenidion $\omega$ free of setal attachments, narrowly baculiform, appressed to palp surface. Postpalpal seta (*ep*; Fig. 13G) spiniform, smooth.

Legs (Figs 6, 15, 19) relatively short, longest (IV) less than 2/3 body length. Pretarsi heterotridactylous, claws with sparse, minute, inconspicuous dorsal dentes. Tarsi spindle-shaped, without tendon guidage tubes. All tibiae and femora I, II clavate, with distinct proximal stalk. Femora and trochanters III, IV broadly expanded with short stalks hidden in adaxial view. Femora III, IV (and in some cases trochanters) with ventral keel or large blade; trochanters III, IV with fin-like basal process (*bpr*; Fig 13H, 22I), with or without prominent teeth or large spines. Porose area (*p.a.*; Figs 6, 22I) developed on adaxial face of each femur and on trochanters III and IV; none on tibiae or tarsi. Setal and solenidial counts as follows: I (1-5-3-4-20) [1-2-2], II (1-4-3-4-16) [1-1-2], III (2-3-2-3-15) [1-1-0], IV (1-2-3-3-12) [0-1-0]; homologies indicated in Table 1; notably, seta *d* absent from genua I–III and from all tibiae and iteral setae present on tarsi I–III. Proral (*p′*, *p″*) and subunguinal (*s*) setae eupathidial on tarsus I; famulus (*e*) small, simple, baculiform. Solenidion $\varphi_1$ of tarsus I flagellate, others vary with species.

**TABLE 1.** Development of leg setae and solenidia in *Anderemaeus sidorchukae* **sp. nov.** and *A. dentatus* **sp. nov.**[1, 2]

| | Trochanter | Femur | Genu | Tibia | Tarsus |
|---|---|---|---|---|---|
| Leg I | | | | | |
| Larva | - | *d*, *bv″* | (*l*), $\underline{d\sigma}$ | (*l*), *v′*, $\underline{d\varphi_1}$ | (*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*), (*pl*), *e*, $\omega_1$ |
| Protonymph | - | - | - | - | $\omega_2$ |
| Deutonymph | - | (*l*) | - | $\varphi_2$ | - |
| Tritonymph | *v′* | - | *v′* | *v″* | (*it*) |
| Adult | - | *v″* | [*d* lost] | [*d* lost] | *v′*, *l″* |
| Leg II | | | | | |
| Larva | - | *d*, *bv″* | (*l*), $\underline{d\sigma}$ | *l′*, *v′*, $\underline{d\varphi}$ | (*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*), $\omega_1$ |
| Protonymph | - | - | - | - | - |
| Deutonymph | - | (*l*) | - | *l″* | $\omega_2$ |
| Tritonymph | *v′* | - | *v′* | *v″* | (*it*) |
| Adult | - | - | [*d* lost] | [*d* lost] | *l″* |
| Leg III | | | | | |
| Larva | - | *d*, *ev′* | *l′*, $\underline{d\sigma}$ | *v′*, $\underline{d\varphi}$ | (*ft*), (*tc*), (*p*), (*u*), (*a*), *s*, (*pv*) |
| Protonymph | - | - | - | - | - |
| Deutonymph | *l′* | *l′* | - | *l′* | - |
| Tritonymph | *v′* | - | *v′* | *v″* | (*it*) |
| Adult | - | - | [*d* lost] | [*d* lost] | - |
| Leg IV | | | | | |
| Protonymph | - | - | - | - | *ft″*, (*p*), (*u*), (*pv*) |
| Deutonymph | - | *d*, *ev′* | *d*, *l′* | *v′*, $\underline{d\varphi}$ | (*tc*), (*a*), *s* |
| Tritonymph | *v′* | - | *v′* | *l′*, *v″* | - |
| Adult | - | - | - | [*d* lost] | - |

[1] Larva unknown for *A. dentatus*, but its leg setation is almost certainly the same as in *A. sidorchuckae*. In brachypyline oribatid mites no setae are added to legs I-III between larva and protonymph.

[2] Setae (Roman letters except famulus *e*) and solenidia ($\sigma$, $\varphi$, $\omega$) are shown where they are first added and are assumed present through the rest of ontogeny, unless noted in brackets. Setae in parentheses represent pseudosymmetrical pairs; dash indicates no addition; underline indicates solenidion is coupled to seta *d*, in same alveolus.

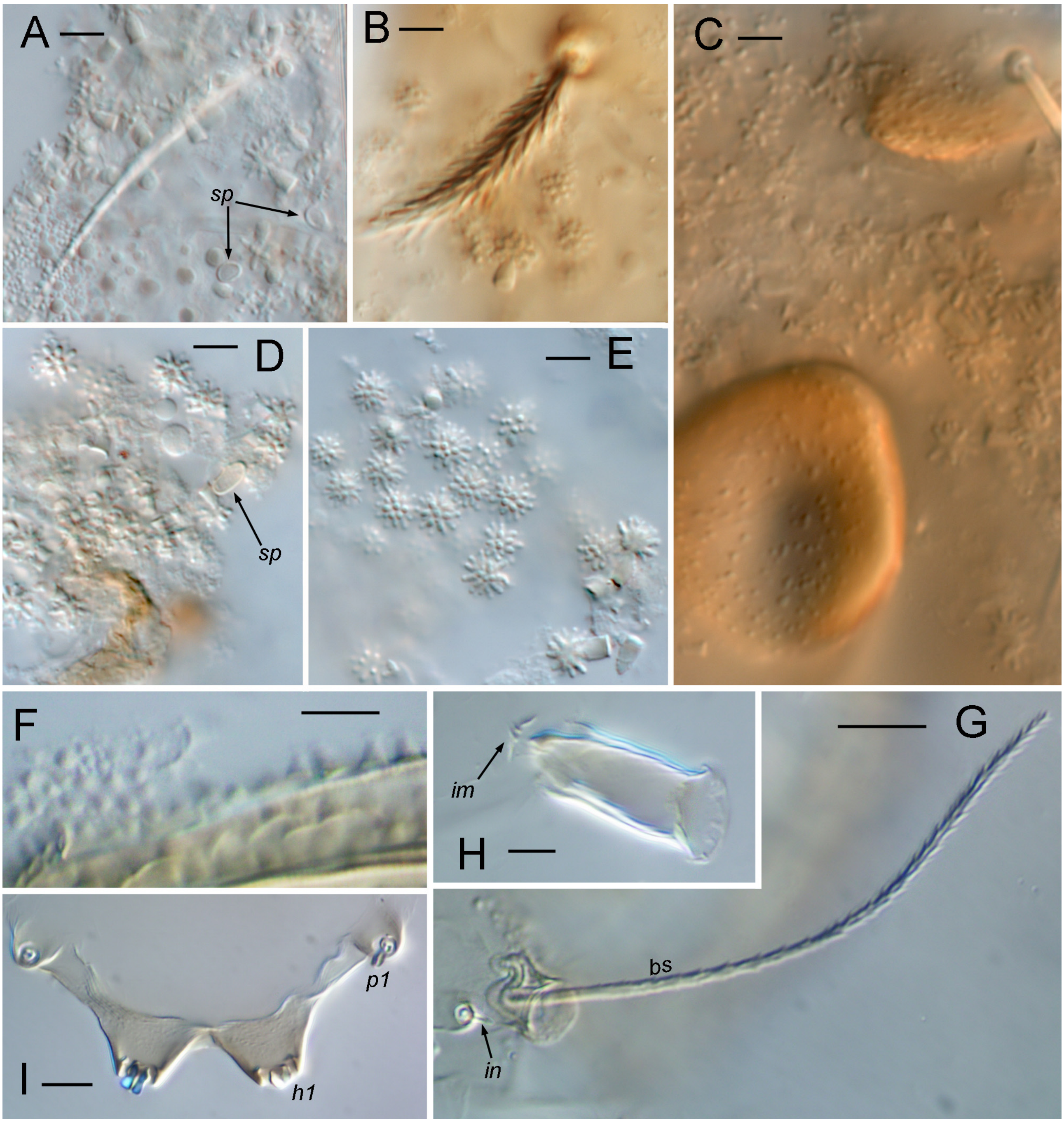

**FIGURE 4.** *Anderemaeus sidorchukae* **sp. nov.**, A–E adult, showing cerotegument, F–I, highly cleared deutonymph: A, anterolateral part of prodorsum (*sp* = spore); B, posterior part of notogaster near seta $h_1$; C, region of aggenital enantiophysis, *e4*; D, E, anterolateral part of prodorsum; F, dislodged cerotegument at edge of prodorsum; G, bothridial and interlamellar setae; H, stalk bearing opening of opisthonotal gland; I, posterior of hysterosoma, ventral view (setae broken). Photomicrographs in transmitted light, DIC. Scale bars: 20 µm (G, I); 5 µm (all others).

*Development*
(Figs 4, 7–9, 16)

Based on all instars of *A. sidorchukae* and nymphs of *A. dentatus*; for emphasis, data on adult included in formulas.

*Facies, cuticle.* Body pyriform, with hysterosoma about twice length of proterosoma; prodorsum distinctly sclerotized, gastronotum without major sclerites. Hysterosoma without permanent dehiscence line. Cuticle colorless to pale tan, smooth. Body and basal leg segments with cerotegument; excrescences in form of dense, short columns or subspherical (Figs 4F, 16C, F); nymphs without exuvial scalps (apheredermous). Without porose apodemes or other tracheal organs.

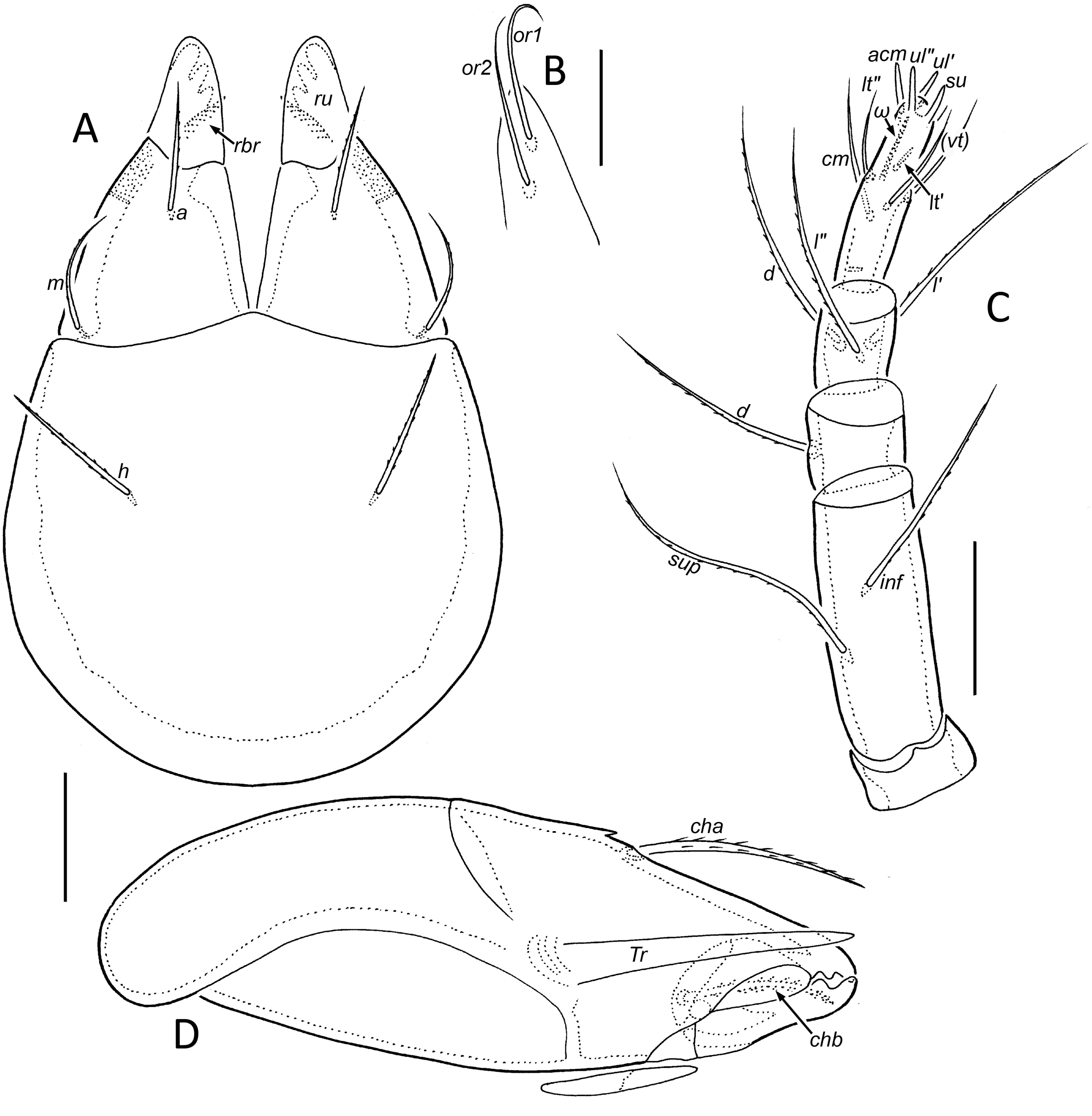

**FIGURE 5.** *Anderemaeus sidorchukae* **sp. nov.**, adult gnathosoma: A, subcapitulum, ventral view (palp omitted); B, left adoral lip; C, right palp, abaxial view; D, left chelicera, adaxial view. Scale bars 20 µm (A, C to same scale; D), 10 µm (B).

*Prodorsum*. Setae *ro* and *le* attenuate, barbed, inserted on small tubercles; tubercle of *le* noticeably projecting in lateral view (Fig. 16B) and extending posteriorly as indistinct ridge (Fig. 16E). Seta *in* long (more than half length of prodorsum) and barbed in larva, minute, spiniform, roughened in nymphs. Seta *ex* attenuate but minute, inconspicuous.

*Gastronotum*. Setal formula 12-12-10, i.e., larva with unideficient setation; nymphs quadrideficient, lacking centrodorsal setae; adult further loses $c_1$, $c_3$. Most gastronotic setae long, finely attenuate to flagellate, barbed; inserted on projecting, lightly sclerotized tubercles varying in size proportionate to seta. Larva with pygidially positioned *dp* flagellate, pair on low mound; centrodorsal and laterodorsal setae, plus $c_1$, $c_3$, subflagellate; row *h* decreasing in length anteriorly (Fig. 7B). Nymphs (Figs 9A, 16A) with *lm* in lateral position (shifting to central position in adult), and pair $h_1$ flagellate, adjacent on weak shared sclerite (Fig. 4I); pair $c_1$ close together, but not on shared sclerite; $h_2$ shorter than $h_3$. Opisthonotal gland opening on small tubercle in larva (Fig. 7A) and in nymphs on long, posterolaterally directed tubular stalk (Figs 4H, 16D), usually weakly flared at opening (see R5); gland contents lightly pigmented. Cupules *ia*, *im*, *ip* normal in form and position; *im* just dorsal to *gla* stalk (Fig. 4H).

*Venter*. Epimeral setation (I–IV, larva to tritonymph: 3-1-2, 3-1-2-1, 3-1-2-2, 3-1-3-3 (none added in adult); epimeral setae attenuate, thin, smooth, except seta *1c* of larva inconspicuous, forming protective scale over Claparède's organ. Genital seta ontogeny (protonymph to adult) 1-3-5-6. Aggenital seta deutonymphal. Paraprocts glabrous (without vestiges) in larva, proto- and deutonymph; adanal (three pairs) and anal (two pairs) setae appear fully formed in proto- and deutonymph, respectively. Genital and adanal setae attenuate, slightly barbed, aggenital and anal setae attenuate, thin, smooth. Cupules *ih*, *ips*, *iad* and *ian* appearing in normal ontogenetic pattern (*ian* lost in adult).

*Gnathosoma*. Generally similar to adult. Subcapitulum slightly longer than wide. Subcapitular (including adoral) setae attenuate, smooth. Seta *inf* of palp femur added in protonymph.

*Legs*. Seta *d* of genua and tibiae well developed in all juveniles (Fig. 8D–F), strikingly long, subflagellate on tibia I of nymphs (Fig. 16E); if coupled with solenidion, then lost without vestige in adult. Iteral setae tritonymphal on tarsi I-III, absent from IV in all instars. Protonymphal tarsus IV with typical seven setae, other segments glabrous. Full ontogeny of setae and solenidia given in Table 1.

## Descriptions

### ***Anderemaeus sidorchukae*** **sp. nov.**

(Figs 1–9)

*Diagnosis*

*Anderemaeus* species with adults 547–669 long. Cerotegument with polyp-like excrescences, having 'bouquet' of many short tentacles. Rostrum with terminal mucro. Lamella simple in form, pair well separated anteriorly, such that mutual distance of cusps (and setae *le*) slightly greater than that of setae *ro*; prolamella absent; transverse prelamellar ridge absent. Seta *in* long, inserted on strong tubercle close to anterior margin of notogaster. Bothridial seta long, baculiform. Notogastral setae short, thick, densely barbed. Femora III, IV with small ventral keel, without spines or teeth; trochanters III and IV dorsodistally with small tooth, III also with strong proximal spine.

This is the only known *Anderemaeus* species combining short notogastral setae with a long, baculiform bothridial seta. The cerotegument excrescences, with many short tentacles, are unique.

*Adult*

*Measurements.* Holotype (male) length 597, maximum notogastral width 398; range (including 2 female, 3 male paratypes) 547–630 × 365–431. Females larger than males: 614–630 × 415–431 vs. 547–597 × 365–398. Two non-type females from Concepción slightly larger: 642 × 456 and 669 × 476.

*Integument*. Cuticle shiny in reflected light (Fig. 3A). Cerotegument (Fig. 4A–E) with larger excrescences mostly polyp-like, with short stalk and head with more than two dozen short arms; smallest excrescences spherical; various extraneous spores often attached, but usually with little organic or mineral debris.

*Prodorsum* (Figs 1–3). Rostrum with terminal mucro, rostral bulge modestly developed. Lamella simple in form, without lateral tooth or prolamella; pair well separated anteriorly, such that mutual distance of cusps (and setae *le*) slightly greater than that of setae *ro*; transverse prelamellar ridge absent. Without noticeable foveation between lamellae. Setae *ro* (51–55), *le* (61–65) and *ex* (28–32) attenuate, weakly barbed; *in* (114–127) acicular, with stronger barbs, inserted on distinct tubercle close to anterior margin of notogaster. Bothridial seta (*bs*; Fig. 1A, 3C) directed laterally to posterolaterally; long (127–135), but shorter than mutual distance of pair; baculiform or slightly tapered distally (weakly spindle-shaped in one non-type specimen; Fig. 3D), with minute, inconspicuous barbs.

