

# Two unusual new species of *Caleremaeus* (Acari: Oribatida) from eastern North America, with redescription of *C. retractus* and reevaluation of the genus

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## Original research

### ABSTRACT

The oribatid mite genus *Caleremaeus* (Caleremaeidae) is widely distributed in the northern hemisphere but has been represented by only three extant and one fossil species. We redescribe the North American *C. retractus* (Banks, 1947) based on adults and nymphs; it is distinguishable from the European type species, *C. monilipes* (Michael, 1882) by its smaller adult size and minor differences in cuticular structure, and by the elongated, tapered form of seta  $h_1$  in nymphs. Two new species are proposed: *C. nasutus* n. sp. from forest soil in Alabama is unique in having adults with a large anterior rostral lobe (juveniles unknown) bearing lamellar setae; the arboreal *C. arboricolus* n. sp. from eastern USA and Canada is unique among described extant species in having adults with femoral sacculles, a transverse ridge bearing lamellar setae and relatively large notogastral setae, and juveniles with a bothridial seta similar to that of the adult. Based on all available data, *Caleremaeus* is redescribed and considered the sole genus in Caleremaeidae. The higher classification of the family is reviewed, and past placement in Ameroidea is rejected in favor of the monofamilial Caleremaeoidea.

**Keywords** Nearctic soil mite; arboreal fauna; Caleremaeidae; eupheredermous juveniles

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‘... *Damaeus monilipes*: the remarkable part of this creature is the form of the legs, particularly the first pair, where the tibia is a globular mass which appears altogether too large for the Arachnid, and gives it the effect of carrying a mace on each side’ (Michael 1882)

## Introduction

*Caleremaeus* Berlese, 1910 (Caleremaeidae) is a distinctive genus of middle-derivative, brachypylous oribatid mites with adult traits that make identification rather easy, even at modest magnification: enlarged first tibiae (see epigram) and a notogaster with a T-shaped pattern of two conspicuous dorsal bulges separated by a foveate sulcus. Only three extant and one fossil-based *Caleremaeus* species have been named, collectively distributed in the western Palaearctic and eastern North America.

The extant type species, *Caleremaeus monilipes* (Michael, 1882), is widely distributed in Europe but it seems absent east of the Ural Mountains (Krivolutsky *et al.* 1995). We

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discount the unexplained listing of this species from tropical Mexico (Vázquez and Prieto Trueba 1999) as an identification error; we have not encountered this species in the western hemisphere, despite much sampling. By contrast, little is known of the other extant species, both of which are similar in many respects to *C. monilipes*. *Caleremaeus divisus* Mihelčič, 1952 is known only from the original collection (arboricolous moss in Tirol, Austria) and the incomplete, poorly illustrated original description. Supposedly it differs from *C. monilipes* in features of prodorsal sculpturing and the size of the notogastral humeral projection, but it has been considered a *species inquirendum* (Schatz and Schuster 2009; Krisper *et al.* 2017). The North American species, *C. retractus* (Banks, 1947) also is known only from its relatively poor original description.

The other named species, *Caleremaeus gleso* Sellnick, 1931, is known only from Baltic amber. The original specimens are not among the material preserved from Sellnick's amber research (Ezhova and Kostyashova 1997) and appear to have been lost. Since its brief description (Sellnick 1931) the species has received no attention in the literature, other than in literature reviews and checklists (e.g. Krivolutsky *et al.* 1990; Labandeira *et al.* 1997).

While *Caleremaeus* seems to have little diversity, there are certainly more than three extant species. For example, based on an integrative analysis including morphometrics and DNA data, Krisper *et al.* (2017 and G. Krisper, personal communication, 2017) indicated that what authors have considered *C. monilipes* is instead a species-complex. This seems consistent with some rather striking differences in size and form, as reported and illustrated in the various published descriptions (*cf.* Michael 1882, 1888; Sellnick 1928; Willmann 1931; Kunst 1971; Bulanova-Zachvatkina 1975; Miko and Travé 1996; Subías and Arillo 2001; Weigmann 2006; Seniczak and Seniczak 2019).

During general studies on Nearctic oribatid mites we have accumulated numerous specimens of the genus. Many had been tentatively identified as *C. retractus*, but others represent three undescribed species, one from western and two from eastern North America, that have features not previously known in the genus. Our main purpose is to describe the latter two new species and to redescribe *C. retractus*, based on studies of adults and nymphs. We precede this with a new diagnosis and description of *Caleremaeus* that incorporates information from all species known to us.

Another goal is to reexamine the family-group classification of *Caleremaeus*. Prior to the proposal of Caleremaeidae by Grandjean (1965b), the principal works on oribatid mites had grouped *Caleremaeus* in Damaeosomidae (in part, modern Oppiidae; Sellnick 1928), Oribatidae (Vitzthum 1931), Eremaeidae (Willmann 1931, Vitzthum 1943, Radford 1950, Baker and Wharton 1952) or Oppiidae (Balogh 1961, 1963). Since 1965, we know of only one different classification: Vázquez and Prieto-Trueba 1999 listed *Caleremaeus* as a genus of Anderemaeidae, but without explanation; it may have been a mistaken inversion, since *Anderemaeus* has been included in Caleremaeidae in some recent literature (see Norton and Ermilov 2019). Both the composition of Caleremaeidae and their position among eupheredermous superfamilies are discussed.

## Materials and methods

**Specimens examined** — Examined *Caleremaeus* specimens and their provenance are detailed below, under the respective species. Adults and juveniles were sorted from stored samples of Berlese-funnel extracts. Juveniles were associated with adults from the same sample using criteria explained by Norton and Ermilov (2014): size and body-leg proportions were consistent with adults; features of the gnathosoma were identical, except for size; a single *Caleremaeus* species was represented by adults in each sample; and adults of no other oribatid mite species with similar size, proportions or gnathosoma were represented. An additional guide was the illustrated habitus of a *C. monilipes* nymph by Michael (1882), whose observations were based on laboratory-reared specimens, and the ontogenetic study of Seniczak and Seniczak (2019).

For comparison and preparation of the generic redescription, we studied European specimens of *C. monilipes* in the first author's collection, including adults from Germany (near Berlin), Spain (Barcelona) and Sweden (Bohuslän), and a single deutonymph accompanying the adults from Sweden. Several specimens of *Hungarobelba visnyai* Balogh, 1938 from Poland were examined for comparison.

Sources and depositories for specimens include the following: *CNC* – the Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada; *MCZ* – the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; *RNC* – the personal collection of Roy A. Norton, Syracuse, New York, USA; *USNM* – the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (currently housed with the U.S. Department of Agriculture collections in Beltsville, Maryland).

**Preparation and documentation** — Most observations and data are from specimens temporarily mounted in cavity slides in a medium of lactic acid diluted with water (2:1; Grandjean 1949). Dissected mouthparts, legs and fragments of body regions requiring close study were permanently mounted in Hoyer's medium for observation with oil-immersion lenses. Compound microscopy employed bright-field, polarized, and Nomarski (DIC) illumination using a Nikon Eclipse E800 compound microscope; line drawings were made with the aid of a drawing tube. Light micrographs were obtained, usually as image stacks, with an AmScope MU800 digital camera mounted on the compound microscope. 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.

Specimens for scanning electron microscopy (SEM Quanta 600 FEI Company TM, Brno, Czech Republic) were removed from alcohol and cleaned by soaking in Terg-a-zyme® solution for 6–12 h, followed by brief (1–2 s) submersion in an ultrasonic bath. Specimens were critical-point dried using the EM CPD300 (Leica Microsystems, Vienna, Austria), mounted on Al-stubs with double sided sticky tape, and gold-coated in a Hummer sputter apparatus.