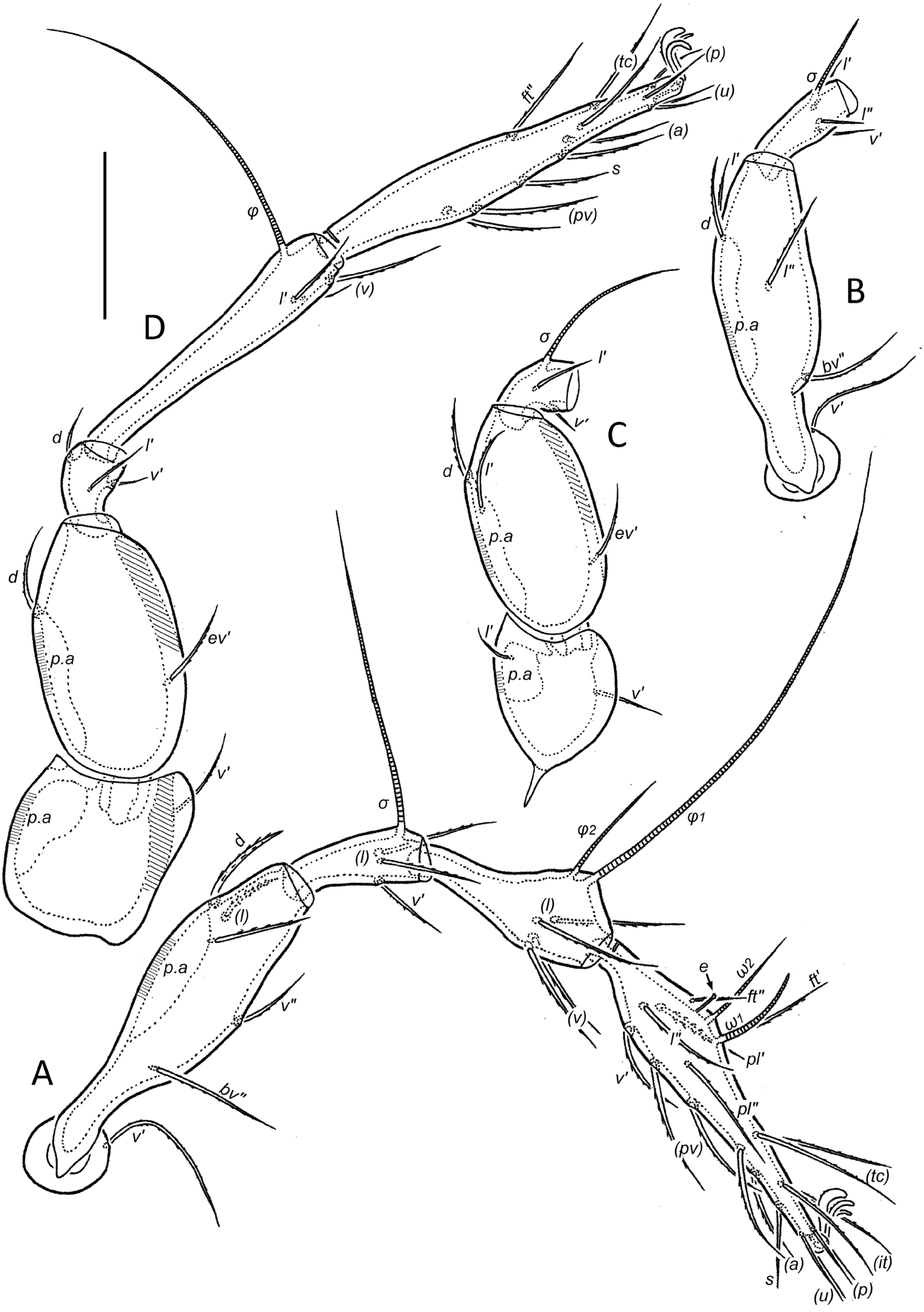

**FIGURE 6.** *Anderemaeus sidorchukae* **sp. nov.**, adult legs (abaxial view): A, right leg I; B, trochanter, femur and genu of right leg II; C, trochanter, femur and genu of left leg III; D, left leg IV. Scale bar 50 µm.

**FIGURE 7.** *Anderemaeus sidorchukae* **sp. nov.**, larva (gnathosoma omitted, legs not shown beyond trochanter): A, dorsal view; B, ventral view; C, lateral view. Scale bar 50 µm.

*Notogaster* (Figs 1, 2). Without noticeable foveolation in reflected light (Fig. 3A). Humeral process present, but not strongly projecting. Notogastral setae comparatively short (32–41), thickened, densely barbed, sometimes slightly dilated medially (Fig. 4B); all inserted on small tubercles. Seta *c* curving posteriorly, ending well short of lyrifissure *ia*; others erect. Setae *lm* and *la* nearly in transverse line (*lm* slightly anterior), *lm* distinctly closer to *la* than to *c*; mutual distance of pair *lm* about four times setal length; $h_2$ medial to $h_3$.

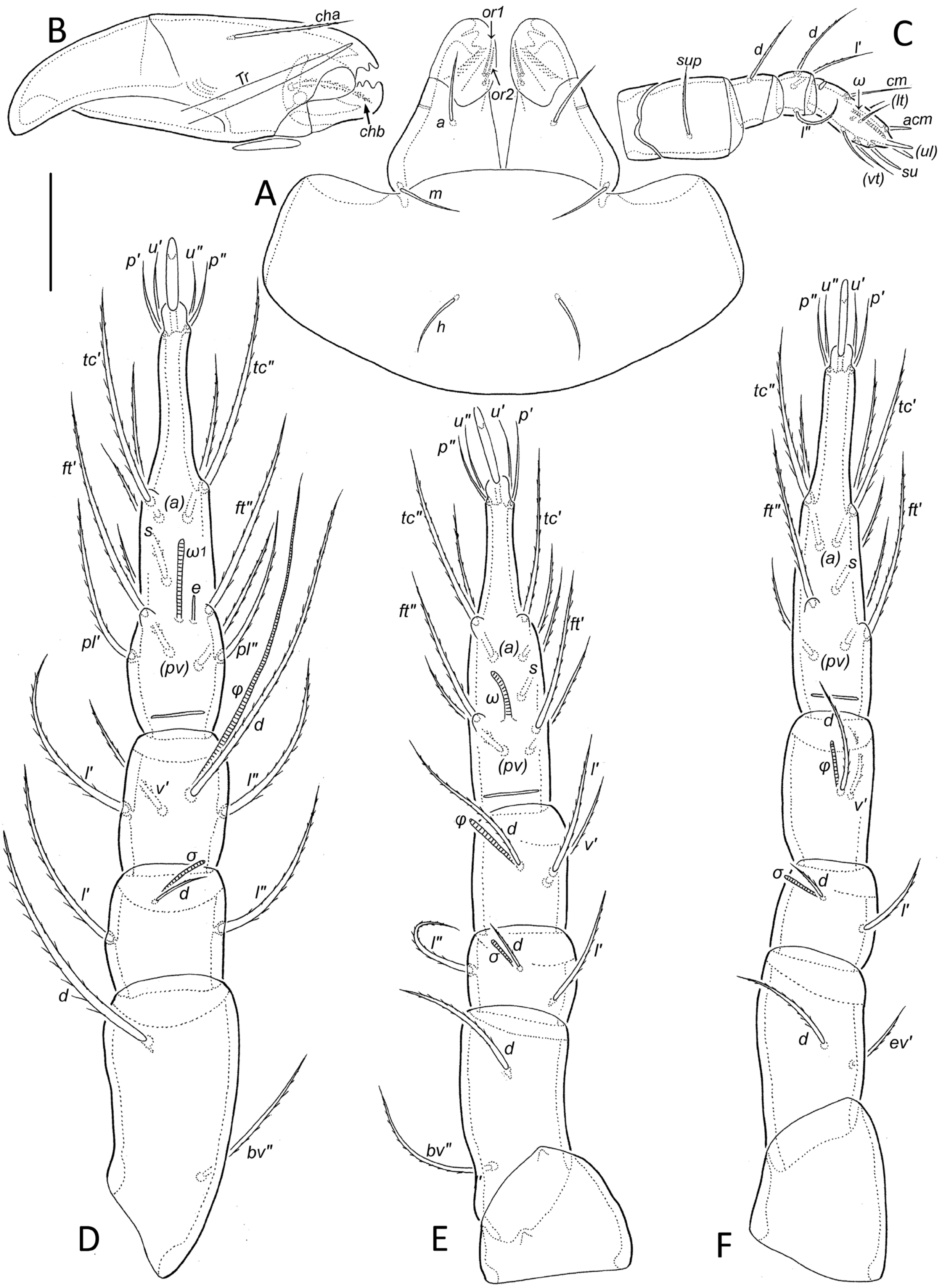

**FIGURE 8.** *Anderemaeus sidorchukae* **sp. nov.**, larva: A, subcapitulum, ventral view (breadth is artifact of strong flattening); B, left chelicera, adaxial view; C, right palp, abaxial view; D, right leg I, dorsal view; E, left leg II, dorsal view; F, left leg III, dorsal view. Scale bar 20 μm.

**FIGURE 9.** *Anderemaeus sidorchukae* **sp. nov.**, nymphs (gnathosoma and legs omitted): A, protonymph, dorsal view; B, protonymph, epimeral region; C, protonymph, posterior venter; D, tritonymph, epimeral region; E, tritonymph, posterior venter. Scale bars 20 µm (A–D to same scale).

*Coxisternum* (Figs 1B, 3F, G). Enantiophysis *e3* present, spanning groove of epimeral border *bo.3*, its anterior tubercle connected by low ridge across epimere III to larger tubercle just posterior to ventrosejugal groove, bearing seta *3b* at base; seta *3c* inserting at base of separate sharp tubercle. Aggenital enantiophysis (*e4*) well developed across border *bo.4*, its posterior tubercle about 3 times as large as anterior; latter, bearing seta *4b*, connected across epimere IV to posterior tubercle of *e3* by low ridge. Epimeral setae thin, attenuate, weakly and sparsely barbed; *3c* and *4c* (28–32) longer than others (20–24).

*Anogenital region* (Figs 1B, 2A). Setae thin, attenuate, smooth or sparsely barbed. Anterior genital seta (20–24) slightly longer than others (16–20); aggenital (20–24), anal (16–20) and adanal (20–24) setae in typical positions. Preanal organ only slightly expanded internally.

*Gnathosoma* (Fig. 5). Subcapitulum longer than wide (123–131 × 86–94). Subcapitular setae attenuate, barbed, *h* (28–32) longer than *a* and *m* (24–28). Adoral setae (12–16) attenuate, smooth. Palps (86–90) and postpalpal seta (8) typical of genus. Chelicerae (123–131) typical of genus; seta *cha* (36–41) longer than *chb* (24–28), both barbed.

*Legs*. Form and proportions of segments shown in Fig. 6. Tarsi significantly (I, II) to slightly (III, IV) longer than respective tibiae. Genua I, II notably longer than III, IV. Femora III, IV elongated, length about twice width, each with small ventral keel (Fig. 3K). Trochanters III, IV dorsodistally with small, triangular tooth; III with additional long proximal spine; IV with small keel in distal half. Form and locations of setae in Fig. 6, summarized in Table 1. Solenidia relatively long: $\sigma$ of genua I subflagellate, $\sigma$ III more than twice segment length; $\varphi$ of tibiae II–IV sub-flagellate.

*Juveniles*
(Figs 7–9)

Length and width of larva 249–265 × 116–132 (n =2), protonymph 348–365 × 199 (n =3), deutonymph 466 × 245 (n =1), tritonymph 581 × 348 (n =1). Bothridial setae in larva and protonymph spindle-form, with long stalk, short lanceolate head and attenuated tip, distinctly barbed; similar or nearly isodiametric (Fig. 4G) in later nymphs.

*Material examined*
Holotype (male): Chile, Maule Region, Talca Province, Alto Vilches, 1160 m a.s.l., 18-I-1985, N. Platnick and O. Francke, from montane forest litter. Paratypes: 5 (2 females, 3 males) from same collection as holotype; 2 (unsexed) from Bio Bio Region, Concepción Province, 6 km south of Concepción, 365 m a.s.l., 22-I-1985, N. Platnick & O. Francke, from pine forest litter. Juveniles (non-type): 7 (2 larvae, 3 proto-, 1 deuto- and 1 tritonymph) with same data as holotype.

*Type deposition*
The holotype is deposited in the SMNH; five paratypes are deposited in the TSUMZ, and one in the UCMZ, preserved in ethanol with a drop of glycerol. One slide-mounted paratype in personal collection of RAN.

*Etymology*
The specific epithet *sidorchukae* honors the late Russian acarologist and paleontologist Ekaterina A. Sidorchuk (see Lindquist & Norton 2019, Rasnitsyn 2019). Katya's absence as a colleague and friend will long be deeply felt.

## ***Anderemaeus dentatus* n. sp.**
(Figs 10–16)

*Diagnosis*
*Anderemaeus* species with adults 614–680. Rostrum with terminal mucro. Lamella with strong triangular tooth projecting anterolaterally, just proximal to small cusp; lamella continuing anteriorly as distinct prolamella; pair strongly

convergent, with mutual distance of setae *le* distinctly less than that of pair *ro*. With distinct transverse prelamellar ridge. Seta *in* long, inserted well anterior to notogastral margin, without supporting tubercle; with isolated subtriangular tubercle posterior to each seta. Bothridial seta long, baculiform. Notogastral setae erect, heavily barbed, relatively long. Femora III, IV with simple ventral keel (III) or large blade (IV); trochanters III and IV with large dorsodistal spine, smaller proximal tooth.

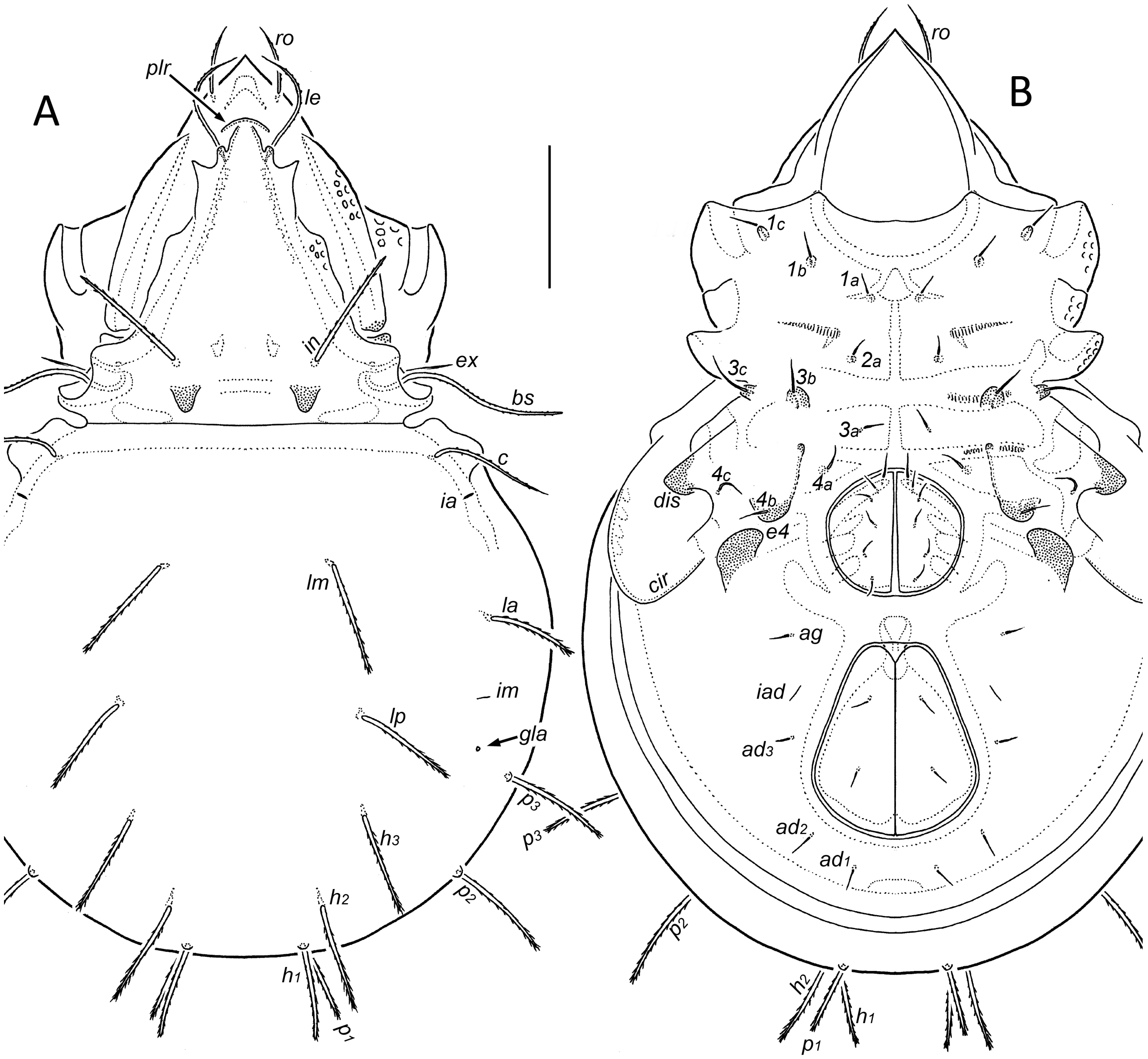

**FIGURE 10.** *Anderemaeus dentatus* **sp. nov.**, adult (gnathosoma and legs omitted): A, dorsal view; B, ventral view. Scale bar 100 µm.

This is the only known *Anderemaeus* species with a strong, conspicuous tooth on the lamella, just posterior to the lamellar seta. Among neotropical species, only *A. chilensis* shares the anteriorly displaced seta *in*, inserted far from the sejugal groove and distant from the pair of triangular tubercles.

*Adult*

*Measurements*. Holotype (female) length 680, maximum notogastral width 431; range (including 4 female, 3 male paratypes) 614–680 × 398–448. Females larger than males: 614–640 × 415–431 vs. 547–597 × 365–398.

*Integument*. Cuticle shiny in reflected light or dulled with organic and mineral debris attached to cerotegument (Fig. 12A, B). Cerotegument (Fig. 13) with larger excrescences columnar to phallus-shaped, covered in dust-like granules (Fig. 13F insert); smaller excrescences amorphous to irregularly granular (Fig. 13B).

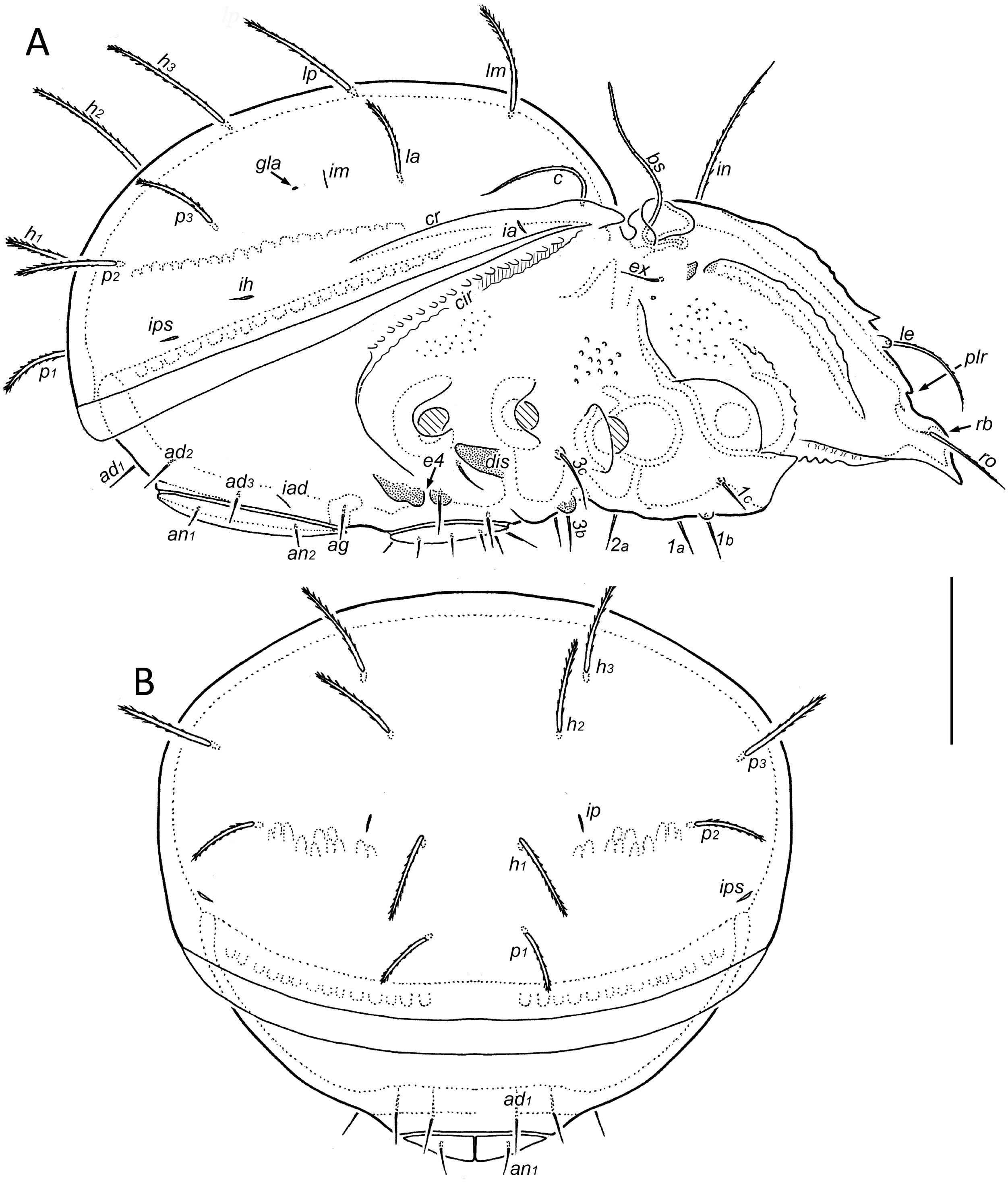

**FIGURE 11.** *Anderemaeus dentatus* **sp. nov.**, adult (gnathosoma and legs omitted): A, lateral view; B, posterior view. Scale bar 100 µm.

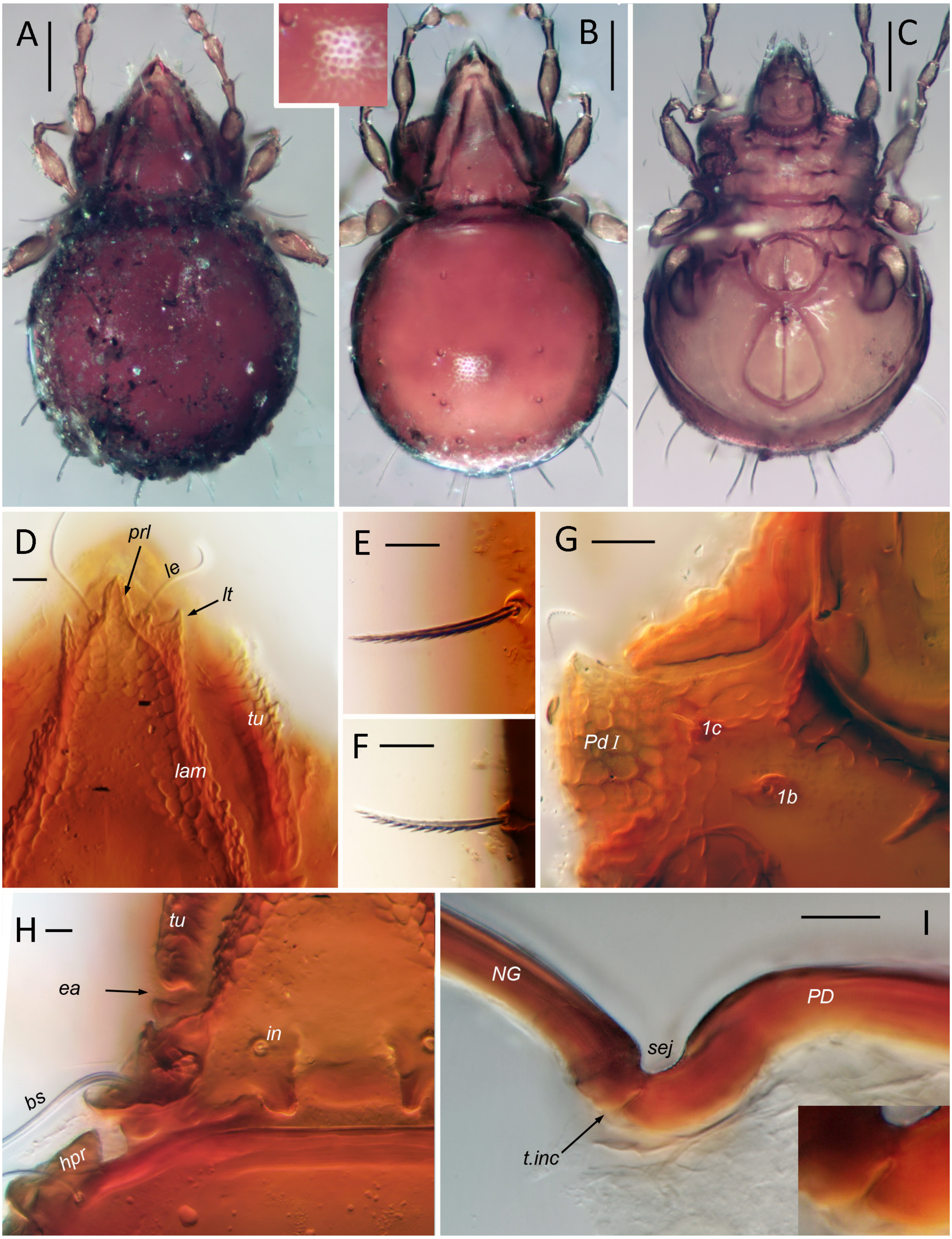

**FIGURE 12.** *Anderemaeus dentatus* **sp. nov.**, adult: A, dorsal view of dark, dirty specimen; B, dorsal view of lighter, cleaner specimen (insert: enlargement from central notogaster, showing shallow foveolae); C, ventral view; D, prodorsum; E, notogastral seta $h_1$; F, notogastral seta $p_1$; G, region of pedotectum I and epimere I, ventral view; H, left sejugal region, dorsal view; I, sagittal section of sejugal region (inset: closeup of transverse incision). Photomicrographs in transmitted light, DIC, except A–C reflected light. Scale bars 100 µm (A–C); 20 µm (all others).

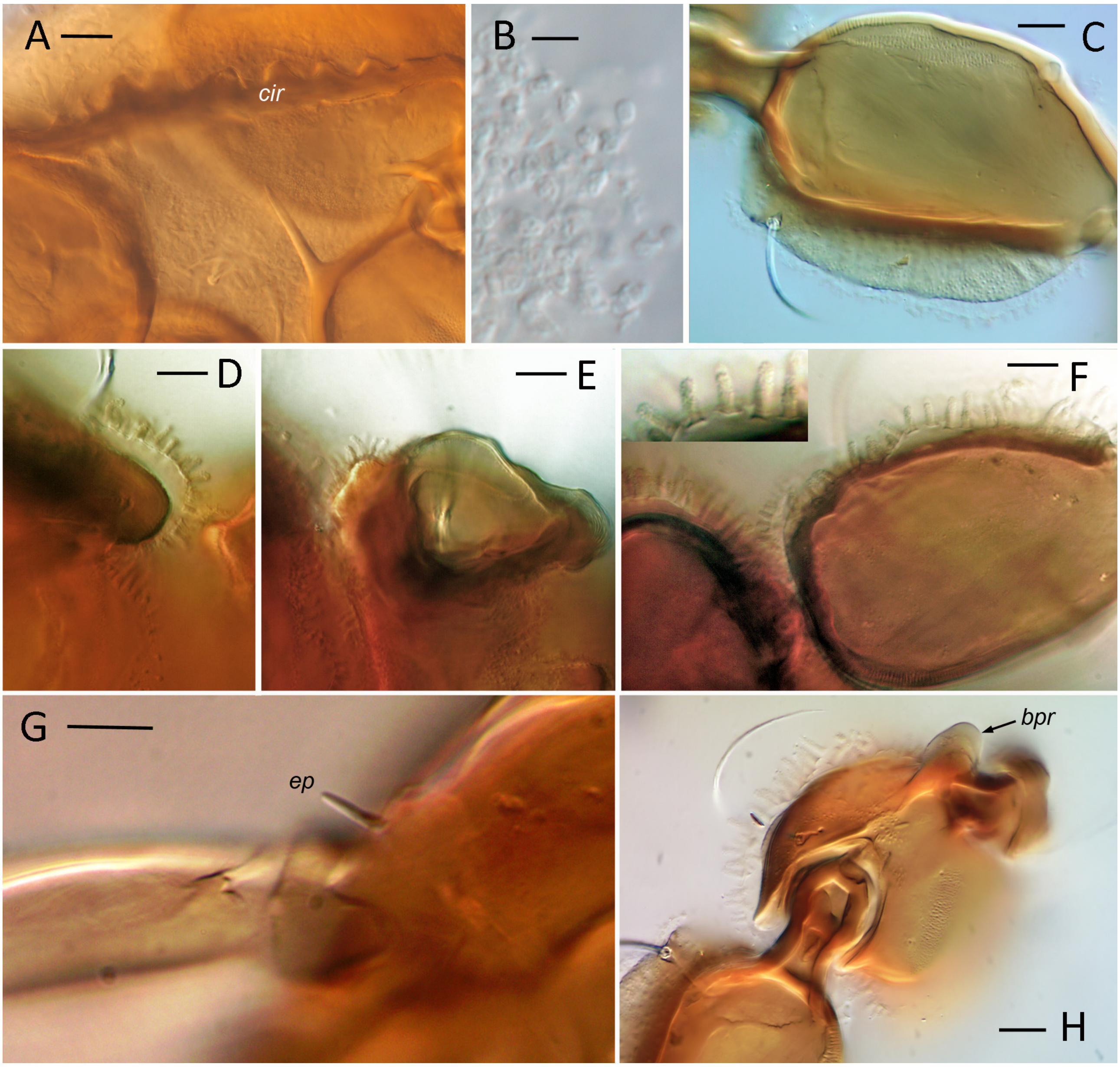

**FIGURE 13.** *Anderemaeus dentatus* **sp. nov.**, adult, cerotegument (separated from cuticle in B, partly dislodged in C, D, F): A, region of circumpedal carina, lateral view; B, lateral podosomal region; C, femur IV; D, humeral tubercle, lateral view; E, bothridium, lateral view; F, partial trochanter and femur III (insert: enlargement of dislodged cerotegument); G, subcapitulum, dorsal view, near base of right palp; H, trochanter and base of femur IV, paraxial view. Photomicrographs in transmitted light, DIC. Scale bars: 10 µm (A, C–H); 5 µm (B).

*Prodorsum* (Figs 10A, 11A). Rostrum with terminal mucro, rostral bulge strongly developed. Lamella with complex form: broadened at mid-length, with additional strong triangular tooth projecting anterolaterally, just proximal to small cusp; continuing anteriorly as distinct prolamella. Space between lamellae distinctly foveate anteriorly; pair strongly convergent, prolamellae nearly touching anteriorly: mutual distance of setae *le* distinctly less than that of pair *ro*. With distinct transverse prelamellar ridge (*plr*), length similar to *ro* mutual distance. Setae *ro* (53–61), *le* (73–86) and *ex* (32–36) thin, attenuate, weakly barbed, *le* usually with accentuated bend. Seta *in* long (118–127), relatively thick, acicular, barbed; inserted without distinct basal tubercle, well anterior of notogastral margin. With isolated, subtriangular interbothridial tubercle located posterior to but distant from each seta *in*. Bothridial setae (118–127) shorter than mutual distance of pair; baculiform or slightly tapered distally, with sparse, inconspicuous barbs, directed laterally or posterolaterally.

*Notogaster* (Figs 10A, 11). With uniform, shallow foveolation visible in reflected light (Fig. 12B insert). Humeral process (*hpr*; Fig 12H) strongly developed. Notogastral setae of medium length ($h_1$, 61–65; $p_1$, 53–57; others 77–86). Seta *c* attenuate, barbed, curving posterolaterally, extending past lyrifissure *ia*; others thickened, erect, heavily barbed (Fig. 13E, F), slightly tapered or sometimes slightly dilated distally, inserted on small tubercles. Seta *lm* distinctly anterior to level of *la*, about equidistant between *la*, *c*; mutual distance of pair *lm* only slightly greater than setal length; $h_2$ aligned with $h_1$, $h_3$.

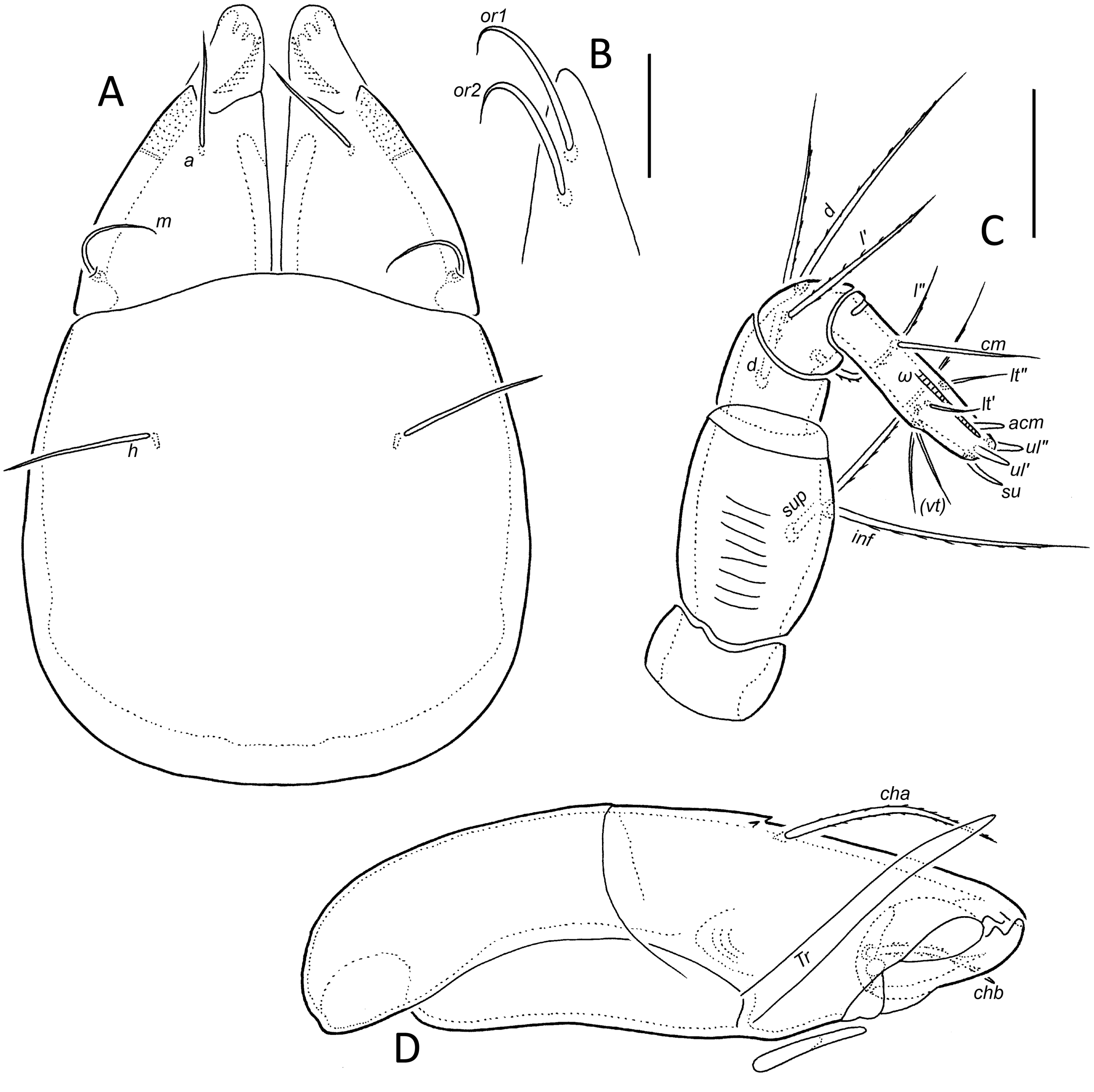

**FIGURE 14.** *Anderemaeus dentatus* **sp. nov.**, adult gnathosoma: A, subcapitulum, ventral view (palp omitted); B, left adoral lip; C, right palp, adaxial view; D, left chelicera, adaxial view. Scale bars 20 µm (A, C to same scale; D), 10 µm (B).

*Coxisternum* (Fig. 10B). Epimere I with small area of foveation in anterolateral corner and on mentotectum (Fig 12G). Enantiophysis *e3* absent, or represented by vaguely-defined, small posterior tubercle only. Tubercles bearing setae *3b*, *3c* strong, isolated, that of *3b* sometimes expressed as low mound extending across sejugal groove. Aggenital enantiophysis (*e4*) well developed across border *bo.4*, its posterior tubercle about twice as large as anterior; latter, bearing seta *4b*, with low ridge running anteriorly across epimere IV. Epimeral setae thin, attenuate, weakly and sparsely barbed; *3c* and *4c* (36–41) longer than others (20–24).

*Anogenital region* (Figs 10B, 11A). Setae thin, attenuate, smooth or sparsely barbed. Anterior genital seta (20–24) longer than others (12–16); aggenital (20–24), anal (12–16) and adanal (20–24) setae in typical positions. Preanal organ only slightly expanded internally.

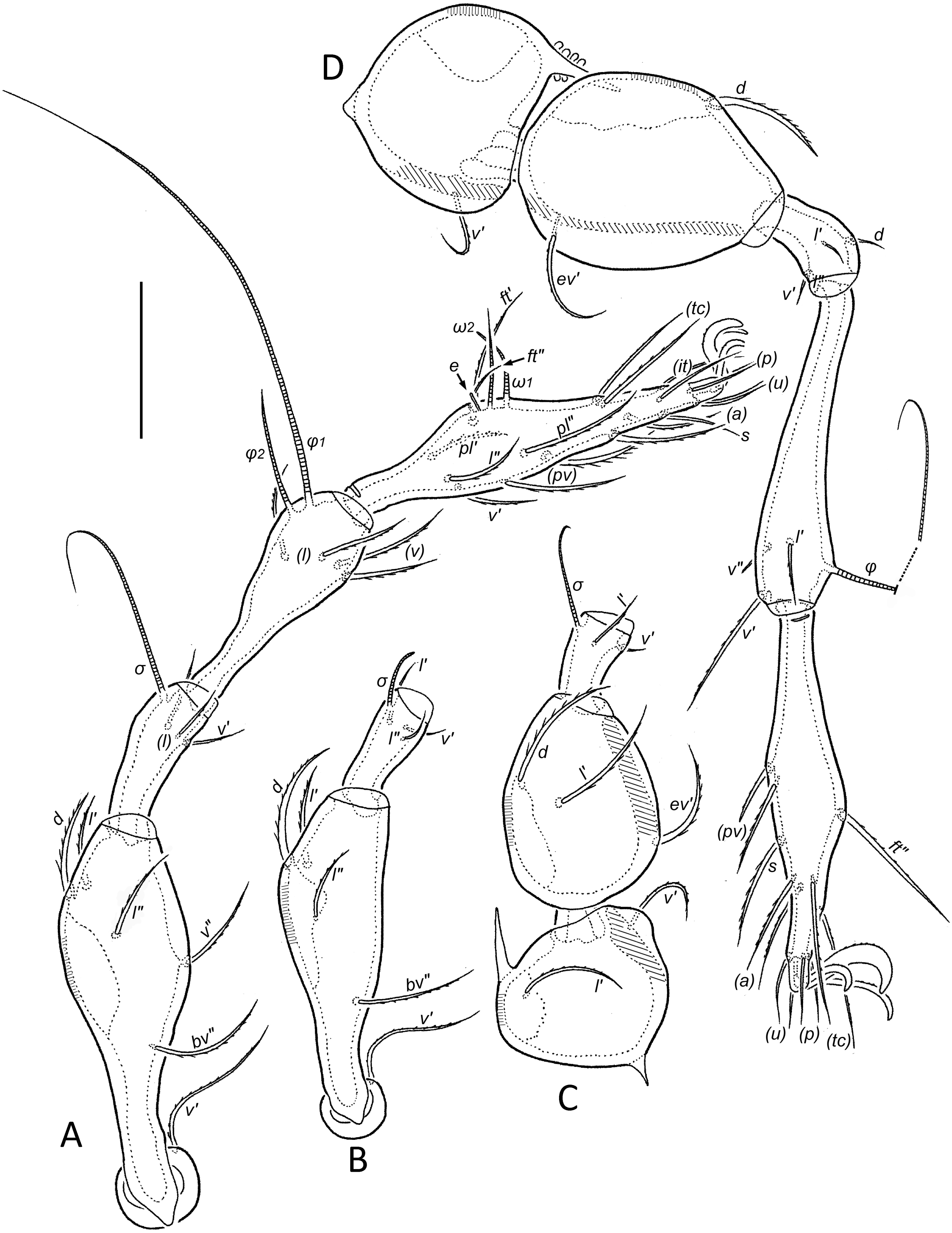

**FIGURE 15.** *Anderemaeus dentatus* **sp. nov.**, adult legs (abaxial view): A, right leg I; B, trochanter, femur and genu of right leg II; C, trochanter, femur and genu of left leg III; D, left leg IV. Scale bar 50 μm.

*Gnathosoma* (Fig. 14). Subcapitulum longer than wide (123–135 × 90–102). Subcapitular setae attenuate, inconspicuously roughened; *h* (28–32) longer than *a* and *m* (20–24). Adoral setae (12–16) attenuate, smooth. Palps (90–94), postpalpal seta (8), and chelicera (123–135) typical of genus; cheliceral setae acuminate to attenuate, barbed, *cha* (36–41) longer than *chb* (24–28).