**Taxonomic context** — The general context is the classification used by Norton and Behan-Pelletier (2009) and Schatz *et al.* (2011), except as noted. A principal digression relates to our use of the superfamily names Eremaeoidea and Zetorchestoidea: these names are fully or partly synonymous according to different concepts in the literature and we use them both below, according to context. Herein, Eremaeoidea is used in the sense of Balogh and Balogh (1992)—including only Eremaeidae and Megeremaecidae—which is how it also seems to have been perceived by Franklin and Woas (1992). Recent classifications (e.g. Schatz *et al.* 2011) have grouped these families with Zetorchestidae under the older synonym Zetorchestoidea, but the molecular study of Lienhard *et al.* (2013) casts doubt on the monophyly of such a taxon. Author and date for species-group taxa are given at the first use of the name; those of supraspecific taxa can be found in Subías (2004).

**Terminology and conventions** — Morphological terminology is mostly that of F. Grandjean (see Travé and Vachon 1975 for references, Norton 1977 for leg setal nomenclature and Travé *et al.* 1996 or Norton and Behan-Pelletier 2009 for overview). Terms are translated from French (Hammen 1980) but Grandjean's original abbreviations and figure notations are often retained. Paired structures are described in the singular unless noted otherwise. Throughout, there are references to numbered 'Remarks on morphology' that conclude the text; each reference is parenthetical, in the form '(R1, R2, etc.).' However, several specific terminology issues are explained here.

*Surface sculpturing.* Impressed surface-sculpture is referred to as *foveate* if circular depressions are relatively large and separated by less than their diameter; *foveolate* sculpture refers to circular depressions that are relatively small and separated by more than their diameter; *scrobiculate* refers to closely-spaced, parallel elliptical depressions (Harris 1979). Projecting

structures are referred to as *knots* if relatively small, simple, dome-shaped, or *tubercles* if relatively large and conspicuous, especially if conical, triangular or tooth-like.

**Lamella and tutorium.** Like Grandjean (1965b), we interpret the two pairs of longitudinal ridge-like structures that are variously developed on the prodorsum of *Caleremaeus* species as homologues of the lamella and tutorium. We refrain from referring to the middle pair of ridges in *Caleremaeus* as ‘costulae’. The latter term appears to have originated in the first of several important synopses by Balogh (1961); he introduced a simplistic dichotomy between a costula (rib-like) and a lamella (blade-like) that still troubles the descriptive literature (Norton and Behan-Pelletier 2009). Clearly, both lamella and tutorium originated as longitudinal ridges, then hypertrophied to flattened, projecting blades in derived groups. The plesiomorphic form is retained in *Caleremaeus* and Megeremaeidae (see R1). When applied to the prodorsum, we believe the term costula is best restricted to describing simple, secondary supporting ridges in taxa that plesiomorphically lack lamellae, as in Oppioidea, for example.

**Measurements and counts** — Body length was measured in dorsoventral aspect, from the tip of the rostrum to the posterior edge of the hysterosoma; width refers to the maximum hysterosomal width in dorsal aspect. Measurements of specific structures or distances are given either as a single number meant to be representative of an average-sized individual, or an estimated range taken from a small sample of several individuals; setae were measured when oriented in a single observational plane (e.g., perpendicular to the surface). Setal and solenidial formulas represent counts per segment for appendages (from leg I to IV; famulus included for tarsus I); epimeral setation is given as number of pairs per podosomal segment (I–IV).

**Abbreviations and notations** — *Prodorsum*. Setae: *ro*, *le*, *in*, *bs*, *ex* – rostral, lamellar, interlamellar, bothridial and exobothridial setae, respectively. Other structures: *apl* – anterior prodorsal lobe; *bo* – bothridium; *cu* – lamellar cusp; *dt* – dorsosejugal tubercle; *eA* – prodorsal enantiophysis; *exv* – alveolar vestige of second exobothridial seta; *lam* – lamella; *mu.gn* – gnathosomal muscles; *not* – anterolateral bothridial notch; *PD* – prodorsum; *rb* – rostral bulge; *rm* – rostral margin; *rph* – rostrophragma; *sej* – dorsosejugal groove; *smc* – submarginal crest; *tu* – tutorium.

*Notogaster; gastronomum*. Setae: *c* (or *c-row*, *c*<sub>1</sub>, *c*<sub>2</sub>, *c*<sub>3</sub> in juveniles); *da*, *dm*, *dp* (centrodorsal setae); *la*, *lm*, *lp* (laterodorsal setae); *h-row* (*h*<sub>1</sub>, *h*<sub>2</sub>, *h*<sub>3</sub>); *p-row* (*p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub>). Other structures: *ab* – transverse anterior bulge; *cgs* – circumgastric scissure; *eH* – humeral enantiophysis; *fov* – foveae of transverse sulcus; *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; *k* – exuvial attachment cornicle of nymph; *kp* – coaptive pocket in larval exuvium to receive protonymph cornicle; *NG* – notogaster; *pb* – longitudinal posterior bulge of adult; *pyb* – pygidial bulge of nymphs; *ts* – transverse sulcus.

*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* – sternal border; *dis* – discidium; *dir* – discidial ridge; *e4* – aggenital enantiophysis, across groove running along *bo.4*; *eL*, *eS* – enantiophyses across sejugal groove (lateral and parastigmatic, respectively); *mf* – medial fossa of coxisternum – *PdI* – pedotectum I.

*Anogenital region*. Setae: *ag* – aggenital seta; *ad*<sub>1</sub>, *ad*<sub>2</sub>, *ad*<sub>3</sub> – adanal setae; *an*<sub>1</sub>, *an*<sub>2</sub> – anal setae. Other 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; *spr* – spermatopositor.

*Gnathosoma*. Setae: *a*, *m* – anterior, middle seta of gena; *h* – hypostomal seta of mentum; *v*, *l*, *d*, *cm*, *acm*, *ul*, *sul*, *vt*, *lt*, *sup*, *inf* – palp setae; *ω* – palp tarsal solenidion; *cha*, *chb* – cheliceral setae. Other structures: *br* – rutellar brush; *Ch* – chelicera; *ch.fr* – cheliceral frame; *ru* – rutellum; *sp* – spicule of chelicera; *Tg* – Trägårdh’s organ.

*Legs*. Setiform organs: *σ*, *φ*, *ω* – solenidia of genu, tibia and tarsus, respectively (with numeric subscript if relevant); *e* – famulus of tarsus I; *d*, *l*, *v* – dorsal, lateral, ventral setae

of whorl, respectively; *ev*, *bv* – basal trochanteral setae; *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl* – tarsal setae. Other structures: *p.a* – porose area; *prt* – protectum; *ret* – retroprotectum; *sac* – sacculus. Parentheses around leg setal notations denote the two members of a pseudosymmetrical pair on a given leg segment, rather than a true bilateral pair (unless otherwise indicated); when denoted separately, prime and second (', ') distinguish the seta on the anterior and posterior face, respectively.

In locality data, counties within USA states and Canadian provinces are indicated by *Co*.