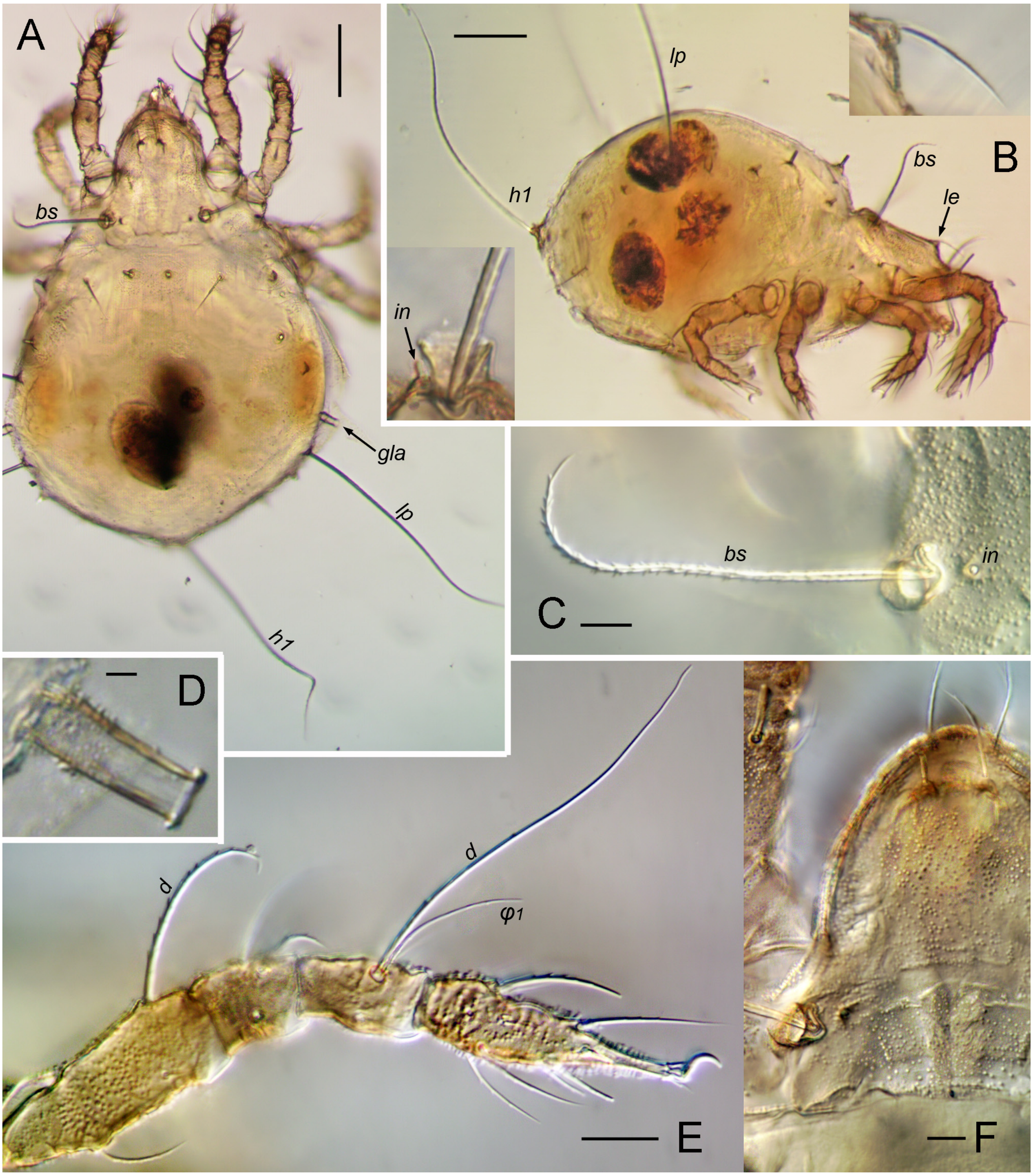

**FIGURE 16.** *Anderemaeus dentatus* **sp. nov.**, nymphs: A, tritonymph, dorsal view (larger hysterosomal setae broken except *lp*, $h_1$); B, same, lateral view (inserts: close-up of seta *le* in upper right, bothridial region in lower left); C, as in A, close-up of bothridial seta; D, as in A, close-up of stalk bearing opening to opisthonotal gland; E, deutonymph, leg I, adaxial view; F, tritonymph, prodorsum, dorsal view. Photomicrographs in transmitted light, DIC. Scale bars:100 µm (A, B); 20 µm (C, E, F); 5 µm (D).

*Legs*. Form and proportions of segments shown in Fig. 15. Tarsi significantly (I, II) to slightly (III, IV) longer than respective tibiae. Genua I, II notably longer than III, IV. Femora III, IV only slightly longer than wide, ventral keel moderate on III, large, blade-like on IV (Fig. 13C), neither with tooth or spine. Trochanters III, IV with prominent dorsodistal spine; III with smaller proximal spine, IV with small proximal tooth. Setation typical of genus; form and locations of setae and solenidia shown in Fig. 15. Solenidion $\sigma$ of genu I subflagellate, distinctly longer than segment; that of other genua shorter than segment (II) or of similar length (III); $\varphi$ of tibiae II–IV subflagellate, equal or only slightly less than segment length.

*Juveniles* (larva unknown)
(Fig. 16)

Length and width of protonymph 310–359 × 199 (n =2), deutonymph 426 × 245 (n = 1), tritonymph 582 × 348 (n=1). Bothridial seta distinctly tapered and consistently, strongly curved anteriad (Fig. 16C).

*Etymology*

The specific name *dentatus* (toothed) is a Latin adjective that refers to the conspicuous tooth on the prodorsal lamella.

*Material examined*

Holotype (female): Chile, Los Lagos Region, Osorno Province, Parque Nacional Puyehue, 4.1 km east of Anticura, 430 m a.s.l., 26-XII-1982, A. Newton and M. Thayer, from Valdivian rainforest litter. Paratypes: 7 (4 females, 3 males) with same data as holotype; 12 (unsexed) from Parque Nacional Puyehue, Aguas Caliente, 425 m a.s.l., 3-I-1985, N. Platnick, O. Francke, from Valdivian forest litter. Other material: Los Ríos Region, Valdivia Province, Rt. 39, 30 km east of Los Lagos, near Panguilulli, 11-III-2005, E. Toledo, col. (13 adults, 1 trito-, 1 deuto-, 2 protonymphs; habitat unknown).

*Type deposition*

The holotype is deposited in the SMNH; five paratypes are deposited in the TSUMZ, one in the UCMZ, preserved in ethanol with a drop of glycerol. The remainder of paratypes are in the personal collection of RAN, three on slides, others in ethanol.

### ***Anderemaeus mataderoensis*** **sp. nov.**
(Figs 17–19)

*Diagnosis*

*Anderemaeus* species with large adults 763–830 × 498–547. Rostrum rounded, without mucro. Lamella without distinct cusp, lateral tooth or prolamella; pair moderately converging, such that mutual distance of setal pairs *le* and *ro* about equal. Transverse prelamellar ridge well developed, immediately anterior to seta *le* insertion. With three large tubercles anterior to sejugal groove, short seta *in* inserted at anterior base of each lateral tubercle. Bothridial seta long, baculiform, weakly barbed. Notogastral setae of medium size, barbed, most erect. Ventral keel of femora III, IV produced distally as large, triangular tooth; trochanters III and IV with short spine.

This is the only known *Anderemaeus* species with a conspicuously short interlamellar seta. Also, no other species is known to have the ventral keel of femora III, IV projected as a conspicuous, sharp tooth, though legs have not been described for most species. Only *A. capitatus* is as large, and it is easily distinguished by its capitate bothridial seta.

*Adult*

*Measurements*. Holotype (female) length 813, maximum notogastral width 531; range (paratypes) 763–830 × 498–547. Without notable gender size difference.

*Integument*. Body color brown to dark brown. Lamellae, tutoria, pedotecta, lateral parts of prodorsum and epimere I foveolate. Cerotegument with excrescences of three types: amorphous, spherical and columnar (diameter and length of excrescences up to 10).

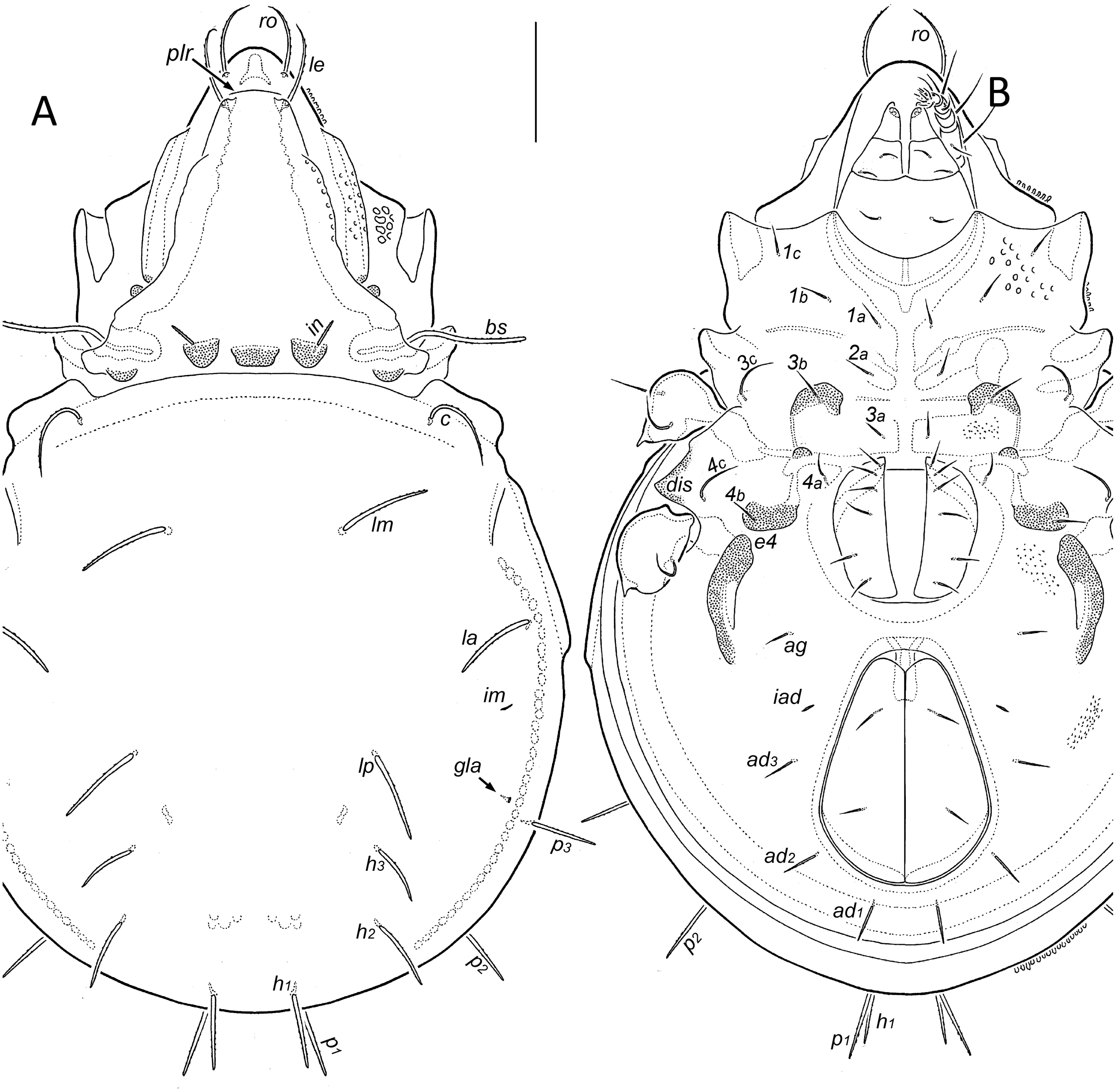

**FIGURE 17**. *Anderemaeus mataderoensis* **sp. nov.**, adult (gnathosoma and legs omitted): A, dorsal view; B, ventral view. Scale bar 100 µm.

*Prodorsum* (Figs 17A, 18A). Rostrum rounded, without mucro. Lamella simple in form, without distinct cusp or prolamella; pair moderately converging, such that mutual distance of setal pairs *le* and *ro* about equal. Rostral bulge strongly developed, transverse prelamellar ridge present immediately anterior to end of lamellae and spanning their mutual distance. Laterorostral carina poorly developed, almost imperceptible in lateral view. With three transversely aligned large tubercles immediately anterior to sejugal groove, each lateral tubercle bearing seta *in* at its base. Setae *ro* (77–86), *le* (90–102) and *ex* (24–28) attenuate, weakly barbed. Seta *in* unusually small (36–41) baculiform, barbed. Bothridium with weak tubercle on posterior surface; bothridial setae (139–151) shorter than mutual distance of pair; baculiform, barbed, directed laterally.

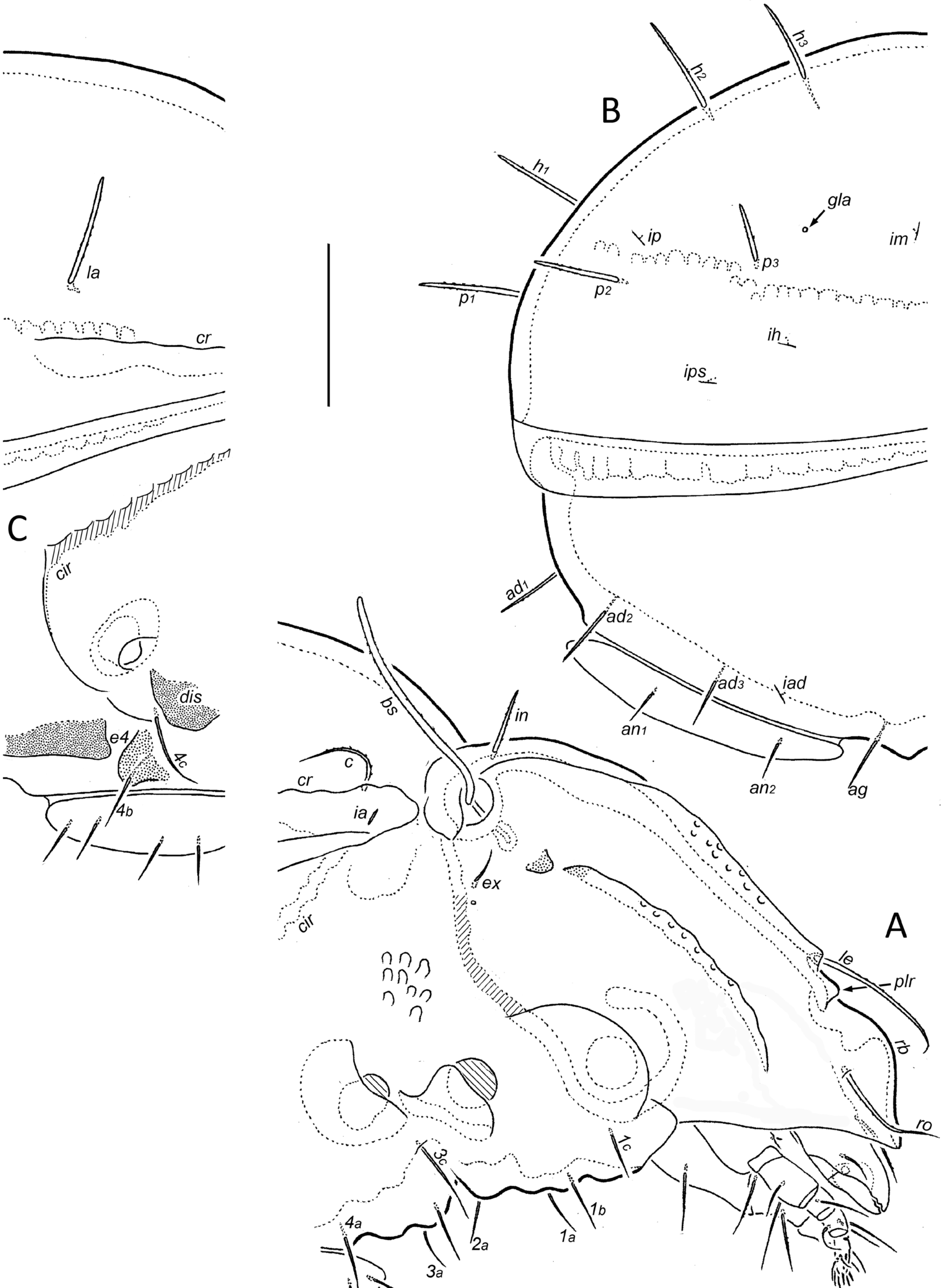

**FIGURE 18.** *Anderemaeus mataderoensis* **sp. nov.**, adult, lateral view: A, anterior half; B, posterior third; C, mid-region. Scale bar 100 μm.

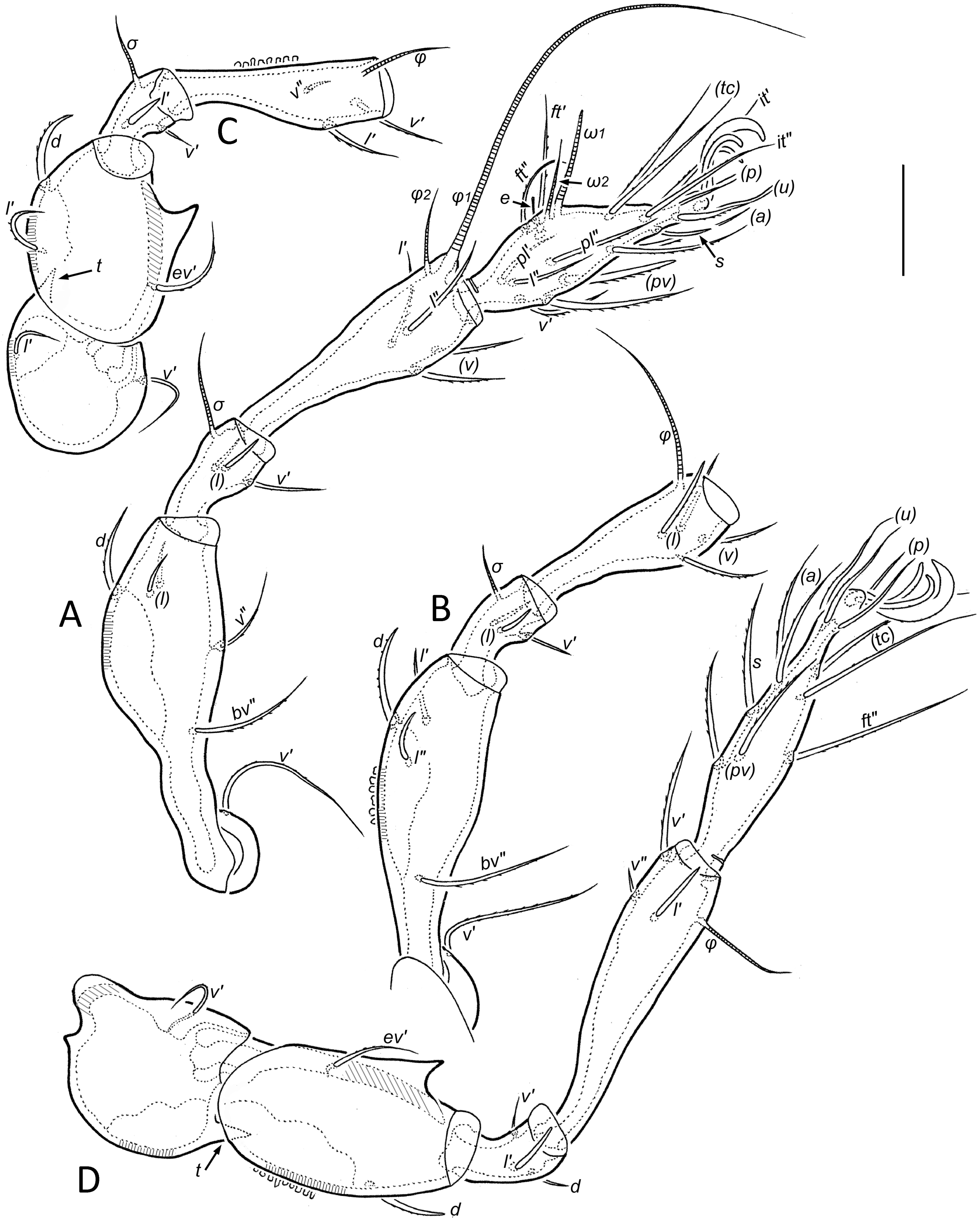

**FIGURE 19.** *Anderemaeus mataderoensis* **sp. nov.**, adult legs (abaxial view): A, right leg I; B, trochanter to tibia of right leg II; C, trochanter to tibia of left leg III (tibia slightly twisted); D, right leg IV. Scale bar 50 µm.

*Notogaster* (Figs 17A, 18). Without noticeable foveolation in reflected light. Humeral process strongly developed, crista moderately so. Notogastral setae of medium size, weakly barbed; *c* (73–82) attenuate, curved posteriorly, others (*la*, *lm*, *lp*, 82–90; $h_1$–$h_3$, $p_1$–$p_3$, 53–61) erect, baculiform to acicular. Seta *lm* displaced anteriorly, far from level of *la* and closer to *c*; mutual distance of pair *lm* about twice setal length; $h_2$ aligned with $h_1$, $h_3$.

*Coxisternum* (Figs 17B, 18A, C). Enantiophysis *e3* represented only by small posterior tubercle. Seta *3b* borne by usually large tubercle, with lateral edge continuing posteriorly as low ridge directed across epimere III; seta *3c* not on distinct tubercle. Aggenital enantiophysis (*e4*) unusually large (Figs 17B, 18C): anterior tubercle, bearing seta *4b*, with medial edge extended anteriorly across epimere IV as low ridge; posterior tubercle elongated, reaching level posterior to seta *ag*. Epimeral setae attenuate, weakly barbed, *3c* and *4c* (53–61) longer than others (28–32).

*Anogenital region* (Figs 17B, 18B). Genital (28–32), aggenital (28–32), anal (20–24) and one pair of adanal ($ad_3$, 28–32) setae attenuate, weakly barbed; adanal setae $ad_1$, $ad_2$, (41–45) slightly thicker, more distinctly barbed. Preanal organ only slightly expanded internally.

*Gnathosoma.* Subcapitulum longer than wide (164–168 × 114–123). Subcapitular setae attenuate, slightly barbed, *a* (32–36) shorter than *m* and *h* (36–41). Adoral setae (16–20) attenuate, smooth. Palps (102–106) and postpalpal seta (6) spiniform, smooth. Chelicerae (164–168) typical of genus; seta *cha* (41–45) longer than *chb* (24–28).

*Legs*. Form and proportions of segments shown in Fig. 19. Tarsi similar in length to respective tibia; all genua of similar size. Femora III slightly longer than wide (1.4:1), femur IV more elongated, about 1.8 x width; each with ventral keel produced distally as large, triangular tooth. Trochanters III and IV each with short, broad dorsodistally spine; IV also with small blunt proximal tooth. Form and locations of setae shown in Fig. 19. Solenidion $\sigma$ of genua I–III shorter than respective segment; $\varphi$ of tibia IV little longer than segment width.

*Juveniles* (unknown).

*Etymology*

The specific name *mataderoensis* refers to the Matadero River, where the new species was collected.

*Material examined*

Holotype (female) and four paratypes (one female and three males): Chirimachay, Matadero River, drift net sample, 14-I-1977 (P. Turcotte). Since all other known *Anderemaeus* species are terrestrial, the occurrence of these specimens in moving water probably reflects an accidental displacement.

*Type deposition*

The holotype and one paratype are deposited in the CNC; three paratypes are deposited in the TSUMZ. All are preserved in ethanol with a drop of glycerol.

## Redescriptions

The following partial redescriptions of *Anderemaeus chilensis* and *A. hammerae* are meant to complement the original descriptions and allow more detailed comparisons with the new species. We also discuss the transfer of *Carabodes tridactylus* Trägårdh, 1907 to *Anderemaeus*.

### ***Anderemaeus chilensis* Hammer, 1962**

(Figs 20–22)

*Anderemaeus* species with adult size 670–786 × 407–504. Cerotegument mostly thin, encrusting, with adherent organic and mineral particles (Figs 20F, 22J), adherent dirt rarely in large masses (Fig. 22K); where distinct, excrescences granular (Fig. 22D) to phallus-like, covered with minute dust-like particles (Fig. 22 E, G, H). Rostrum with terminal mucro and prominent rostral bulge (Fig. 20F). Lamella simple in form, broadest in middle third, without lateral tooth but with distinct tubular cusp and long prolamella; main part of lamellar pair moderately converging, mutual distance of setal pair *le* slightly greater than that of *ro*, but prolamellae (Fig. 20D, F) converging strongly,

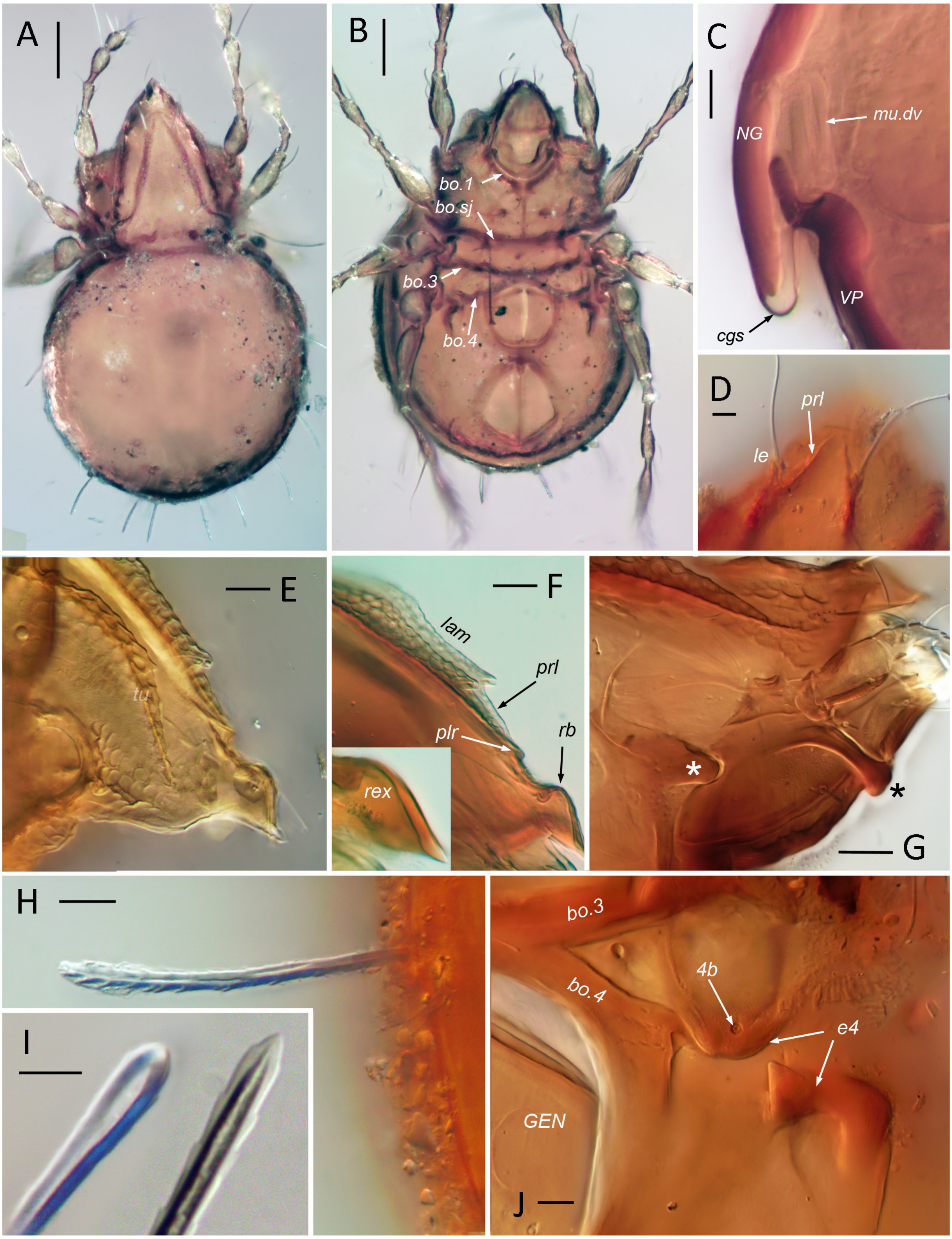

**FIGURE 20.** *Anderemaeus chilensis* Hammer, 1962, adult: A, dorsal view; B, ventral view; C, left part of transverse section through mid-region of hysterosoma; D, anterior region of holotype prodorsum, dorsal view; E, prodorsum of dissected specimen, right lateral view; F, parasagittal section of anterior proterosoma, cut to right of lamella (setae *le* broken), internal view (insert: close-up of rostral bulge); G, same, cut to right of tutorium, showing condyle (white asterisk) articulating with subcapitulum, and rebordered margin of mentum (black asterisk); H, notogastral seta $h_1$ of holotype; I, tip of bothridial seta, holotype on left, specimen from Tome, Chile on right; J, left aggenital region, ventral view. Photomicrographs in transmitted light, DIC, except A, B reflected light. Scale bars 100 µm (A, B); 20 µm (C–G); 10 µm (H, J); 5 µm (I).

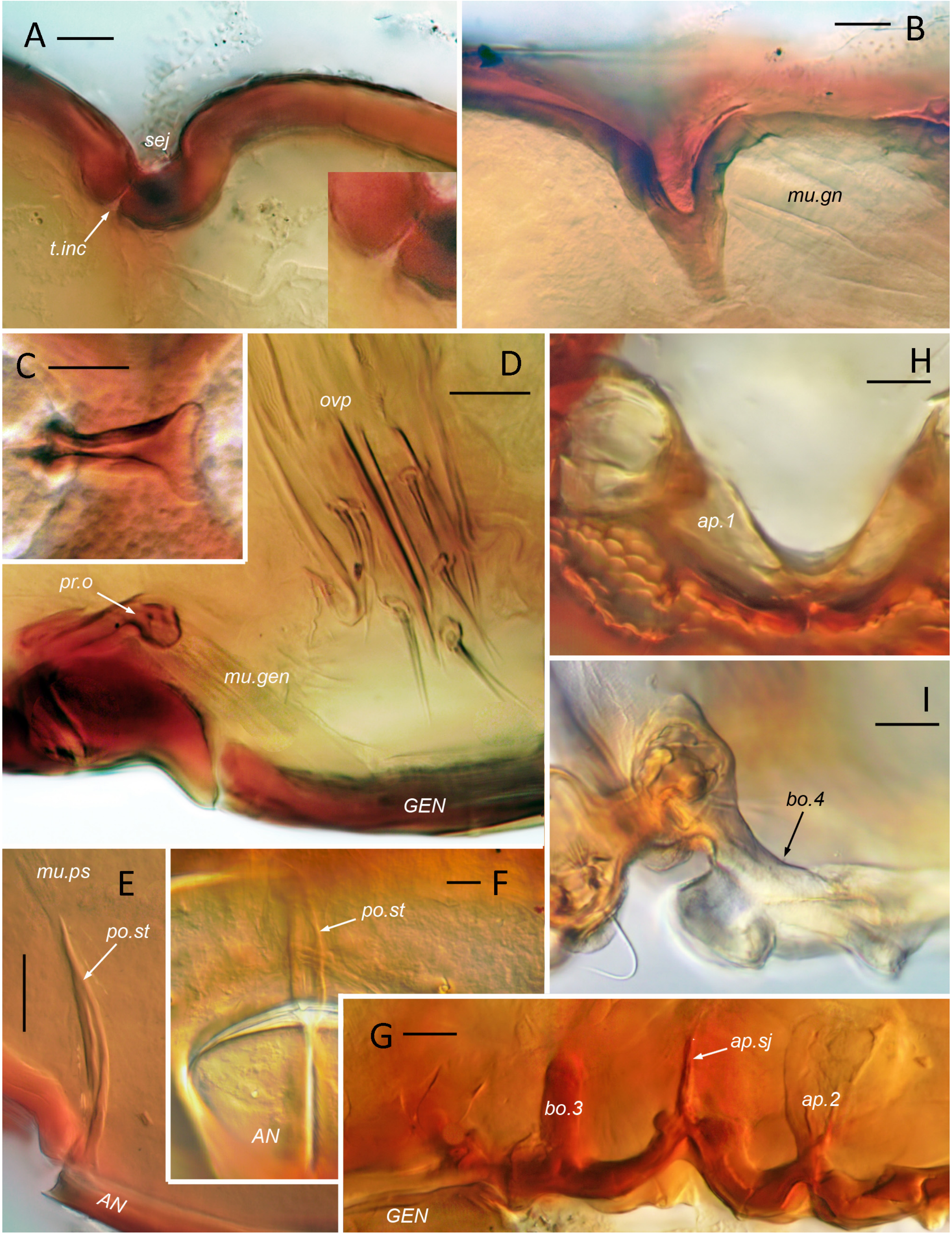

**FIGURE 21.** *Anderemaeus chilensis* Hammer, 1962, adult: A, parasagittal section near midline (insert: enlargement of transverse incision); B, same, just medial to bothridium, such that sejugal groove cut at angle; C, preanal organ, internal view, anterior to right; D, genital region of parasagittal section of hysterosoma, cut just lateral to ovipositor, internal view; E, same, but showing posterior part of anal plates; F, external posterior view of anal region; G, parasagittal section of podosoma cut at edge of right genital plate, anterior to right, internal view; H, transverse section of podosoma in strongly cleared specimen, anterior view of apodemes I; I, same, region of left acetabulum IV, posterior view. Photomicrographs in transmitted light, DIC. Scale bars: 20 µm.

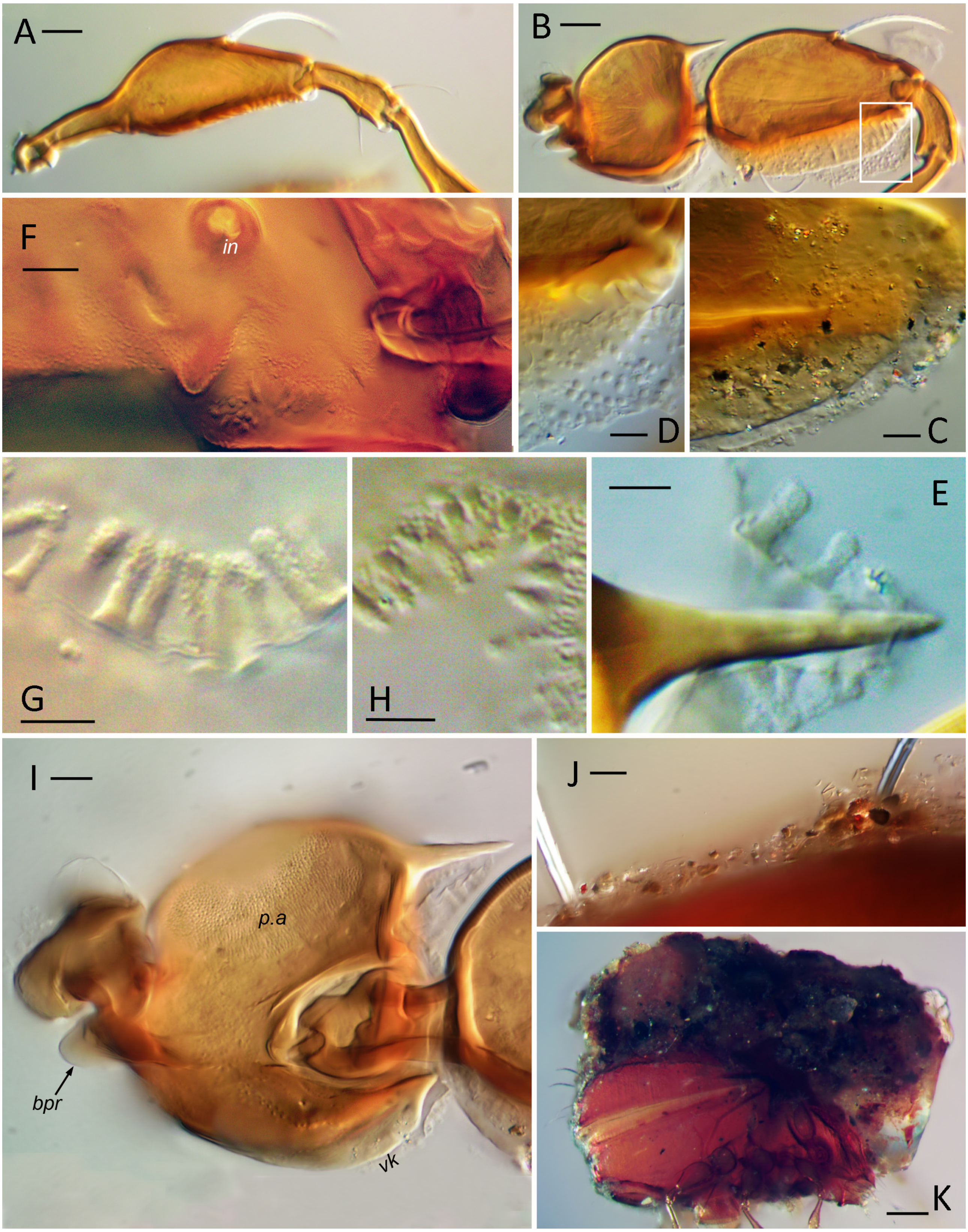

**FIGURE 22.** *Anderemaeus chilensis* Hammer, 1962**.**, adult: A, leg I, proximal half; B, leg IV, proximal half; C, D, framed region of B, in different specimens; E, dorsal spine of trochanter IV, with dislodged cerotegument; F, right sejugal region, dorsal view; G, cerotegument dislodged from mid-prodorsum; H, same, from epimere I; I, trochanter IV, enlarged from B; J, notogastral surface between setae $h_2$, $h_3$; K, unusual specimen with heavy dirt load. Photomicrographs in transmitted light, DIC. Scale bars: 100 µm (K); 20 µm (A, B, F); 10 µm (I, J); 5 µm (C–E, G, H).

nearly touching at tips. With distinct transverse prelamellar ridge but without laterorostral carina (Fig. 20E). Seta *in* long, inserted on small tubercle well anterior to notogastral margin; with additional larger, subtriangular tubercle midway between each *in* and margin (Fig. 22F). Bothridial seta long, baculiform, slightly tapered to slightly expanded distally (Fig. 20I), with minute, inconspicuous barbs. Humeral process well developed. Notogastral setae relatively large (*lm* ~100), mostly (except *c*) erect, isodiametric to weakly clavate (Fig. 20H), distinctly and densely barbed. Aggenital enantiophysis (*e4*) usually with small tooth at medial corner of posterior tubercle (Fig 20J); enantiophysis *e3* absent; tubercle of seta *3b* expressed as low mound extending across sejugal groove, *3c* without tubercle. Anterior border of subcapitular mentum strongly rebordered by unusually thickened edge (Fig. 20G). Legs with tarsi longer than respective tibia on I, II but similar in length on III, IV; genua I, II longer than III, IV (Fig. 22A, B). Femora III, IV respectively 1.4, 1.6 x longer than wide; each with distinct ventral blade, not produced as tooth or spine. Trochanters III and IV with large dorsodistal spine; III with ventrodistal keel and separate small, sharp proximal tooth; IV with larger blade, extending entire ventral length and produced proximally as tooth. Solenidion $\sigma$ of genu I subflagellate, distinctly longer than segment; $\varphi$ of tibiae II–IV subflagellate, equal or only slightly less than segment length. Preanal organ distinctly expanded internally (Fig. 21C), often almost T-shaped.

### ***Anderemaeus hammerae*** **Mahunka, 1980**

(Figs 23, 24)

*Anderemaeus* species with adult size 580–680 × 383–436. Cerotegument, dense and often slightly pigmented, excrescences mostly polyp-like, with several tapered arms, or bullet-shaped (Fig. 24D–G, I); little or no adherent particulate debris. Rostrum with terminal mucro and moderate rostral bulge. Foveation present between lamellae in anterior half of prodorsum. Lamella simple, with distinct tubular cusp and short prolamella; latter pair converging more strongly than lamellae. Mutual distance of setal pair *le* slightly greater than that of *ro*. Prelamellar ridge weakly developed or absent. Tutorium extended unusually far anteriorly onto rostrum as carina (Fig. 23F). Seta *in* long (~120), baculiform, nearly smooth, with extremely minute, inconspicuous barbs (Fig. 23E); each seta inserted on strongly-projecting tubercle, about its width removed from notogastral margin. Bothridium (Figs 23G, 24C) with series of conspicuous, rounded tubercles posteriorly; bothridial seta (75–80) much shorter than *in*, virtually smooth, with distinct pyriform head. Notogaster covered with shallow foveolae (Fig. 23A); humeral process strongly developed, with oblique dorsal carina (Fig. 24C). Notogastral setae relatively long (*lm* ~75–80), mostly (except *c*) erect, heavily barbed, isodiametric or acicular (Fig. 24F). Enantiophysis *e3* present (Fig. 24H), posterior tubercle extended as ridge across epimere IV to merge with *e4*; tubercle of seta *3b* distinct, with opposing small tubercle across sejugal groove to form ventrosejugal enantiophysis (*ev*). Legs (Fig. 24A, B) all with tarsus slightly longer than respective tibia; genua I, II longer than III, IV. Femora III, IV about 1.7 times longer than broad, each with ventral keel, enlarging to narrow blade distally, not produced as tooth or spine. Trochanter III with modest proximal (anterior pointing) spine (Fig. 24I) and dorsodistal tooth; IV only with dorsodistal tooth. Solenidion $\sigma$ of genu I subflagellate, distinctly longer than segment; $\varphi$ of tibiae II–IV subflagellate, equal or only slightly less than segment length. Preanal organ (Fig. 23B, insert) slightly expanded internally, often vase-like.