## Redescription of *Caleremaeus*

Berlese (1910) provided no diagnosis when *Caleremaeus* was proposed, but simply referred to the type species, *C. monilipes*. In early synopses (e.g. Sellnick 1928, Willmann 1931), genus-level characters were not distinguished. Nor did Grandjean (1965b) distinguish generic traits when he gave an extended diagnosis for the newly proposed Caleremaeidae, based only on *C. monilipes*. Generic characters seem not to have been isolated until Bulanova-Zachvatkina (1975) listed a single generic trait: the unique notogastral topography. Norton (1978) proposed including *Veloppia* as a second genus of Caleremaeidae and considered Grandjean's (1965b) diagnosis of this family as a diagnosis of *Caleremaeus*. Subsequently Subías and Arillo (2001) and Weigmann (2006) distinguished Caleremaeidae and *Caleremaeus* with brief diagnoses. Below, we use the latter three works and our own observations to propose a new diagnosis and expanded description of *Caleremaeus*. Parts relating to adults are based on all species known to us, both described and undescribed; those relating to nymphs are based on only *C. monilipes*, *C. retractus* (*sensu stricto*; additionally the 'retractus' group from New York) and *C. arboricolus*; those relating to the larva are from *C. arboricolus* and the 'retractus' group from New York, as well as the larval exuvial scalp of *C. retractus*, and literature data on *C. monilipes*. For *C. monilipes*, published information on adults is from references given above (Introduction), while that on juveniles is mainly from Michael (1882), Grandjean (1965b) and Seniczak and Seniczak (2019; but see R12).

## *Caleremaeus* Berlese, 1910

Type species: *Damaeus monilipes* Michael, 1882 (p. 16). The original combination often has been given in the literature as *Notaspis monilipes*, but this was a later recombination by Michael (1888).

**Etymology** — Berlese (1910) did not indicate the etymology of *Caleremaeus*, but the stem *eremaios* is Greek (meaning solitary) and is the basis for the older genus name *Eremaeus* Koch, 1835. The prefix 'cal', if also based on Greek, would be from *kalos*, meaning beautiful. While less likely, Berlese might have mixed languages: if 'cal' were Latin-based it could relate to the habitat of the type species *C. monilipes*, which Michael (1882) collected from rotten wood (Latin: *cala*, piece of wood).

**Diagnosis** — Brachypylna with small to medium-sized adults (length 306–475 µm), overall shape elongate-pyriform in dorsoventral view. Integument with enveloping cerotegument, usually with dense, dome- to mushroom-shaped excrescences; sclerotized procuticle partly foveate to foveolate. Prodorsum with or without paired, ridge-like lamella and tutorium; with or without prodorsal enantiophysis. Rostrum with strongly developed submarginal crest. Bothridial seta with basal stalk and flattened, expanded head. Dorso- and pleurophragmata absent. Notogaster without porose organs; anterior margin nearly straight, with small dentate tubercles or knots; with distinct humeral process opposing tubercle(s) on posterior wall of bothridium to form humeral enantiophysis; with strong topography consisting of relatively flat lateral region and two strong bulges (transverse anterior bulge and longitudinal posterior bulge) separated by foveate transverse sulcus; with 10 pairs of setae, marginal to submarginal. Pedotectum I present, II absent; propodolateral apophysis absent; discoidal ridge usually present, distinct discidium present or absent; circumpedal carina absent; lateral, parastigmatic



and aggenital enantiophyses present; coxisternum with distinct medial fossa between setae *4a*. Subcapitular rutellum atelobasic. Legs relatively short, tibiae I, II unusually large, with narrow basal stalk and swollen distal bulb, I with dorsodistal process; pretarsi monodactylous; seta *d* absent from genua I–III and all tibiae; iter al setal pair present on tarsi I–II, only *it''* on III, none on IV. Nymphs plicate, eupheredermous, gastrontum with papilliform attachment cornicle; setal pair *h*<sub>1</sub> adjacent on extension of pygidial sclerite; paraprocts atrichous in larva, proto- and deutonymph.

## Adult

**Facies, cuticle** — Small to medium-sized (length 306–475 µm) Brachypylina, with overall elongate-pyriform shape in dorsoventral view (Figs 1, 8, 13). Integument with enveloping cerotegument conspicuously covering all exposed surfaces, mostly with dome- to mushroom-shaped excrescences of various sizes and densities (Figs 2C–D, 10B–C); prodorsal and notogastral setae usually with some type of isotropic coating or basal cerotegument nodule (Figs. 9J–K, 16A–D). Sclerotized procuticle medium-brown when mature, becoming paler, yellowish with alcohol preservation; partly foveate to foveolate. Usually with little or no adhering debris; exuvial scalps of juveniles not retained on notogaster.

**Prodorsum** (Figs 1, 2, 8, 9, 13–15, 18) — With or without ridge-like lamella and tutorium (R1); with or without prodorsal enantiophysis (*eA*); with one (usually) to three pairs of small dorsosejugal tubercles (*dt*) anterior to sejugal groove, approximately aligned with seta *in*. Rostrum entire, broadly rounded to subtriangular in dorsal view. Rostral bulge (*rb*) conspicuous (e.g., Figs 1B, 2I, M, 9H) or not (Fig. 15E–F); ventral face of bulge and rostraphragma with (Figs 2K–M; 15F–H) or without embossed pattern (R2). Rostrum with shelf-like submarginal crest (Figs 2L, 3G, 15E, 18A; *smc*) extending from near acetabulum I to insertion of seta *ro* or beyond, forming most of lateral contour in dorsoventral view; without genal tooth or incision. Without dorsophragma or pleurophragma, gnathosomal muscles inserting directly on prodorsal cuticle (*mu.gn*; Fig. 9H); dorsal cheliceral retractor muscle attachments marked by paired longitudinal row of internal sigillae in oval to quadrilateral region between bothridia, usually with posterolateral corners of region marked by tubercle pair *dt* (Fig. 1A) or most medial tubercle if several present (Fig. 9E). Bothridium strongly projecting above surface, with well-sclerotized wall, broad anterolateral notch (Figs 9D, 14E; *not*), and one or more blunt teeth or tubercles on posterior wall; with two chambers—wide outer chamber smooth-walled in distal half, with several well-spaced circular ridges in proximal half; narrow inner chamber with dense fine striations, those of first part circular but abruptly changing to longitudinal in deeper, innermost part (Fig. 2F); without tracheal organ. Bothridial seta directed dorsolaterally, with basal stalk and flattened, expanded head, each occupying about half setal length; stalk smooth, head densely squamose with subtriangular, distally blunt scales, or with more vague ridges and elevations (Figs 2E, 9D–F, 14E). Seta *in* relatively small, at most about half mutual distance of pair; seta *le* inserted far distally, near or beyond level of *ro*, on cusp or other form of projection. Vestige of second bothridial seta (Figs 9I, 15E; *exv*) present (R3).