### ***Anderemaeus tridactylus*** **(Trägårdh, 1907) comb. nov.**

Trägårdh (1907) proposed *Carabodes tridactylus* based on a single specimen collected from moss on the subantarctic 'Observatory Island', near Staten Island (Isla de los Estados), Tierra del Fuego, Argentina. It has not been recollected and, despite the rather detailed original description and relatively clear illustrations, for more than a century the species has remained in *Carabodes*. It was not mentioned in Fredes' (2018) recent checklist of oribatid mites of Argentina. Recently, Subías (2017) indicated that *C. tridactylus* was a member of *Anderemaeus*, which is clearly correct. However, this work is an unpublished electronic update of his 2004 checklist, and according to the International Code of Zoological Nomenclature it cannot be used a source of valid nomenclatural acts. Therefore, after consultation with Dr. Subías, we make the formal recombination herein.

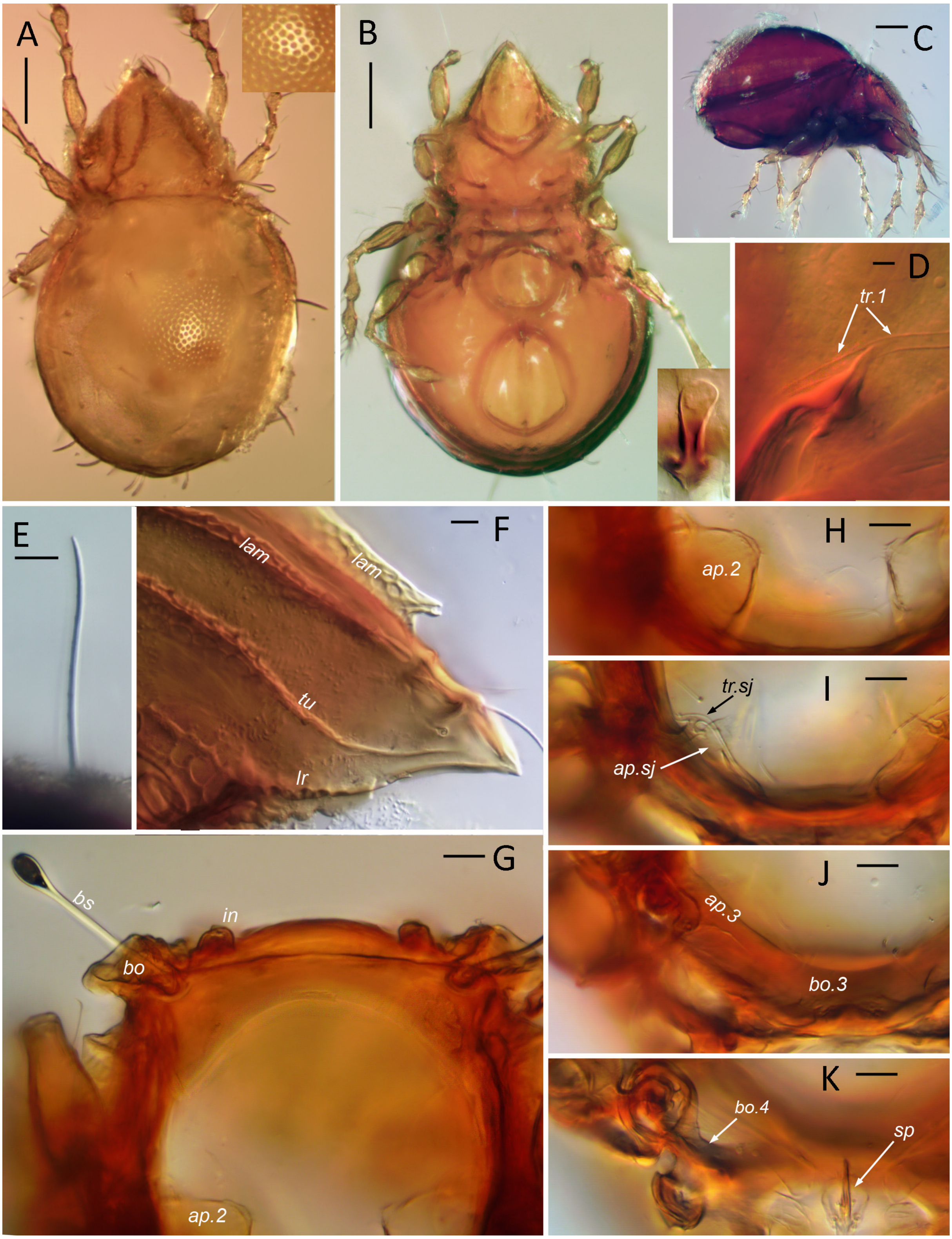

**FIGURE 23.** *Anderemaeus hammerae* Mahunka, 1980 adult: A, dorsal view (insert: enlargement from central notogaster, showing shallow foveolae); B, ventral view (insert: preanal organ, ~45 µm long ); C, lateral view of dark specimen; D, part of acetabulum I, showing bifid tracheal trunk, internal view, dissected specimen; E, interlamellar seta; F, prodorsum lateral view (slightly dorsal, seta *le* broken from cusp); G, transverse section of strongly cleared specimen, cut behind sejugal region, posterior view (setae *in* broken); H, same, ventral region showing apodemes 2; I, same, shallower focus showing sejugal apodemes; J, same, shallower focus showing apodemes 3; K, same, shallower focus showing acetabulum IV and spermatopositor. Photomicrographs in transmitted light, DIC, except A, B reflected light. Scale bars: 100 µm (A–C); 20 µm (E–K); 5 µm (D).

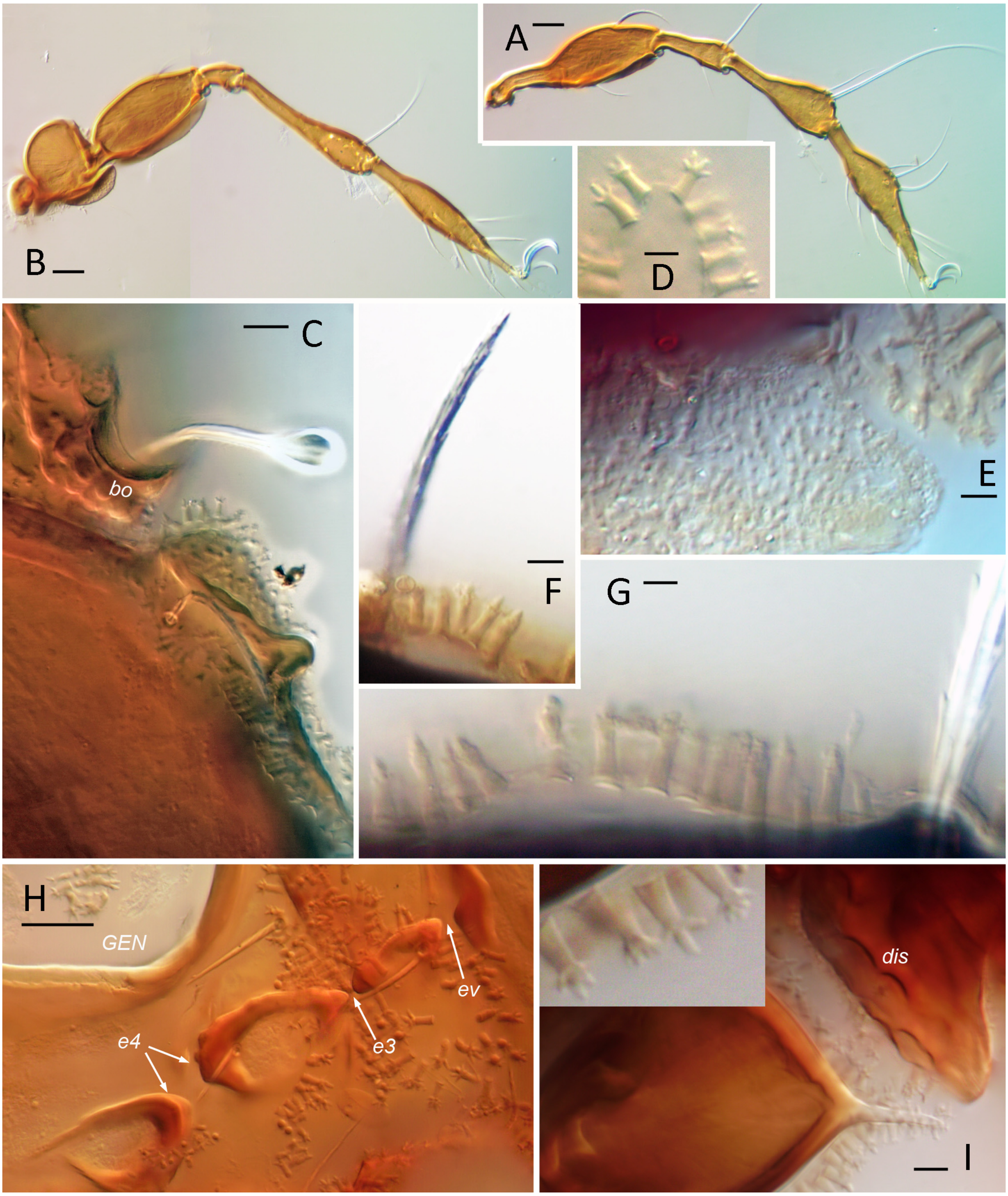

**FIGURE 24.** *Anderemaeus hammerae* Mahunka, 1980, adult: A, leg I, B, leg IV; C, bothridial region, dorsal view; D, cerotegument dislodged from pedotectum I; E, cerotegument dislodged from genital plate (left) and aggenital region (right); F, region of notogastral setae $h_3$, with dislodged cerotegument; G, same, region of notogastral seta $h_2$; H, region of epimeres III, IV, anterior to right; I, discidium and part of trochanter III, ventral view, anterior to right (insert: enlargement of cerotegument excrescences). Photomicrographs in transmitted light, DIC. Scale bars: 20 µm (A, B, C, H); 5 µm (all others).

While terminology has changed, Trägårdh's (1907) description and figures closely match the traits of *A. hammerae*, known from the southern tips of Argentina and Chile. Mahunka (1980) did not cite Trägårdh's work and seems to have been unaware of *C. tridactylus*. Only one trait prevents us from proposing a synonymy: Trägårdh described setae as follows: 'interlamellar hairs hairy, straight and blunt, situated as far from the middle as from the pseudostigmatic organs [i.e., the bothridial setae].' While seta *in* of *A. hammerae* (Fig. 22E) does have barbs, these are consistently minute and extremely difficult to discern, even with oil-immersion lenses and contrast-illumination, and the setae could not reasonably be characterized as 'hairy'. Since in all other *Anderemaeus* species known to us, the barbation of seta *in* is distinct at even modest magnification, it seems most reasonable to consider both to be valid species.

## Key to known species of *Anderemaeus*

1. Small species, less than 450 total length; notogaster with *p*-row of setae less than 1/3 length of dorsal setae and differently shaped. Length 344–443. . . . . . . . . . . . . . . . . . . . . . *Anderemaeus australiensis* J. & P. Balogh, 1983. Distribution: Australia.
- Larger species, greater than 600 total length; *p*-row similar to dorsal setae in shape and length or only slightly shorter. Neotropical species. . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Bothridial seta with length equal or greater than that of seta *in*; with weakly developed head (diameter at most 2–3 times that of stalk), or baculiform, or slightly tapered . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
- Bothridial seta distinctly shorter than *in*; with well-developed, distinct head, 5 or more times broader than stalk. . . . . . . . . . 10

3. Bothridial seta as long as mutual distance of pair, filiform, with minute swollen head; notogastral setae unusually long, subflagellate, distinctly barbed; lamellae strongly convergent, nearly touching anteriorly; rostrum rounded. Length 652–689 . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus hidasii* P. Balogh, 1995. Distribution: Brazil.
- Bothridial seta shorter, distinctly less than their mutual distance; notogastral setae not flagellate; lamellae and rostrum various . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

4. Lamella without distinct cusp or prolamella; rostrum rounded . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
- Lamella with small cusp bearing seta *le*, with or without prolamella; rostrum rounded or pointed . . . . . . . . . . . . . . . . . . . . . . 6

5. Seta *in* unusually short, hardly exceeding width of tubercle at its base; notogastral setae relatively short (*lm* reaching only about halfway to insertion of *la* in dorsal view). Length 763–830 . . . . . *Anderemaeus mataderoensis* **sp. nov.** Distribution: Ecuador.
- Seta *in* normal, longer than mutual distance of pair; notogastral setae relatively long (*lm* reaching insertion of *la* in dorsal view). Length 718–720 . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus sturmi* Balogh & Balogh, 1985). Distribution: Colombia

6. Dorsosejugal region with pair of large, triangular tubercles; prolamella long, distinct; notogastral setae of row *h* well-aligned. . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
- Dorsosejugal region without tubercles, or with small basal tubercles just large enough to support seta *in*; prolamella short or absent; *h* row not aligned ($h_3$ displaced laterally). . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

7. Rostrum pointed, with small mucro; seta *in* inserted distinctly anterior to each tubercle; bothridial seta baculiform to slightly tapered; prolamellae strongly converging . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
- Rostrum rounded; seta *in* inserted at base of each tubercle; bothridial seta weakly expanded distally as small head; prolamellae nearly parallel. Length 650. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus monticola* Hammer, 1958. Distribution: Argentina, Bolivia (dubious record in China, see above).

8. Lamella with strong lateral tooth, just proximal to cusp; preanal organ only slightly expanded internally. Length 614–680 . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus dentatus* **sp. nov.** Distribution: Chile.
- Lamellae without lateral tooth; preanal organ strongly expanded internally, nearly T-shaped. Length 670–786 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus chilensis* Hammer, 1962. Distribution: Chile, Argentina, Mexico.

9. Bothridial seta expanded distally as distinct, small head; short prolamella present; notogastral setae of moderate length (*c* about as long as humeral process, mutual distance of pair *lm* about twice setal length). Length 750. . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus magellanis* Hammer, 1962. Distribution: Argentina, Chile.
- Bothridial seta baculiform to slightly tapered distally; prolamella absent; notogastral setae unusually short (*c* shorter than humeral process, mutual distance of pair *lm* about four times setal length). Length 547–630 . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus sidorchukae* **sp. nov.** Distribution: Chile.

10. Head of bothridial seta capitate, surface granulate; rostrum rounded, without mucro; lamella without distal cusp; setal pair *ro* with mutual distance greater than that of *le*; with pair of large, approximate tubercles in dorsosejugal region, width about equal to mutual distance of pair. Length 746–812 . . . . . . . . . . *Anderemaeus capitatus* J. & P. Balogh, 1985. Distribution: Colombia.
- Head of bothridial seta pyriform, virtually smooth; rostrum pointed; lamella with distinct cusp; mutual distance of *ro* less than that of *le*; dorsosejugal region with only exaggerated basal tubercle of seta *in*, mutual distance of tubercle pair about four times

their width. Length 580–680 (subantarctic species). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

11. Seta *in* virtually smooth . . . . . . . . . . . . . . . . . . . . . . . *Anderemaeus hammerae* Mahunka, 1980. Distribution: Argentina, Chile.
\- Seta *in* with noticeable barbs . . . . *Anderemaeus tridactylus* (Trägårdh, 1907) **comb. nov.** (see above). Distribution: Argentina.

## Classification of *Anderemaeus*

### *History of family-group classification*

Ideas about the family and superfamily classification of *Anderemaeus* have varied significantly over time and according to author (Table 2). When first proposed by Hammer (1958), *Anderemaeus* was not associated with a family, but Balogh (1961, 1965) soon included it in a broad concept of Oppiidae (Oppioidea). Subsequently, Balogh (1972) proposed several new families within Oppioidea, including Anderemaeidae, which then comprised three genera: *Anderemaeus*, *Cristeremaeus*, and *Carabodoides* (= *Epieremulus*). Later, Balogh & Balogh (1985) transferred *Yungaseremaeus* from Oppiidae to Anderemaeidae. Balogh & Balogh (1992) added *Luxtoneremaeus* and, without explanation, transferred Anderemaeidae to Eutegaeoidea; they also removed *Amazoppia,* which had been included briefly in Anderemaeidae (Balogh & Balogh 1988). Norton & Behan-Pelletier (2009) did not question the concept of Balogh & Balogh (1992), except they followed Marshall *et al.* (1987) in considering the name Eutegaeoidea a junior synonym of Cepheoidea, so they used the latter name. In the last decade there has been much confusion over the availability of the names Cepheidae and Cepheoidea, due to homonymy; herein we retain these names in the usage of Schatz *et al.* (2011), pending a recently proposed resolution (Halliday & Norton 2019; see R6).

**TABLE 2.** Past family-group classifications of the oribatid mite genus *Anderemaeus* Hammer, 1958

| Source | Family | Superfamily |
|---|---|---|
| Balogh 1961, 1965 | Oppiidae | Oppioidea |
| Balogh 1972[1] | Anderemaeidae | Oppioidea |
| Balogh & Balogh 1992 | Anderemaeidae | Eutegaeoidea |
| Franklin & Woas 1992 | Anderemaeidae | Eremaeoidea |
| Colloff & Halliday 1998 | Anderemaeidae | Polypterozetoidea |
| Woas 2002 | Caleremaeidae *sensu lato*[2] | not given[3] |
| Subías 2004 | Caleremaeidae *s. l.* | Eremelloidea |
| Norton & Behan-Pelletier 2009[4] | Anderemaeidae | Cepheoidea |
| Oliveira *et al.* 2017 | Caleremaeidae *s.l* | Ameroidea |

[1] Followed by Fujikawa (1991)

[2] Most authors have considered Caleremaeidae to be monogeneric (i.e., *sensu stricto*; *s.s.*) but a broader context—Caleremaeidae *sensu lato* (*s.l.*)—was proposed by Woas (2002) and further expanded by Subías (2004); see text.

[3] See text for explanation.

[4] This is the classification of Balogh & Balogh (1992) except that Eutegaeoidea was considered a junior synonym of Cepheoidea; however, the latter name is invalid due to homonymy, and in need of emendation (Halliday & Norton 2019; see R6).

Woas (2002) presented a different and somewhat confusing view of Anderemaeidae, which he considered a heterogeneous family. He indicated (p. 52) that C*risteremaeus*, *Yungaseremaeus* and '*Anderemaeus* (in part)' should be transferred to Caleremaeidae, though he considered the placement tentative for the latter two genera. His expanded concept is referred to below as Caleremaeidae *sensu lato* (*s.l.*); it does not include *Veloppia*, as suggested by Norton (1978). Woas' (2002) classification was presaged by comments of Franklin & Woas (1992), who had noted similarities between the transferred genera and *Caleremaeus* (aggenital enantiophysis, tubular preanal organ) while arguing against their past inclusion in Oppioidea. Subías & Arillo (2001) had also briefly considered the possible synonymy of Anderemaeidae and Caleremaeidae, but made no definitive statement.

Woas (2002) did not clearly identify the species of *Anderemaeus* that should be excluded from this transfer, but he implied that *Anderemaeus forsteri* Balogh & Balogh, 1985 was not a typical *Anderemaeus* species; he seemed unaware that Balogh & Balogh (1992) previously had transferred *A. forsteri* to *Luxtoneremaeus*. Woas implied (by referencing Hammer's 1958 paper) that the type species, *A. monticola*, should be among those transferred to Caleremaeidae; thus, he seems to have subsumed Anderemaeidae within Caleremaeidae, leaving behind two taxa—*A. forsteri* (i.e. *Luxtoneremaeus*) and *Carabodoides* (= *Epieremulus*)—that previously had been included. However, there is a confusing contradiction in his list of Amazonian oribatid mites (p. 284): here, he included *Carabodoides* in Anderemaeidae as the only genus of the family present in that region. Woas (2002) did not indicate a superfamily placement for his Caleremaeidae *s. l.* but considered it among the 'Eupheredermata' (pp 51, 284). Earlier, Franklin & Woas (1992) had tentatively suggested including the genera in Eremaeoidea (sensu Balogh & Balogh 1992).