**Notogaster** — Without octotaxic system of porose organs. Fully fused to prodorsum across distinct dorsosejugal groove (Fig. 2M); circumgastric scissure broad posteriorly, but gradually narrowing anteriorly to efface in humeral region. Length about 1.2–1.3 times width, varying slightly with hysterosomal distension: slightly angular posteriorly when contracted; nearly truncate anteriorly with several to dozen knots or tubercles along margin (Fig. 3A–C). Humeral process (*hpr*) conspicuous, triangular in dorsal view, opposing bothridial tubercle(s) to form humeral enantiophysis (*eH*) across sejugal groove; not extended posteriorly as longitudinal carina ('crista'). Without marginal tectum. With strong topographic relief (Figs 2A–B, M; 14A), comprising relatively flat marginal zone and two tandem medial bulges separated by distinct transverse sulcus; anterior bulge (*ab*) transverse, between notogastral margin and sulcus, with setae of pair *c* on either side; larger posterior bulge (*pb*) longitudinal, tapering to nearly reach posterior margin. Bulges smooth (but see comments about *C. gleso* below, under

*C. arboricolus* n. sp.), transverse sulcus with irregular row or narrow band of distinct foveae. Notogastral setae small to medium-sized; 10 pairs, six (*c*, *la*, *lm*, *lp*, *h*<sub>3</sub>, *h*<sub>2</sub>) forming single file in submarginal zone (Figs 1A–B, 8A, 13A); one pair (*h*<sub>1</sub>) inserting close together at posterior end of central bulge; three pairs (*p*<sub>1</sub>, *p*<sub>2</sub>, *p*<sub>3</sub>) inserting along posterior margin. With typical five pairs of lyrifissures; *ia* lateral to seta *c*, *im* near seta *lm*, obliquely oriented; *ip* lateral to central bulge, between setae *p*<sub>1</sub> and *h*<sub>2</sub> (Fig. 9M); *ih* and *ips* anterior to seta *p*<sub>3</sub>, positioned in tandem along posterolateral margin at approximate level of setae *lp*, *h*<sub>3</sub>, respectively (Fig. 1B). Opisthonotal gland opening (*gla*) inconspicuous, posterior to *im*.

**Coxisternum and lateral podosoma** (Figs 1B, 8B, 13B) — Coxisternum with well-defined transverse grooves associated with internally-marked epimeral borders (Fig. 14B). Muscle sigilla of coxisternum strongly developed, leaving most borders well defined in transmitted light (Fig. 3F): border *bo.4* chevron-shaped, i.e. oblique on each side of midline; sternal border (*bo.st*) wide in epimere I, narrow in II and III. Apodemes 1–3 of typical size and form (Fig. 10E); without apodeme 4. Epimere IV with distinctly impressed, unpaired medial fossa (Fig. 3F; *mf*). Ventral and lateral podosoma with multiple tubercles: sejugal groove spanned by lateral enantiophysis (*eL*) dorsal to leg insertions and parastigmatic enantiophysis (*eS*) below insertions (R4); aggenital enantiophysis (*e4*) present, spanning groove along *bo.4*. Epimeres III, IV with (Fig. 3F) or without (Fig. 8B) well-defined ridges marking lateral depressions coapted to leg trochanters. Epimeral setation 3-1-3-3; seta *3c* inserted on posterior tubercle of *eS*, *4b* on anterior tubercle of *e4* (R5). Pedotectum I small, with normal, scale-like form (R12); pedotectum II absent. With or without discrete discidium (*dis*), usually with oblique discoidal ridge (*dir*) between acetabula III, IV running toward sejugal region (Figs 3F, 9I, 16E–F). Circumpedal carina absent. Tracheal system normal: trachea 1 and sejugal trachea bifurcated, trachea 3 simple.

**Anogenital region** (Figs 1B, 8B, 13B) — Curvature of ventral plate interrupted posteriorly by vague, rounded process, usually accommodated by vague notch in notogastral margin. Genital aperture subrectangular, well separated from anal aperture; latter wider posteriorly, pyriform to subpentagonal. Genital aperture of male proportionally smaller than that of female (relative to anal aperture: length 0.7, width 0.8 in male, 0.9, 1.0 in female). With 4–6 pairs of genital setae in single file near medial margin, distance between setae increasing posteriorly; single aggenital seta near posterolateral corner of each genital plate; two pairs of anal setae, near medial margin of plate; three pairs of adanal setae, *ad*<sub>1</sub>, *ad*<sub>2</sub> posterior to anal plate, *ad*<sub>3</sub> at about its mid-length. Preanal organ (*pr.o*; R6) with basal plate subtriangular, exposed between closed anal plates (Figs 8B, 14B); internalized apophysis (Fig. 3F, H, I) short, tubular to slightly expanding or tapering distally (i.e. internally). Lyrifissure *ian* absent; *iad* close to anterolateral corner of anal plate, parallel to margin (Fig. 3E). Posteromedial corner of each anal plate with long, narrow strut (Fig. 3J, *po.st*) extending internally to serve as attachment for postanal suspensor muscle (*mu.ps*). Ovipositor (Fig. 10F–H) of normal form and moderate size, length similar to body height when fully extended; three distal lobes long, narrow, occupying about half length beyond fold; with usual nine pairs of setae: three pairs of acute to acuminate coronal setae (ca. 10–12 µm), and four setae on each lobe; distal setae ( $\psi_1$ ,  $\tau_1$ ) attenuate (ca. 20–30 µm), more proximal setae ( $\psi_2$ ,  $\tau_{2-4}$ ) acuminate (ca. 10–15 µm). Spermatopositor (Fig. 10D; *spr*) short, with typical form for Brachypylina; with seven pairs of acuminate to attenuate setae (ca. 6–10 µm) having typical distribution including pairs  $\psi_1$ ,  $\psi_2$  being closely adjacent posteriorly; mid-level seta (probably  $\tau_1$ ) with alveolus distinctly larger than others (Fig. 10D, insert). Genital papillae with normal form, homogeneous.

**Gnathosoma** — Subcapitulum (Fig. 1C) diarthric, without axillary saccule at base of palp; rutellum (*ru*) atelobasic, with broad ventral lobe, two dorsal teeth and rutellar brush (*br*); setation normal, with single pair of hypostomal (*h*), two pairs of genal setae (*a*, *m*) and two pairs of inconspicuous adoral setae on narrow lateral lips; postpalpal seta baculiform, slightly curved. Palp (Fig. 1D) five-segmented with elongated cylindrical tarsus, about same length as genu and tibia combined; chaetome (trochanter to tarsus) 0-2-1-3-9(1), with tarsal setae relatively long, except *acm*, *su* and pair (*ul*) short, thick, eupathidial; solenidion  $\omega$  independent, baculiform,

nearly prone (R12). Chelicera (Figs 5E, 17D) without specialization: chelate dentate, with chela occupying about quarter total length; with few or no spicules (*sp*) on main body; with usual dorsal (*cha*) and abaxial (*chb*) setae and tapering Trägårdh's organ (*Tr*) on adaxial face.

**Legs** (Figs 4-5, 11, 17) — Relatively short, about 0.4–0.5 times body length; legs II, III slightly shorter than I, IV. Articulations simple, without tecta except for partial retrotectum at base of femora I, II (Fig. 11B–C; *ret*) and trochanters III, IV, and partial ventrodistal protectum on trochanters III, IV (Fig. 5B–C; *prt*). Trochanters III, IV short, broad, somewhat asymmetrically mushroom shaped, short stalk hidden in lateral view; with porose area on adaxial face. Femora without ventral carinae, bulbous middle region gradually tapering distally, variously narrowed proximally to form short stalk; bulb with porose area or sacculle. Genua with proximal half slightly narrowed, all similar in length. Tibiae I, II conspicuously bulbous distally, abruptly narrowed to short proximal stalk attached dorsally; tibia I distinctly deeper than tarsus I in lateral view, with broad dorsodistal apophysis bearing solenidia; tibia II with depth similar to tarsus II or only slightly greater; tibiae III, IV gradually tapered proximally. Tarsus I abruptly tapered distally at midlength, IV tapered gradually, II, III intermediate. Tibiae, tarsi without porose organ. Pretarsi monodactylous. Leg chaetome consistent among species (R7, R12), with salient features as follows. Solenidial counts (legs I–IV, genu, tibia, tarsus): 1-1-1-0, 2-1-1-1, 2-1-0-0; genual solenidia and tibial solenidion  $\phi_2$  short, baculiform,  $\phi_1$  flagellate ('tactile'), tarsal solenidia tapering but blunt ('ceratiform'). Setal counts (legs I–IV, trochanter to tarsus, famulus included.): 1-1-2-1, 4-4-3-2, 3-2-1-2, 4-4-3-3, 20-16-14-11; homologies in Table 1. Seta *l''* of femora I and II very low on adaxial face. Seta *d* absent from genua I–III and from all tibiae. Tarsus I with proral (*p*) and subunguinal, *s*, setae eupathidial; fastigial setae differently shaped: *ft'* nearly straight or slightly and gradually curved; *ft''* smaller, bent at oblique angle or distally subflagellate (Figs 4A, 11E, 17C). Iteral pair present on tarsi I–II, only *it''* present on III, no iterate seta on IV; proximal accessory setae present on tarsi I (*l''*, *v'*) and II (*l''*); seta *a'* absent from tarsus IV. Famulus, *e*, isodiametric, baculiform.