Without direct reference, Subías (2004) appears to have embraced the essential idea of Woas (2002)—that Anderemaeidae should be incorporated into Caleremaeidae—and made further modifications. He transferred the remaining genera of Anderemaeidae (sensu Balogh & Balogh 1992) to Caleremaeidae, even though Woas (2002) expressly had excluded *Epieremulus* (as *Carabodoides*) from Caleremaeidae *s.l.* and seems to have excluded *Luxtoneremaeus* (*A. forsteri*) by implication. Like Woas (2002), Subías (2004) correctly stressed the need for disintegrating the broad early concepts of Oppioidea but, as part of a reorganization, he proposed the heterogeneous superfamily Eremelloidea, which comprised eight rather disparate families, including Caleremaeidae *s.l.* This classification seems to have been unused by other authors, and in unpublished online annual updates Subías (2016 and following) abandoned Eremelloidea and grouped Caleremaeidae *s.l.* with Eremaeoidea, as suggested earlier by Franklin & Woas (1992), though his concept of this superfamily seems much broader than theirs.

Two classifications of Anderemaeidae are shown in Table 2 but are not discussed further. Colloff & Halliday (1998) included Anderemaeidae in Polypterozetoidea but presented no discussion or rationale. When first recognized (Balogh 1961), Polypterozetoidea was monofamilial, but Balogh (1972) expanded it to a small collection of unrelated families. While the content has changed (e.g. Schatz *et al.* 2011), the superfamily remains heterogeneous. We see no characters that suggest the inclusion of Anderemaeidae, other than a couple of widespread traits noted below, and to our knowledge no one else has used this classification. Most recently, Oliveira *et al.* (2017) included Anderemaeidae in Ameroidea; this was inadvertent, due to a conflation of classifications, and can be dismissed. They accepted Woas' (2002) inclusion of *Anderemaeus* in Caleremaeidae *s.l.*, while also accepting the inclusion of Caleremaeidae *s.s.*in Ameroidea by Norton & Behan-Pelletier (2009), who had treated Anderemaeidae as a family of Cepheoidea. Ameroidea includes *Ctenobelba*, the only other brachypyline genus known to have nymphs with opisthonotal glands opening on a distinct projection (see R5), but there are no other relevant similarities.

We examine this history in two steps. First, we critique and reject Woas' (2002) idea that *Anderemaeus* and *Caleremaeus* are confamilial, using traits of both adults and juveniles. Juveniles of *Caleremaeus* were known superficially from Michael's (1882) description and illustration of *C. monilipes* (Michael, 1882), and various details of its ontogeny were provided by Grandjean (1954, 1965). Juveniles of *Anderemaeus* were unknown until the present study. We assume these species are representative of their respective genera, especially regarding the cited traits, which normally would not vary among species of an oribatid mite genus. Second, *Anderemaeus* is compared to each of the superfamilies with which it has been associated, and also to Gustavioidea for reasons explained below. These comparisons are not exhaustive, focusing instead on a few characters known to differ among the taxa. Character states are derived from the literature, complemented by observations of material in the authors' collections, as needed. General sources include Balogh & Balogh (1992), Grandjean (1954, 1965), Woas (2002), Weigmann (2006) and Norton & Behan-Pelletier (2009). Other important sources are indicated where relevant.

### Are *Anderemaeus* and *Caleremaeus* confamilial?

Woas (2002) emphasized three shared traits that he thought linked *Caleremaeus* to *Anderemaeus*. One was the complex of four blade- or ridge-like projections on the prodorsum—a pair of prodorsal lamellae (or large costulae) that are flanked by a pair of similar tutoria. The suggested similarity might also have included the presence of a prodorsal enantiophysis (*ea* or *A*) formed by the posterior corner of the tutorium and a closely opposing tubercle, though he did not mention it specifically. A second was the shared presence of a paired aggenital enantiophysis (*e4* or *U*), which spans the posterior border of epimere IV. The third is what Woas (p. 52) called 'a large preanal organ almost touching the rear margin of the genital opening.' The latter description seems rather equivocal, since it ignores the specific structure of the organ, and the relative distance between the anal and genital plates would also affect interpretation of the character. Franklin & Woas (1992) had more specifically characterized the shared form as 'tubular'. Such hollow organs often are called 'caecum-like' when formed as simple tubes or pouches.

As seen in Table 3, none of these traits is unique to Woas' (2002) expanded concept of Caleremaeidae *s.l.*, which included four genera: *Caleremaeus*, *Cristeremaeus*, *Anderemaeus* and *Yungaseremaeus*. The complex of paired, ridge- or bladelike lamellae and tutoria is widespread in Brachypylina and seems plesiomorphic in the context of these genera, and indeed Woas' (2002) general approach was to recognize 'levels of organization', which allows paraphyletic groups based on symplesiomorphies. Unknown to Woas (2002), this complex is not universal in *Caleremaeus*: for example, the lack of both lamella and tutorium in an undescribed species from the USA (Norton & Behan-Pelletier 2009, their Fig. 15.43) probably represents a loss. This indicates at least some level of homoplasy in the character even at the genus-level.

**TABLE 3.** Distribution of selected characters in *Anderemaeus*, *Caleremaeus* and relevant superfamilies. (+ = trait present, - = trait absent)

| | *Anderemaeus* | *Caleremaeus* | Eremaeoidea[1] | Cepheoidea[2] | Gustavioidea |
|---|---|---|---|---|---|
| lamella (or presumed homologue) | + | +/-[3] | +/- | +/- | + |
| tutorium | + | +/-[3] | +/- | +/-[4] | +/- |
| prodorsal enantiophysis (*ea*) | + | +/- | +/- | - | - |
| pedotectum II | + | - | + | + | +/- |
| phragmata | - | - | - | - | +/- |
| humeral process | + | + | - | + | +/- |
| circumpedal carina | + | - | - | +/- | +/- |
| hollow preanal organ | + | + | + | + | +/- |
| aggenital enantiophysis (*e4)* | + | + | - | +/- | - |
| dorsosejugal fusion | + | + | - | +/- | +/- |
| palp $\omega$ coupled to *acm* | - | - | - | +/- | +/- |
| rutellum atelobasic | - | + | - | - | +/- |
| trochanter III-IV spines | + | - | +/- | + | - |
| centrodorsal setae present (nymphs) | - | - | - | - | +/- |
| scalps retained (nymphs) | - | + | + | + | +/- |
| nymphal cuticle plicate | - | + | + | - | +[5]/- |

[1] Eremaeoidea is used here in the sense of Balogh & Balogh (1992), including only Eremaeidae and Megeremaeidae, which is how it also seems to have been perceived by Franklin & Woas (1992). Recent classifications (e.g. Schatz *et al.* 2011) have included these families with Zetorchestidae, under Zetorchestoidea, but the molecular study of Lienhard *et al.* (2013) casts doubt on the monophyly of such a grouping.

[2] Despite a problem with homonymy, the name Cepheoidea is retained and used in the sense of Schatz *et al.* (2011), while a solution is pending (Halliday & Norton 2019; see R6).

[3] The lamella-tutorium complex (and enantiophysis *ea*) is undeveloped in an undescribed North American species (illustrated by Norton & Behan-Pelletier 2009; their Fig. 15.43).

[4] In their diagnosis of Cepheoidea, Norton & Behan-Pelletier inadvertently stated that the tutorium is absent; in fact, it can be present (e.g. Cepheidae, Eutegaeidae), or absent (e.g. Microtegeidae).

[5] Juveniles of most gustavioid taxa have a relatively smooth cuticle, but that of *Dendrozetes* (Peloppiidae) is plicate (Lindo *et al*. 2010).

We view the tubular preanal organ as another symplesiomorphy among the four genera. Overall, this organ takes many forms, one of which is a solid apodematal internalization with diverse shapes, found in many highly-derived oribatid mites (e.g. Poronota). However, it seems to have originated as a simple invagination from the flat preanal plate that, in macropyline groups, serves as the origin for genital plate retractor muscles (Grandjean 1969). A simple short caecum, elongated tube or internally-expanded hollow invagination (vase-like, bifid, or even T-shaped) is typical of early- to middle-derivative Brachypylina, including most Hermannielloidea, Neoliodoidea, Eremaeoidea, Plateremaeoidea, Damaeoidea and numerous other groups. The tubular or slightly expanded form can be found in at least some members of all the taxa shown in Table 3, and it cannot be considered a synapomorphy supporting a close relationship of *Anderemaeus* and *Caleremaeus*.

The prodorsal and aggenital enantiophyses also have scattered taxonomic distributions. The former typically is associated with the tutorium (e.g. *Anderemaeus*, *Caleremaeus*, *Megeremaeus*, *Veloppia*), but it also occurs in the absence of the lamella-tutorium complex or its analogs (e.g., Pheroliodidae, Hungarobelbidae and the amerid genus *Gymnodampia*). The aggenital enantiophysis has a similarly scattered distribution outside Woas' four genera. In addition to *Veloppia*—which Woas' (2002) suspected was more closely allied with Hungarobelbidae than with Caleremaeidae *s.l.*—it is present in some taxonomically dispersed genera currently grouped in the cepheoid families Cepheidae (*Eupterotegaeus*), Microtegeidae (*Microtegeus*, *Suctotegeus*), Cerocepheidae (*Dicrotegaeus*, *Bornebuschia*), Eutegaeidae (*Neoeutegaeus*) and Nosybeidae (*Topalia*, *Lamellocepheus*). It also occurs in at least one genus of Polypterozetoidea (*Nodocepheus*), and Carabodoidea (*Fissicepheus*) while being absent from most members of these superfamilies.[1] The apparent homoplasy indicated by the scattered distribution of the prodorsal and aggenital enantiophyses may result from several adaptive convergences; such structures probably assist in holding localized plastrons when a mite is temporarily underwater (see R7). However, it seems equally likely that these structures appeared early in brachypyline evolution and that at least some of the scattered absences represent independent losses.

The three traits highlighted by Woas (2002) are common to *Anderemaeus* and *Caleremaeus* but considering their much wider distribution they are not convincing evidence that the two genera are confamilial. Two shared traits that Woas did not consider should also be addressed. One is the fusion of prodorsum and notogaster, which also exists in *Caleremaeus* (Norton & Behan-Pelletier, in prep.). However, such fusion exists in some members of all superfamilies considered in Table 3, except for Eremaeoidea, so it is an evolutionarily labile trait. Another is the sharing of a longitudinal ridge or carina, low on the lateral face of the rostrum. *Caleremaeus* species have a ridge running posteriorly from the insertion of seta *ro* that is distinctly removed from the rostral margin (Miko & Travé 1996), while some *Anderemaeus* species have a laterorostral carina that continues the rostral margin posteriorly, onto the parietal wall of acetabulum I. We view these as different structures, of independent origin.

In contrast to these similarities, several traits of *Anderemaeus* seem to be apomorphies that are not shared with *Caleremaeus* but rather are found in more derived taxa of Brachypylina. One relates to scalp retention by nymphs. In the terminology of Grandjean (1954), *Caleremaeus* has 'eupheredermous' nymphs (Michael 1882)—i.e., they are among the diverse group of early- and middle-derivative taxa that carry exuvial gastronotic 'scalps' of previous instars in a pagoda-like stack (see R8). Woas (2002) assumed that *Anderemaeus* juveniles were eupheredermous but, lacking data, he considered the relationship with *Caleremaeus* tentative. In fact, *Anderemaeus* nymphs lack scalps: they are 'apheredermous' but are unusual in being 'dorsodeficient' (lacking setal pairs *da*, *dm*, *dp*), like most eupheredermous taxa. This derived combination of traits—apheredermy with dorsodeficiency—was previously known in only one superfamily of Brachypylina, the Gustavioidea, as discussed below.

A second derived trait of *Anderemaeus* relates to cuticle of the juveniles. A plicate cuticle is found in the probable outgroup of Brachypylina (Hermanniidae) and in many early- to middle-derivative brachypyline taxa. The latter include eupheredermous taxa such as Neoliodoidea and Eremaeoidea, in which nymphal cuticle is plicate except for that lying underneath the exuvial scalps (Behan-Pelletier 1993; Norton & Franklin 2018, Remark #2 therein), and *Caleremaeus* shares this plesiomorphic trait (Norton & Behan-Pelletier, in prep.). The juvenile cuticle of *Anderemaeus* lacks any evidence of plication.

A third derived trait of *Anderemaeus* that *Caleremaeus* lacks is the paired circumpedal carina (= peripodal line) of adults, which usually delimits the posterior extent of a slight concavity in the lateral podosoma, into which legs are folded and appressed during defensive posture (Grandjean 1931). Its taxonomic distribution has not been fully catalogued, but the carina is present in most Poronota (absent from Licneremaeoidea and several more derived families: Stelechobatidae, Zetomotrichidae, Neotrichozetidae). It also is developed to various extent in several 'pycnonotic' (= non-poronotic) taxa that seem closely allied with Poronota, including Microzetidae, Charassobatidae and Limnozetoidea. The carina is plesiomorphically absent from most pycnonotic Brachypylina, including *Caleremaeus*, but is present in nearly all Gustavioidea (absent from *Pyroppia* and relatives, see below), in many Cepheidae, and in the polypterozetoid family Nodocepheidae.

A fourth derived trait of *Anderemaeus* is the presence of sharp spines on trochanter IV, and usually III of adults. These are well-developed in Eremaeoidea and in many members of the cepheoid families Cepheidae and Eutegaeidae.

A fifth derived trait of *Anderemaeus* is the absence (loss) of coronal setae on the ovipositor. These setae are

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[1] In an overview of oribatd mite morphology, Norton & Behan-Pelletier (2009, their Fig. 15.6F) illustrated the general position of *e4* by modifying a published image of Damaeidae; *e4* was added without indicating that no known Damaeidae possess it.

plesiomorphically present in *Caleremaeus*, but that is also true of all superfamilies considered in Table 3. The loss of these setae is relatively rare, with most known examples being in Oppioidea—with which Anderemaeidae shares no other notable apomorphies—and certain families of the poronotic superfamily Oripodoidea (Ermilov 2010).

At first consideration, the pantelobasic rutellum—i.e. attached across the width of the gena—might be viewed as another derived trait of *Anderemaeus*. In *Caleremaeus* the rutellum is atelobasic, attached to the gena only laterally. Grandjean (1957) presented atelobasy, which is found in many macropyline taxa, as being ancestral to pantelobasy, but even the earliest-derivative Brachypylina—e.g. Hermannielloidea, Neoliodoidea, Plateremaeoidea—possess a pantelobasic rutellum. The atelobasic form is found in some middle-derivative groups—e.g. Damaeidae, Hungarobelbidae (Miko & Travé 1996), even the gustavioid genus *Dendrozetes* (Lindo *et al.* 2010)—and in these it is more parsimonious to consider atelobasy as a reversal. Atelobasy in *Caleremaeus* can be viewed similarly.

We conclude that *Anderemaeus* is a more derived genus of Brachypylina than is *Caleremaeus*, and the two genera are not close relatives. The several similarities noted by Woas (2002) are either symplesiomorphies that are shared with other taxa or are function-based convergences that evolved in multiple taxa. Therefore, we recommend reverting to the past recognition of Caleremaeidae and Anderemaeidae as distinct families.

### *Notes on genera of Anderemaeidae*

At present, we follow the concept of Anderemaeidae given by Balogh & Balogh (1992), comprising *Anderemaeus* and the four genera listed below, but it is unlikely to withstand close future scrutiny. To determine which genera should remain will require the discovery of their juveniles as well as more detailed morphological knowledge of adults. Brief current assessments follow, but only those for *Cristeremaeus* and *Epieremulus* are supported by direct observations of adults.

*Luxtoneremaeus* (i.e. *A. forsteri*) is a monotypic genus that almost certainly will remain in Anderemaeidae. Woas (2002) dismissed it from his Caleremaeidae *s.l.* because it has a modified lamella-tutorium complex, but the only real difference seems to be the presence of a translamella. This is not a convincing basis for dismissal, since numerous other brachypyline families include species both with and without this structure (e.g. Liacaridae, Mochlozetidae, Ceratozetidae). No other difference with *Anderemaeus* is evident from illustrations (Balogh & Balogh 1985): characteristic features like the rectangular humeral tubercle, the large discidium and the aggenital enantiophysis are present, and the medial part of a circumpedal carina seems indicated in the sketchy ventral figure.

*Yungaseremaeus*, another monotypic genus, probably also will remain in Anderemaeidae. As originally described (Balogh & Mahunka 1969), its dorsal features match those of *Anderemaeus*, but ventral structures have been presented in a conflicting manner. The venter of the type species, *Y. longisetosus* Balogh & Mahunka, 1969, was not illustrated in the original description, but in their family review Balogh & Balogh (1985) included a ventral drawing (their Fig. 4A); it lacks both a discidium and aggenital enantiophysis and bears little resemblance to the venter of *Anderemaeus* or *Luxtoneremaeus*. Also, six setae are shown on each genital plate, contradicting the written description (five). Probably this illustration is an error, made from a different mite species. In their later compendia (Balogh & Balogh 1992, 2002) the same authors included an entirely different ventral illustration (their Fig. 154D and plate 194, Fig. 11, respectively) that clearly shows the discidium and enantiophysis, as well as the described number (five pairs) of genital setae. No circumpedal carina is illustrated, but its absence needs confirmation: this feature often is omitted from sketchy figures.

*Cristeremaeus* is the only genus that Woas (2002) added to Caleremaeidae *s.l.* unequivocally. Like *Anderemaeus* it has the lamella-tutorium complex, a rectangular humeral apophysis, prodorsal and aggenital enantiophyses. The notogaster and prodorsum seem fused, with a sejugal groove and anteriorly-narrowing circumgastric scissure, as in *Anderemaeus*, though this was not proven by sagittal sectioning as only several specimens were available. Other than monodactylous pretarsi, the legs are similar to those of *Anderemaeus*; they are relatively longer and thinner than in *Caleremaeus* and lack a dorsodistal tubercle on tibia I. Unlike *Anderemaeus*, legs III and IV have neither trochanteral spines nor ventral keel on femora; more significantly, is there is no trace of a circumpedal carina. Its inclusion in Anderemaeidae probably will remain equivocal until juveniles are found, but the transfer to Caleremaeidae cannot be supported.

*Epieremulus* (= *Carabodoides*) probably will be removed eventually from Anderemaeidae. Adults have a pair of medial, low, ridge-like lamellae (often called 'costulae'), but instead of a distinct tutorium there are one or two pairs of less-defined ridges, and the prodorsal enantiophysis is absent. The notogaster lacks a humeral process; instead, there is a conical tubercle on the posterior slope of the dorsosejugal furrow (not on the notogaster proper) that opposes a bothridial tubercle.[2] The aggenital enantiophysis is present (*E. geometricus*) or absent, and there is no circumpedal carina. Trochanters III and IV lack spines and femora lack ventral keels. The preanal organ is hollow and strongly T-shaped. Tibia I is unlike that of *Anderemaeus*, having a large dorsodistal tubercle bearing the solenidia.

*Superfamily position of Anderemaeidae*

Because the composition of Anderemaeidae is uncertain, we briefly examine below how well the type genus, *Anderemaeus*, fits the characters of Eremaeoidea, Cepheoidea and Gustavioidea. Superfamily concepts are those summarized by Norton & Behan-Pelletier (2009) and Schatz *et al.* (2011), except that Eremaeoidea is used in the narrower sense of Balogh & Balogh (1992; see footnote, Table 3); concepts of Subías (2004 and unpublished online updates) differ in some details. We do not critique the original placement of *Anderemaeus* in Oppioidea (Table 2), as this was well-rejected by Franklin & Woas (1992) and Woas (2002), though they were unaware of at least one shared derived trait, the loss of coronal setae on the ovipositor (see above). Nor do we analyze its placement in Eremelloidea (Subías 2004), Polypterozetoidea (Colloff & Halliday 1998) or Ameroidea (Oliveira *et al*. 2017), as these associations seem untenable (see above).

*Anderemaeus* vs Eremaeoidea. Eremaeidae and Megeremaeidae comprised this group in the treatment of Balogh & Balogh (1992). This seems to have been the sense used by Franklin & Woas (1992) and Woas (2002), and to which they considered adding Caleremaeidae (*s.l*). These authors focused on similarities of *Anderemaeus* with Megeremaeidae, particularly the lamella-tutorial complex and hollow, tubular preanal organ, which we consider plesiomorphic (see above). Unlike *Anderemaeus*, adult eremaeoids lack the derived circumpedal carina, and juveniles are eupheredermous and plicate. *Anderemaeus* species lack the apomorphic traits of Eremaeoidea, including adults with ventral neotrichy and both tibial and tarsal porose areas, and juveniles with tracheal organs (Behan-Pelletier 1990, 1993). They do share an unusual symplesiomorphy: the presence in adults of a vestige of the second exobothridial seta (*em* in Behan-Pelletier 1993).