## Juveniles

Figures 6–7, 12

**Facies, cuticle** — Preserved specimens colorless to light tan. Unsclerotized regions of gastronomic cuticle plicate, except smooth underneath exuvial scalps of nymphs; plicae generally vertical laterally, vaguely circumferential around opisthonotal gland opening and paraprocts. Hysterosomal line of dehiscence not evident. Cerotegument distinct, enveloping, with short excrescences of various sizes generally similar to those of adults or merged into irregular masses.

**Prodorsum** — With several ridges or folds, longitudinal laterally and transverse medially; one of latter bearing setal pair *le*. Rostrum usually truncate anteriorly (Fig. 7F). With normal setation, all but bothridial seta (*bs*) short to medium length. Bothridium and *bs* fully developed in all instars; bothridium projecting, cylindrical to slightly funnel-shaped, thin-walled, without tracheal organ; *bs* similar to that of adult, or narrower and proportionally longer.

**Gastronotum** — Larva dorsally with strong topography comprising elevated anterior rim, three distinct tandem medial bulges and low, slightly bifid pygidial bulge (Figs 6A–B; 12A); with normal 12 pairs of setae: setae of pairs *da*, *dm*, *dp* adjacent on respective medial bulges, pair *h<sub>1</sub>* on pygidial bulge. Gastronotum of nymphs with margins not covered by scalps, forming somewhat flattened rim, protruding most distinctly in anterior region (Figs 6B, 12C); without medial bulges; pygidial sclerite present, with bulge (Figs 6B, 7E; *pyb*) anteriorly and separate posterior lobe made terminally bifid by adjacent tubercles bearing setae *h<sub>1</sub>*. Nymphs with typical eupherederm gastronomic setation of 12 pairs, having lost dorsocentral setae (*da*, *dm*, *dp*) while gaining pseudanal setae *p<sub>1</sub>*, *p<sub>2</sub>*, *p<sub>3</sub>*. Pair *h<sub>1</sub>* conspicuously enlarged in nymphs (R8). Exuvial scalps of previous instars tightly attached (R9) by means of small, papilliform, lightly sclerotized, centrally located cornicle (Fig. 7G; *k*); protonymphal cornicle inserting in coapted pocket (Figs 6A, 12A, F; *kp*) of larval scalp, under front slope of medial bulge bearing seta *dp*;



cornicle of other nymphs nesting into previous respective cornicle (Fig. 12F). Scalps strongly reticulate or not, with setation typical of eupheredermis: scalp of larva with  $c_1$ ,  $c_2$ ,  $da$ ,  $dm$ ,  $dp$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_1$ ; of proto- and deutonymph with  $c_1$ ,  $c_2$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_{1-3}$ ,  $p_1$ .

**Coxisternum** — Without brachytracheae or other representation of apodemato-acetabular tracheal system. With lightly sclerotized demi-epimeres, separated by broad band of soft cuticle having distinct to vague longitudinal plicae and rows of cerotegument granules (Fig. 12G). Claparède's organ of larva typical, emerging through slit-like opening, with seta  $lc$  formed as protective scale;  $lc$  normal in nymphs. Epimeral setation (larva to tritonymph; no change in adult): 3-1-2, 3-1-2-1, 3-1-2-2, 3-1-3-3; setae  $1a$ ,  $2a$ ,  $3a$ ,  $4a$  all on soft medial cuticle, others on epimeral sclerite; seta  $4a$  delayed to deutonymph, in normal manner (R5).

**Anogenital region** — Genital setation varies with species: protonymph with one pair, deutonymph with two or three, tritonymph with four or five. Aggenital seta first formed in deutonymph. Paraprocts atrichous in larva, proto- and deutonymph: setal rows  $p$ ,  $ad$ ,  $an$  first formed in proto-, deuto- and tritonymph, respectively. Ontogeny of cupules normal, cupule added with respective setal row;  $ian$  formed in tritonymph but half size of others (about diameter of setal alveolus), lost in adult.

**Gnathosoma** — Similar to that of adult, except for weaker sclerotization of subcapitulum making labiogenal articulation indistinct. Palp femoral seta  $inf$  first formed in protonymph.

**Legs** — With size proportions as in adult but most segments somewhat more tubular; tibia I with strong, cylindrical dorsodistal apophysis. Ontogeny of leg chaetome given in Table 1, with salient features as follows. Seta  $d$  present on all genua and tibiae, coupled in same alveolus with respective solenidion on all but genu IV; except on tibia I, seta and solenidion very short, equal in length or  $d$  very slightly longer (Figs 7N, 12J, 18D), solenidion difficult to see in some orientations. Seta  $d$  and  $\phi_1$  of tibia I both long, inserting on dorsodistal apophysis;  $\phi_1$  flagellate,  $d$  2/3 to 3/4 as long, with barbs or cilia having clear, velum-like coating of various distinctness (Figs 7L, 12I). Protonymphal leg IV setation 0-0-0-0-7, with typical tarsal complement of ( $p$ ), ( $u$ ), ( $pv$ ),  $ft''$ . On tarsus I, setae ( $p$ ) appear to be eupathidial from larva (uncertain in early instars), but  $s$  formed as normal seta, becoming eupathidial only in adult;  $s$  located proximal to pair ( $a$ ) in nymphs, but displaced distal to them when eupathidial, as usual. Ontogeny of iter setae complex: pair forms in tritonymph on tarsus I and in adult on II, with solitary  $it''$  tritonymphal on III (R7, R12).

## Caleremaeus retractus (Banks, 1947)

*Carabodoides retracta* Banks, 1947; p. 123. [Nomen nudum in Pearse 1946, p. 148]

*Caleremaeus retractus* (Banks, 1947); Marshall *et al.* 1987, p. 225

**Etymology** — Banks (1947) presented no explanation of the species epithet, and there are no hints in his description. Marshall *et al.* (1987) treated 'retracta' as an adjective and emended the name accordingly.

**Type locality** — The type specimens (below) derived from a study of soil animals of the Duke Forest (Durham Co., North Carolina) by Pearse (1946). The Duke Forest is somewhat fragmented and, since four different locations and habitats were studied, the exact origin of the types is unknown.