*Anderemaeus* vs Cepheoidea. The original placement in Cepheoidea (Balogh & Balogh 1992) was not explained, but probably it related largely to conspicuous similarities (e.g. the lamella-tutorium complex and humeral process, both typical of Cepheidae). As currently composed, the superfamily seems heterogeneous and without consistent, defining traits. For example, the circumpedal carina is developed to various degrees in some Cepheidae but not in others, is equivocally present (vaguely formed) in some Eutegaeidae and is absent from other cepheoid families (e.g. Microtegeidae, Cerocepheidae). The aggenital enantiophysis is present (Microtegeidae, Cerocepheidae, some Eutegaeidae, some Cepheidae) or absent (e.g. most Cepheidae, Eutegaeidae). *Anderemaeus* lack three derived traits found in Cepheidae—a notched or divided pedotectum I, partial fusion of palp tarsal solenidion with seta *acm* ('imperfect double-horn'), and (usually) a near-circular arrangement of notogastral setae—but these also are absent from other cepheoid families, such as Microtegeidae (Ermilov *et al.* 2010) and Cerocepheidae (Ermilov & Minor 2015). We are not aware of any cepheoid taxon that possesses a prodorsal enantiophysis, but otherwise each character of adult Anderemaeidae can be found somewhere within the broad current concept of Cepheoidea; i.e., there is no obvious reason to exclude the family. Juveniles have been described only for Cepheidae, and these are eupheredermous.

*Anderemaeus* vs Gustavioidea. No one has proposed *Anderemaeus* as a member of Gustavioidea, but the latter includes all species previously known to have dorsodeficient nymphs that are also apheredermous. Since *Anderemaeus* shares this rare trait combination, a comparison is warranted.

Concepts of Gustavioidea have expanded over time. Peloppiidae (= Ceratoppiidae, Metrioppiidae) and Liacaridae (*sensu lato*, including Xenillidae) long have been considered close relatives. They were included in Balogh's (1961) first concept of Liacaroidea, along with Astegistidae and Tenuialidae, and remained as the superfamily expanded—under the senior synonym Gustavioidea—to include also Gustaviidae, Multoribulidae and usually Kodiakellidae (Balogh 1972; Balogh & Balogh 1992; Subías 2004; Schatz *et al.* 2011).

In this sense, Gustavioidea includes taxa with a diversity of nymphal morphology, such that they would be spread among three of Grandjean's (1954) five brachypyline sections. Tenuialidae, Gustaviidae and *Birsteinius* (a genus equivocally assigned to Liacaridae) are 'normal' (dorsodeficient) euepherederms (section 2). Known Peloppiidae and

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[2] Ermilov & Anichkin (2014) illustrated the notogaster of *Epieremulus budupensis* Ermilov & Anichkin, 2014 as having a strong pair of conical humeral tubercles (their Fig. 15A, B), but this was an error; the tubercles are on the posterior part of the sejugal groove, below the margin of the notogaster.

most Liacaridae (*Liacarus*, *Dorycranosus*, *Xenillus*, *Adoristes*) are dorsodeficient apheredermes (section 3). Astegistidae (at least *Furcoribula*; Ermilov & Kolesnikov 2012) are 'normal' (integidorsal) apheredermes (section 4).

Norton (1983) considered dorsodeficient apheredermy to be apomorphic, derived from normal (dorsodeficient) eupheredermy by the loss of scalp retention, and a small amount of molecular data support this idea (Schäffer *et al.* 2010). In fact, if one removes their exuvial scalps, nymphs of Tenuialidae (Seniczak *et al.* 2018) and Gustaviidae (Ermilov 2010; Ermilov *et al*. 2013) appear much like those of some members of Peloppiidae, such as *Metrioppia* (Grandjean 1931) and *Hauseroceratoppia* (new observation).[3] They share the long, marginally positioned gastronotic setae on distinct tubercles with pair $h_1$ adjacent in the pygidial region, a relatively smooth gastronotic cuticle, and nymphal regression of prodorsal seta *in* (see R9). This set of traits is shared by various brachypyline families with eupheredermous nymphs but *Anderemaeus* is the only non-peloppiid apheredermous taxon known to have them. Nymphs of other members of Peloppiidae either have a different facies (*Ceratoppia*; Seniczak & Seniczak 2010) or are unknown (e.g. *Pyroppia*, *Parapyroppia* and *Paenoppia*, a subset that we informally and temporarily will call 'pyroppiines').

Adult traits are less supportive of a close relationship between *Anderemaeus* and Peloppiidae, or Gustavioidea in general. Most gustavioids, including many Peloppiidae, have the derived circumpedal carina, though it is absent from some Peloppiidae (e.g. pyroppiines and *Dendrozetes*) and from Kodiakellidae. However, this carina is rather widespread in other derived superfamilies of Brachypylina (see above). *Macquarioppia* (=*Macquariella*)—a genus that Wallwork (1963, 1964) considered rather primitive among Peloppiidae (=Metrioppiidae)—has a humeral projection but it does not resemble that of *Anderemaeus*, nor does the knife-like projection of Tenuialidae. To our knowledge, no gustavioids have either the prodorsal or aggenital enantiophysis, and while some have trochanters II-IV with dorsodistal angles, they lack noticeable spines.

Other similarities between *Anderemaeus* and Gustavioidea adults usually are inconsistent and are plesiomorphic, in our view. (1) Like *Anderemaeus*, gustavioids have paired lamellae and tutoria, though the pyroppiine genera and *Dendrozetes* have lost the latter. (2) Gustavioids collectively have a wide variety of preanal organs, but the plesiomorphic hollow, tubular form of *Anderemaeus* is to our knowledge present only in Astegistidae. (3) As with Cepheoidea, Gustavioidea exhibit different states of association between eupathidial seta *acm* with solenidion *ω*. In pyroppiine Peloppiidae, as well as in Tenuialidae, Liacaridae and Astegistidae, the two structures have the plesiomorphic state of independence, as in *Anderemaeus*. By contrast, in Gustaviidae and some other Peloppiidae (*Ceratoppia*, *Hauseroceratoppia*) there is an imperfect double-horn. (4) Dorso- and pleurophragmata are derived apodemes projecting internally from the posterior border of the prodorsum that serve as origins for gnathosomal muscles. These are plesiomorphically absent from *Anderemaeus*, in which gnathosomal muscles insert directly on the prodorsal surface cuticle, and also are absent from some Peloppiidae (e.g. *Dendrozetes*, *Ceratoppia*). But at least the pleurophragmata are present in most gustavioid families, including most Peloppiidae (*Metrioppia*, *Hauseroceratoppia*, *Pseudoceratoppia*, the pyropiinae genera). They are widespread also in Poronota and other relatively derived Brachypylina (reviewed in Norton & Behan-Pelletier 2009, Norton & Franklin 2018). (5) A characteristic apomorphy of many adult Gustavioidea, absent from *Anderemaeus*, is the paired aggenital taenidium. In most instances it is a groove, covered by a 'minitectum' lying transversely between acetabulum IV and the genital plates (Grandjean 1968, 1969, 1971). The minitectum is found in Astegistidae, Gustaviidae and Tenuialidae (though it may be incomplete in the latter), and in some Liacaridae (e.g. *Stenoxenillus*, some *Liacarus* and *Xenillus*). Liacaridae that lack a minitectum have a narrow, ribbon-like band of modified cuticle that occupies this position, typically with dense microtubercles in contrast to a smooth surrounding surface (e.g. *Dorycranosus*, *Opsioristes*, *Adoristes*, many *Xenillus*, some *Liacarus*); the band can be slightly depressed as a weak groove, or not. While most Peloppiidae have a taenidium and minitectum, the pyroppiine genera have no modifications in this region, not even a band of modified cuticle, nor do Kodiakellidae. Outside Gustavioidea, the aggenital taenidium and minitectum is found in *Conoppia* and Thyrisomidae. The former is an unusual genus currently in Cepheidae (see R10); the latter is usually included in Oppioidea, but this needs reexamination.

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[3] Wallwork (1963, 1964) indicated that nymphs of the peloppiid genus *Macquarioppia* (=*Macquariella*) are similar to those of *Metrioppia*, but to our knowledge he never illustrated or described them.

*Conclusions*

*Anderemaeus* and *Caleremaeus* are not close relatives and should not be considered confamilial. At present, there is no clear reason to include *Anderemaeus* in Eremaeoidea or in the recently recognized Caleremaeoidea (which seems based on only *Caleremaeus*; Weigmann 2006). Based on adult morphology, we can identify no synapomorphies that support including *Anderemaeus* in either Cepheoidea or Gustavioidea, but neither relationship is precluded, mainly because the current concept of each superfamily is so broad as to encompass taxa that collectively possess all or most traits of *Anderemaeus* adults, albeit in a mosaic fashion. Juvenile morphology more strongly supports Gustavioidea as containing the closest relatives of *Anderemaeus*, as there is at least one plausible synapomorphy. The dorsodeficient apheredermy of nymphs is a derived trait known only from *Anderemaeus* and the gustavioid families Peloppiidae and Liacaridae. Various members of Peloppiidae share the nymphal facies of *Anderemaeus*—with elongated, marginalized gastronotic setae, including adjacent pair $h_1$, and nymphal regression of prodorsal seta *in*—that is not found among Liacaridae.

Grandjean (1954) recognized that their relatively conservative morphology gives juveniles of Brachypylina special value in deciphering phylogenetic relationships. Since then, various taxonomic problems have been solved, or at least better-informed, by the discovery and incorporation of data on juveniles (Travé 1964; Norton & Ermilov 2014). We therefore propose the transfer of *Anderemaeus*, and consequently Anderemaeidae, to Gustavioidea. When they are more completely known, certain other genera currently included in this family may be excluded (see above).

One reason for uncertainty is that the monophyly of each superfamily—Cepheoidea and Gustavioidea—is itself equivocal. Traits listed in diagnoses (e.g. Norton & Behan-Pelletier 2009) might be present in only a part of the included families or may remain unexamined in some of them. Nor do available DNA data lend support, though only a few relevant taxa have been examined. In trees from several studies using the 18S rRNA gene, representatives of neither superfamily form a discrete clade (Maraun *et al.* 2009; Dabert *et al.* 2010; Krause *et al.* 2016; Xue *et al.* 2017). Overall, while most families in pycnonotic Brachypylina seem conceptually sound, most currently-recognized superfamilies are not (e.g. Norton & Franklin 2018), having been first assembled more for purposes of identification and cataloging than as reflections of phylogenetic relationships.

## Remarks

1. *Anderemaeus* species have a bulge (*rb*, Fig. 20F) above the rostral excavation that is usually conspicuous. The excavation (*rex)*, common in brachypyline oribatid mites, results from an abrupt thinning of the ventral ('internal') face of the solid rostral limb, between the rostral setae; it accommodates distal gnathosomal elements when the subcapitulum is elevated during the defensive posture. Under transmitted light, in dorsal view, the thinner cuticle makes the excavation conspicuous and it can be mistaken for a large fenestration or incision and is often drawn with solid lines. For two reasons, we believe that Balogh & Balogh (1983) made such an error when describing *A. australiensis*, which they wrote had a 'broad incision.' First, in lateral view (their Fig. 13C) the rostrum shows the typical bulge, characteristic of *Anderemaeus*, so almost certainly the limb excavation is also present. Second, a real incision would be visible from below, but in their ventral view (Fig. 13B) the rostrum is entire.

2. While the notogaster appears to be separated from the prodorsum in dorsal aspect, sagittal sections show that these regions are fused at the bottom of the distinct sejugal groove (*sej*; Figs 12I, 21A). Marking the fusion is a deep, narrow, transverse incision (*t.inc*) from the internal face of the cuticle, leaving only the external third of the exocuticle intact. We interpret this as an elastic hinge, a line of flexing that accommodates changes in hysterosomal volume. Such fusions probably are under-reported in taxa having a deep dorsosejugal groove, since the line of fusion is rather hidden. Also, at least in the case of *Anderemaeus*, the incision allows the notogaster to be easily removed during dissection, which can give a false impression of integrity.

3. We use the notations for setae of epimere IV proposed by Norton & Franklin (2018; Remark #15 therein). They showed that Grandjean's (1934; see also Sidorchuk & Norton 2010) widely used method of designating setae according to ontogenetic appearance is unnecessary and confusing, and masks an interesting ontogenetic delay of the most medial seta. Seta *4b* appears in the protonymph, exactly aligned with *3b* (Fig. 9B); *4a* appears in the deutonymph, and *4c* in the tritonymph, each aligned perfectly with the metamerically homologous seta on epimere III (Fig. 9D).

4. All known *Anderemaeus* species have six pairs of genital setae as adult. The original ventral illustration of *A. capitatus* by Balogh & Balogh (1985; their Fig. 1B) shows only five pairs, but in a footnote (p. 44) they indicated that the most anterior pair was omitted.

5. The strange projection of the opisthonotal gland opening of *Anderemaeus* nymphs on a long, narrow stalk is unique among oribatid mites. In general, this gland serves a defensive function (Heethoff *et al.* 2011), and usually it opens flush with the body surface in both adults and juveniles. Previously-known examples of a projected opening are few, and in each case the opening is on a short, funnel-like extension: they include all instars of Parhypochthoniidae, adults of Hermanielloidea, and juveniles of *Ctenobelba* (Ameroidea: Ctenobelbidae; Grandjean 1965). The phylogenetic distance among these three taxa shows that projected openings have evolved multiple times, and we believe *Anderemaeus* juveniles represent a fourth instance.

6. The mite family name Cepheidae is a junior homonym (Schatz *et al.* 2011). According to Art. 55.3 of the International Code of Zoological Nomenclature (ICZN 2000), such cases—caused by similar but not identical generic names—must be referred to the Commission. The problem cannot be resolved by simple replacement with existing family-group synonyms, as has been attempted recently: Compactozetidae for Cepheidae and Eutegaeoidea for Cepheoidea (e.g. Norton & Ermilov 2014). Halliday & Norton (2019) have submitted a proposal to the International Commission of Zoological Nomenclature that would emend the spelling of Cepheidae (and Cepheoidea) while retaining the original authority and date (Berlese 1896). Pending resolution by the Commission, we retain the long-established usage herein.

7. An enantiophysis—two tubercles that oppose each other, usually across a cuticular groove—can be formed at numerous places on the adult body (Grandjean 1960; Norton 1978). Such structures probably assist in holding localized plastrons when a mite is temporarily underwater (Chen *et al.* 2004), and the scattered taxonomic distribution of the prodorsal and aggenital enantiophyses, noted above, may result at least in part from several adaptive convergences.

Similarly, Grandjean (1968) suggested that the aggenital taenidium-minitectum serves a respiratory function during submersion in water by connecting air in the progenital cavity with an air film (plastron) in the acetabular region, where the tracheal stigmata open. If true, it would be functionally similar to the aggenital enantiophysis, which could anchor an air film in the same position. Is there an evolutionary transition between an aggenital enantiophysis spanning a shallow groove and a full aggenital taenidium with minitectum? The condition in the tenuialid genus *Hafenreferria* argues against such a derivation, since the minitectum is incomplete medially and appears to be an extension of acetabulum IV (Grandjean 1969).

8. Nymphal scalp retention and a dorsodeficient gastronotic setation (loss of centrodorsal setae *da*, *dm* and *dp* after the larva) usually are co-occurring traits; this seems adaptive since mechanoreceptors should be irrelevant if hidden underneath closely appressed scalps, and the setae could interfere with retention. But while the correlation is strong (Grandjean 1954) it is not perfect. In a few taxa, centrodorsal setae are retained under the stack of scalps. The plicate nymphs of the licneremaeoid genus *Dendroeremaeus* (Dendroeremaeidae) are integridorsal, but with highly reduced centrodorsal setae; surprisingly, they can retain all scalps through the tritonymph, despite their anteriorly incomplete line of dehiscence, which is usually associated with apheredermy (Behan-Pelletier *et al.* 2005). While scalp-retention in *Dendroeremaeus* appears to be inconsistent, there are at least two brachypyline genera—*Charassobates* and *Tegoribates*—whose plicate nymphs consistently carry scalps while retaining small centrodorsal setae (Grandjean 1958; Behan-Pelletier 2017). As these are isolated examples within large, otherwise apheredermous superfamilies (Licneremaeoidea and Achipterioidea, respectively), they probably represent independent derivations of scalp-retention. Scalps also are retained by nymphs of the poronotic family Oribatellidae, most of which are integridorsal (exceptions in Behan-Pelletier & Walter 2012), but are held away from the body rather than being appressed to it (Grandjean 1954).

Another expression of character-independence is that described above for Peloppiidae (= Ceratoppiidae, Metrioppiidae), Liacaridae and *Anderemaeus*: dorsodeficiency in apheredermous nymphs. The hypothesis that this trait evolved from eupheredermy by the loss of scalp retention in nymphs (Norton 1983) can explain postlarval dorsodeficiency, but it is not sufficient for the case of the peloppiid genus *Dendrozetes*, in which the larva is also dorsodeficient. No known eupheredermous taxon has a larva lacking centrodorsal setae, and obviously no *Dendrozetes* ancestor could have carried a scalp in its first active instar. So, this unique setation seems the result of an ontogenetic acceleration of centrodorsal suppression, which starts in the protonymph in all other known instances (see also R9).

Large-scale questions on the plasticity of nymphal gastronotic traits remain unanswered. Is integridorsal apheredermy always ancestral to eupheredermy, which is then always ancestral to dorsodeficient apheredermy? Probably it is not that simple. For at least one genus of Ameroidea (*Gymnodampia*) a reversal seems likely: they have nymphs with integridorsal apheredermy, but otherwise seem to be positioned in the midst of eupheredermous taxa (Chen *et al.* 2004). One would have to invoke loss of scalp retention and also the loss of setal suppression, e.g. a neotenic retention of the centrodorsal setae in the nymphs. Astegistidae presents a similar problem: they have typical gustavioid adult traits, including the minitectum, yet have nymphs that are integridorsal apherederms (Ermilov & Kolesnikov 2012); is the latter plesiomorphic, or does it represent a form of reversal?

9. Nymphal regression of the interlamellar seta—normal-sized in larva and adult, but conspicuously reduced in nymphs—is a common pattern in eupheredermous taxa. It might be explained as avoiding interference between seta and scalps, with the seta ‘released’ from this constraint in the adult. It occurs in eupheredermous gustavioids (Gustaviidae, Tenuialidae, the liacarid genus *Birsteinus*) but is absent from integridorsal gustavioids (Astegistidae) and also some dorsodeficient taxa (most Liacaridae). The interference argument is weakened by the fact that numerous Damaeidae taxa retain scalps also in the adult, but seta *in* reverts to full size anyway. No eupheredermous taxon expresses regression of the seta in the larva, but it occurs in some Peloppiidae (*Ceratoppia*, *Dendrozetes*); interference obviously cannot explain the diminutive setal form in these apheredermous taxa.

10. *Conoppia* species have the facies of Gustavioidea—well rounded, with dark, relatively smooth cuticle and very short notogastral setae—but, surprisingly, the genus has never been included in any constituent family. Prior to Grandjean’s (1954) now-classic ‘Essai’ *Conoppia* was included in a very heterogeneous Eremaeidae (along with *Ceratoppia* but separate from Liacaridae, Tenuialidae, Gustaviidae), while *Cepheus* and relatives usually were included in a broad concept of Carabodidae (e.g. Vitzthum 1940–1943; Radford 1950; Baker & Wharton 1952). With no detailed discussion, Grandjean (1954) transferred *Conoppia* to Cepheidae, presumably based on its eupheredermous nymphs, with large, leaflike gastronotic setae, as well as adult traits such as an imperfect palpal double-horn and a large but divided pedotectum II.

However, Grandjean (1954, p. 434) stated that *Conoppia* was distinguished from other cepheids in the adult by several characters that were instead shared with *Ceratoppia* (Gustavioidea: Peloppiidae); of these, he specified only one: what he called a ‘pretarsus’ (adesmatic distal articulation) on tarsi II-IV. Earlier (Grandjean 1942), he had noted another similarity of these genera: an unusual ontogenetic change in the coupled seta *d* and solenidion of leg tibiae and tarsi. But probably the most striking trait of *Conoppia* shared with *Ceratoppia* (but not with other Cepheidae) is the aggenital minitectum, which he described in detail only much later (Grandjean 1969). *Ceratoppia* is unusual among gustavioids in having pedotectum I divided in the middle by a notch—a typical trait of Cepheidae—and like that of *Conoppia* it bears a sharp spine (Seniczak & Seniczak 2010; Lindo 2011). Such an interesting mix of traits suggests that *Conoppia* may be especially instructive when examining the phylogenetic relationship between Cepheoidea and Gustavioidea, but still we know surprisingly little about the adult and juveniles of this widespread genus.

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