**Type material** — Banks (1947) reported two specimens in the type series. The holotype (original designation as 'type') is a slide-mounted specimen in the arachnid collection of the MCZ. The label bears the following data in Banks' handwriting: 'Duke Forest N. Car.; #475; Pearse; *Carabodoides retracta* Bks; 3018 type.' The mite is broken by crushing but has an estimated total length of about 320  $\mu$ m. The second specimen is a paratype in the mite collection of the USNM. It is a gravid female, also broken, with an estimated original length of 340  $\mu$ m and with the following label data in Banks' handwriting: 'Duke Forest, N.C. 238, Pearse, Jan. *Carabodoides retracta* Bks. Paratype.' The measurements contrast significantly with the '.55 to .6 mm' reported by Banks (1947).

**Other material examined** — Approximately 40 topotypic adults (24 females, 10 males, several undetermined) with the following data: North Carolina, Durham Co., Duke Forest (35° 58.9' N, 78° 56.6' W), 4-V-1979, L.J. Metz, col., from loblolly pine (*Pinus taeda* Linn.) and hardwood forest litter. Also available for study were 30 nymphs and more than 300 adults from a nearby location that we consider near-topotypes: North Carolina, Durham Co., G.W. Hill Demonstration Forest (36°12.1' N, 78°52.9' W), 1973 (various dates), L.J. Metz col., from loblolly pine forest litter and upper soil.

**Diagnosis** — *Caleremaeus* species with adults having total length 306–340 µm. Prodorsum with well-developed distal cusps. Each cusp longer than wide, pair usually close together and basally-connected; tip pointed, oblique beyond insertion of seta *le*. Lamella well defined proximally, with variable development more anteriorly; turtorium well developed, enantiophysis *eA* present. Usually with single small pair of dorsosejugal tubercles. Notogastral setae small (most 11–14 µm), inconspicuously barbed beyond basal cerotegument nodule. Epimeral groove

**Table 1** Ontogeny of leg setae and solenidia in *Caleremaeus* species<sup>1, 2</sup>.

	Trochanter	Femur	Genu	Tibia	Tarsus
<b>Leg I</b>					
Larva	-	<i>d</i> , <i>bv</i> "	( <i>l</i> ), <u><i>dσ</i></u>	( <i>l</i> ), <i>v</i> ', <u><i>dφ</i></u> ⊥	( <i>ft</i> ), ( <i>tc</i> ), ( <i>p</i> ), ( <i>u</i> ), ( <i>a</i> ), <i>s</i> , ( <i>pv</i> ), ( <i>pl</i> ), <i>e</i> , <i>ω</i> <sub>1</sub>
Protonymph	-	-	-	-	<i>ω</i> <sub>2</sub>
Deutonymph	-	( <i>l</i> )	-	<i>φ</i> <sub>2</sub>	-
Tritonymph	<i>v</i> '	-	<i>v</i> '	<i>v</i> "	( <i>it</i> )
Adult	-	-	[ <i>d</i> lost]	[ <i>d</i> lost]	<i>v</i> ', <i>l</i> "
<b>Leg II</b>					
Larva	-	<i>d</i> , <i>bv</i> "	( <i>l</i> ), <u><i>dσ</i></u>	<i>l</i> ', <i>v</i> ', <u><i>dφ</i></u>	( <i>ft</i> ), ( <i>tc</i> ), ( <i>p</i> ), ( <i>u</i> ), ( <i>a</i> ), <i>s</i> , ( <i>pv</i> ), <i>ω</i>
Protonymph	-	-	-	-	-
Deutonymph	-	( <i>l</i> )	-	<i>l</i> "	-
Tritonymph	<i>v</i> '	-	-	<i>v</i> "	-
Adult	-	-	[ <i>d</i> lost]	[ <i>d</i> lost]	<i>l</i> ", ( <i>it</i> )
<b>Leg III</b>					
Larva	-	<i>d</i> , <i>ev</i> '	<i>l</i> ', <u><i>dσ</i></u>	<i>v</i> ', <u><i>dφ</i></u>	( <i>ft</i> ), ( <i>tc</i> ), ( <i>p</i> ), ( <i>u</i> ), ( <i>a</i> ), <i>s</i> , ( <i>pv</i> )
Protonymph	-	-	-	-	-
Deutonymph	<i>v</i> ', <i>l</i> '	<i>l</i> '	-	<i>l</i> ' <sup>3</sup>	-
Tritonymph	-	-	-	<i>l</i> ' <sup>3</sup> , <i>v</i> "	-
Adult	-	-	[ <i>d</i> lost]	[ <i>d</i> lost]	<i>it</i> "
<b>Leg IV</b>					
Protonymph	-	-	-	-	<i>ft</i> ", ( <i>p</i> ), ( <i>u</i> ), ( <i>pv</i> )
Deutonymph	-	<i>d</i> , <i>ev</i> '	<i>d</i> , <i>l</i> '	<i>v</i> ', <u><i>dφ</i></u>	( <i>tc</i> ), <i>a</i> ", <i>s</i>
Tritonymph	<i>v</i> '	-	-	<i>l</i> ', <i>v</i> "	-
Adult	-	-	-	[ <i>d</i> lost]	-

<sup>1</sup> Adult data are based on all studied species and populations, including *C. monilipes* from Sweden, Germany and Spain. Ontogenetic data are from *C. arboricolus* n. sp. (topotypic population), *C. retractus* (near-topotypic population), a species in the 'retractus group' (New York population; see text), and *C. monilipes* (Norwegian population; see Seniczak and Seniczak 2019 and corrections in R12); from each population all instars were studied, except no larva was available from the *C. retractus* near-topotypic population.

<sup>2</sup> Setae (Roman letters) and solenidia (*σ*, *φ*, *ω*) 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 solenidium is coupled to seta *d*, in same alveolus.

<sup>3</sup> Seta *l*' of tibia III is invariably deutonymphal in *C. arboricolus*, *C. retractus* and the 'retractus group' from New York. By contrast, in *C. monilipes* *l*' first forms along with *v*" in the tritonymph, according to Seniczak and Seniczak (2019); appropriately, *l*' is absent from both tibiae III of our single deutonymph from Sweden.

2 usually without bordering tubercles or knots; ventrosejugal groove with only enantiophysis *eS*. Female with five pairs of genital setae, male with 4–6. Leg femora each with porose area. *Nymphs* with bothridial seta elongate, nearly as long as prodorsum, squamose in distal half but without distinct head; gastronomic seta *h*<sub>1</sub> with length similar to that of *bs*, narrow, barbed throughout, pair closely parallel and distinctly bowed; exuvial scalps appearing reticulated in transmitted light.

## Adult

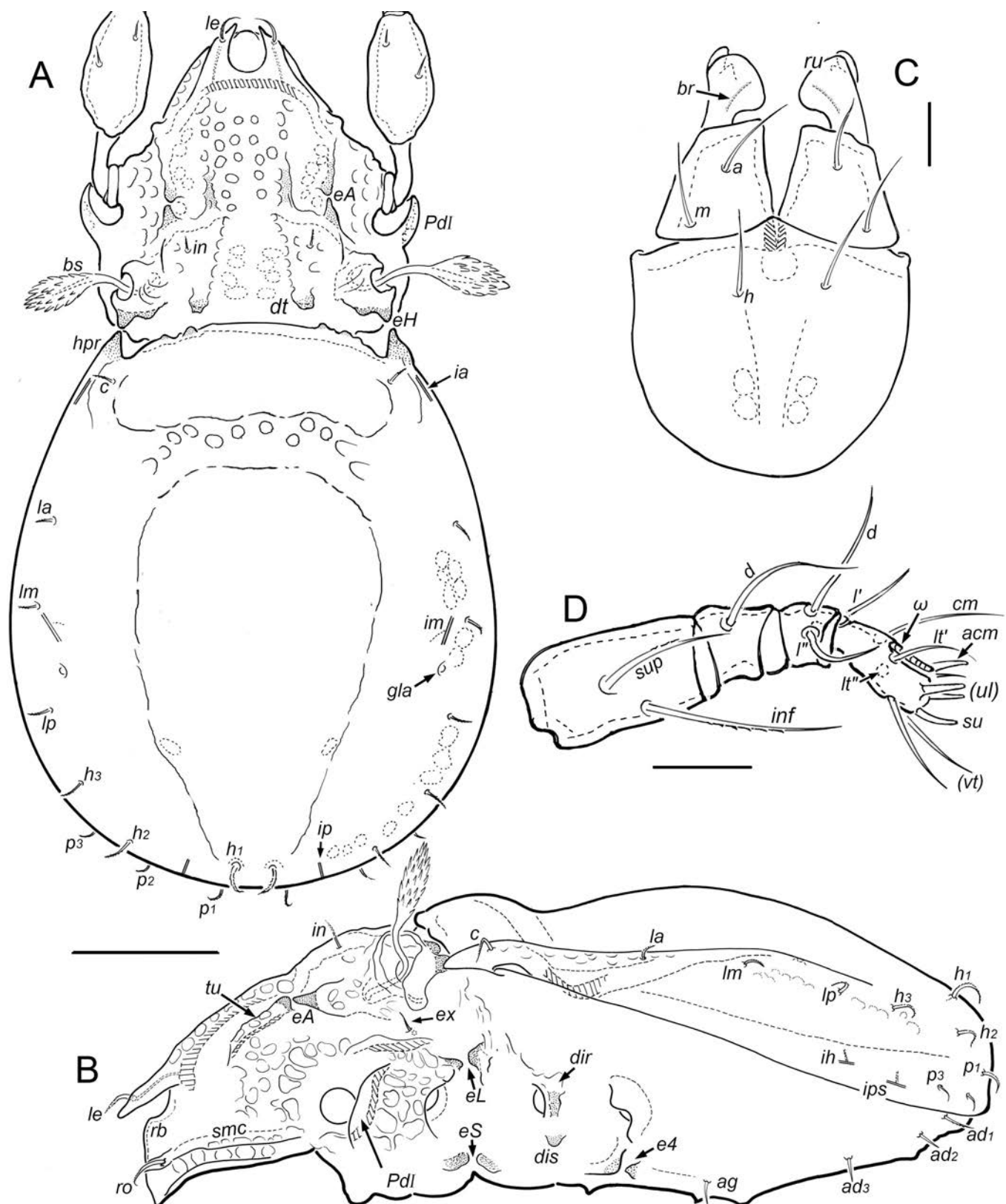
Figures 1–5

**Dimensions** — Total length of 20 measured topotypes 306–340 µm (mean 324); maximum width 172–203 µm (mean 189). Female (n = 10) length 323–340 µm (mean 333), maximum width 191–203 µm (mean 198); male (n = 10) length 306–328 µm (mean 313), width 172–191 µm (mean 179).

**Integument, setae** — Cerotegument excrescences mostly in form of near-spherical nodule with short, thick stalk (like unopened ‘button’ mushroom). Nodules relatively uniform in size according to location: largest on mid-notogaster, 4–6 µm diameter (Fig. 2A, C, D), often well-spaced; slightly smaller (~3 µm) anteriorly and laterally on notogaster, densely packed, usually touching; smallest (~1–2 µm) on prodorsum, venter and legs; basal cerotegument layer on venter microgranular between nodules. Most dorsal setae (except *bs*) short, inconspicuous, acuminate; basal third hyaline, smooth, penetrating distinct, usually shaded, cerotegument nodule; distal region pigmented, with minute barbs on outer curvature (e.g. Figs 2G, 3D). Most ventral setae simple, nearly straight, without pigment or distinct cerotegument nodule.

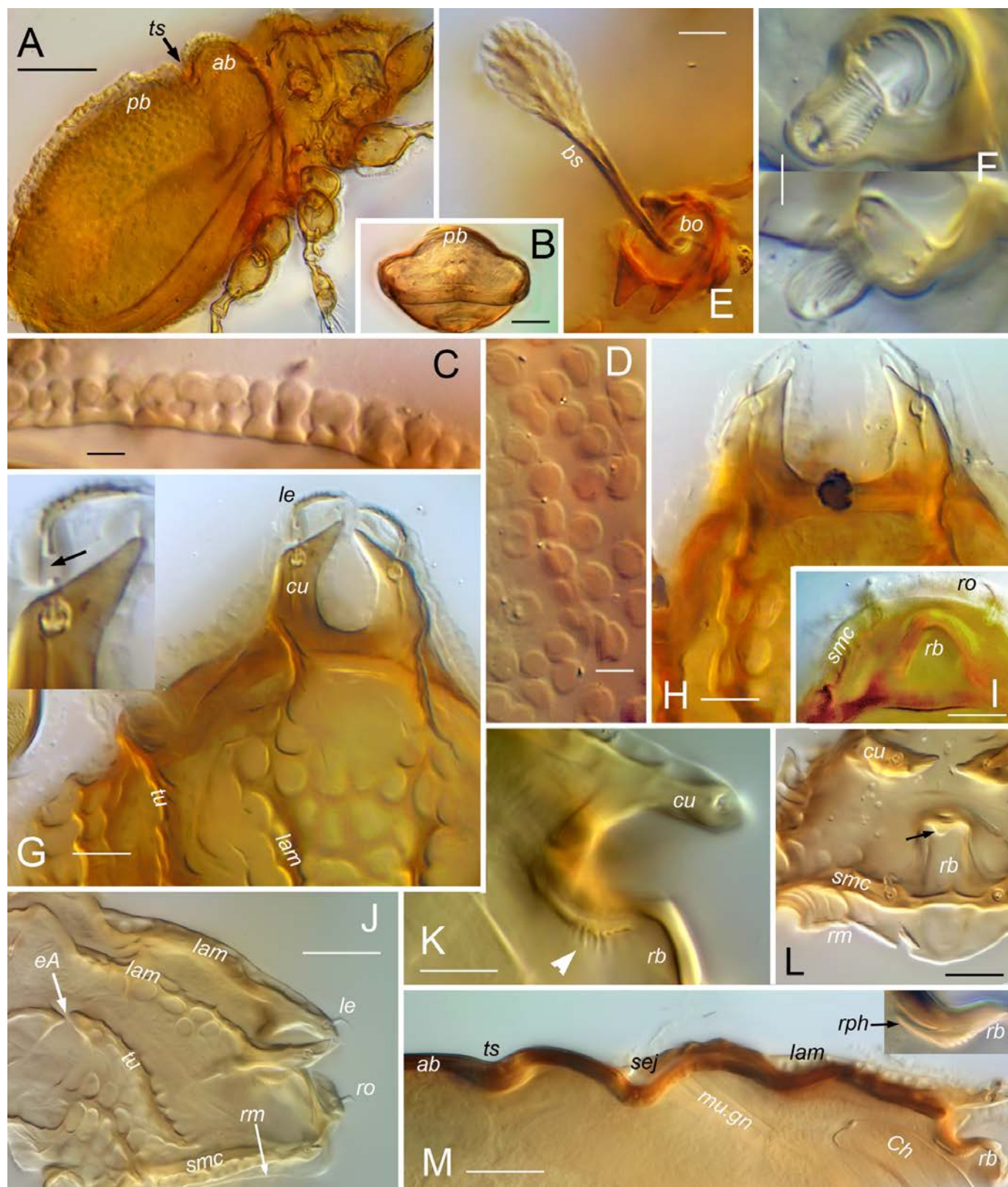
**Prodorsum** — Surface usually foveolate, with well-spaced circular depressions mostly 5–8 µm diameter (Fig. 1A), foveate in some (Fig. 2G); tip of rostrum and subtriangular posteromedial region (with muscle sigilla) mostly smooth. With basally-connected pair of strongly projecting cusps (Fig. 2G; *cu*), longer than wide, each bearing lamellar seta (*le*) near tip; lateral margin of cusp distal to *le* insertion sharply oblique, forming pointed tip directed anteromedially at variable, often asymmetrical angle; paired tips often pincer-like, separated by only 2–8 µm. Cusp pair usually appear connected basally, with U-shaped inner margin, separated by less than their length, rarely with wider separation (Fig. 2H). Submarginal crest (*smc*) extending beyond insertion of rostral seta (*ro*), completely around front of rostrum (Figs 1B, 2J, I, 3G); cuticle scrobiculate immediately below crest. Rostral bulge (Fig. 2I, K, L) conspicuous, with embossed pattern on ventral surface. Lamella well defined posteriorly (level of acetabulum I); with variable development more anteriorly, either extending onto base of cusps (Fig. 2H) or (more commonly) effacing proximal to cusps (Figs 1A, 2G). Tutorium effacing anteriorly, well developed posteriorly to form anterior part of prodorsal enantiophysis *eA* (Fig. 1B); posterior tubercle of *eA* well-defined, conical, nearly touching tutorium. Short longitudinal ridge present laterally, between seta *ex* and acetabula I, II (Fig. 1B). With single pair of small, rounded to subrectangular dorsosejugal tubercles, located at corners of smooth sigillar region (Fig. 1A; *dt*); tubercle sometimes doubled or bilobed (Fig. 3B–C). Bothridial seta (*bs*; ~55–60 µm) projecting dorsolaterally, slightly curved just outside bothridium, remainder straight; squamose head comprising half its length, lightly pigmented, usually with acute tip; stalk smooth, unpigmented (Figs 1A, 2E). Posterior wall of bothridium with strong, conical, tooth-like tubercle directed at humeral process of notogaster, and second more medial tubercle, usually smaller (Figs 1A, 3B–C). Seta *le* (~15 µm; Fig. 2G) strongly curved medially, tips of pair overlapping or not according to form of cusps; *ro* (~15 µm) curved anteroventrally, inserting on submarginal crest at level slightly posterior to *le*; seta *in* (15–20 µm; Fig. 3G) slightly curved or nearly straight, mutual distance 4–5 times length; seta *ex* (~15 µm) inserted between bothridium and short lateral ridge. Setal vestige *exv* ventral or posteroventral to *ex*, nearly touching its alveolus.

**Notogaster** — Length about 1.2 times width; usually evenly rounded posteriorly. Foveae mostly limited to transverse sulcus and to anterolateral region between setae *c* and *la* (Fig.



**Figure 1** *Caleremaeus retractus* (Banks), adult: A – dorsal view (legs mostly omitted); B – lateral view (gnathosoma, legs and anal, genital plates omitted); C – subcapitulum, ventral view (adoral lips and palps omitted); D – palp, abaxial view. Scale bars: 50 µm (A, B); 10 µm (C, D).





**Figure 2** *Caleremaeus retractus* (Banks), transmitted-light micrographs of near-topotypical adults: A – dorsolateral view; B – posterior view; C – cerotegument separated from notogaster, lateral view; D – same, dorsal view (face-on); E – bothridium and bothridial seta (head face-on); F – optical sections of bothridium; upper image focused fine circular striations of inner chamber, lower image on longitudinal striations of deepest part of inner chamber; G – anterior region of prodorsum, dorsal view (insert = enlargement of seta *le*, arrow to break in seta emphasizing surrounding cerotegument nodule); H – same, different specimen, showing cusp variation; I – anterior region of specimen in G, deeper focus showing rostral bulge and submarginal crest; J – prodorsum, dorsolateral view (gnathosoma removed; setae *le* and *ro* represented only by birefringent core); K – specimen in J, deeper focus on rostral bulge (arrowhead to transverse striae of embossed pattern on inner surface of rostral bulge); L – rostral region of dissected specimen, anterior view (black arrow to central ridge of embossed pattern on inner face of rostral bulge); M – parasagittal section of prodorsum and anterior hysterosoma (insert = enlarged base of rostral bulge and rostraphragma). Scale bars: 50 µm (A, B); 20 µm (J, M); 10 µm (E, G-I, K, L); 5 µm (C, D, F).



3A). Humeral process (*hpr*) medium-sized (8–10 µm long), tip usually not reaching bothridial tubercle across sejugal groove. Anterior margin (between *hpr*) irregular, with series of 4–12 small tubercles (up to 4 µm long), weak knots, or slight bulges (Fig. 3A–C). Most setae with form of prodorsal setae noted above, 11–14 µm; *h*<sub>1</sub> with same form, but usually slightly larger (12–18 µm), medially curled, mutual distance of pair about equal to length; *p*<sub>2</sub>–*p*<sub>3</sub> smaller (6–8 µm) and differently shaped, smooth, without pigment or basal cerotegument nodule (Fig. 3D). Lyrifissures *ia*, *im*, *ip* relatively large (10–14 µm; Fig. 3B), *ips*, *ih* smaller (~6 µm).

**Venter and lateral podosoma** — Foveate in acetabular region and lateral parts of coxisternum (Fig. 3F), and usually in single transverse row behind smooth mentotectum; coxisternum without foveae centrally; with irregular muscle sigilla on inner face of cuticle. Laterosejugal enantiophysis (*eL*) with strong conical to rounded tubercles. Epimeral groove 2 usually smooth. Enantiophysis *eS* variable in size, tubercles overlapping or not reaching each other; without other tubercles or knots along ventrosejugal groove. With strong, sculpted discoidal ridge (*dir*) posterior to acetabulum III and separate conical discidium (*dis*) below it, near lateral end of epimeral border 3 (Fig. 1B). Lateral coaptive ridges well-formed, connecting posterior tubercle of *eS*, discidium, and (usually) anterior tubercle of *e4* (Fig. 3F). Epimeral setae acuminate to attenuate (~12–15 µm). Aggenital enantiophysis (*e4*) strongly developed. Medial fossa of epimere IV often with small pair of projections on margin (Fig. 3F). Anogenital region relatively smooth, but with inconspicuous fine striation in adanal region (Fig. 3E). Apophysis of preanal organ slightly tapered to slightly expanded (Fig. 3F, H, I). Females consistently with five pairs of genital setae; males variable, 4–6 (of 18 male plates examined, nine with 4 setae, eight with 5, one with 6; asymmetrical in five of nine individuals). Anogenital setae acuminate; aggenitals and genitals ~6–7 µm, anals ~5–6 µm; adanals ~6–9 µm (*ad*<sub>1</sub> longest). Lyrifissure *iad* ~12 µm (Fig. 3E).

**Gnathosoma** — Subcapitulum smooth or with few scattered foveolae; hypostomal (*h*, ~14 µm) and genal (*a*, *m*, ~15–18 µm) setae attenuate. Chelicera ~80 µm long, with 0–2 small spicules; setae *cha* (~22 µm), *chb* (~15 µm) attenuate, barbed.

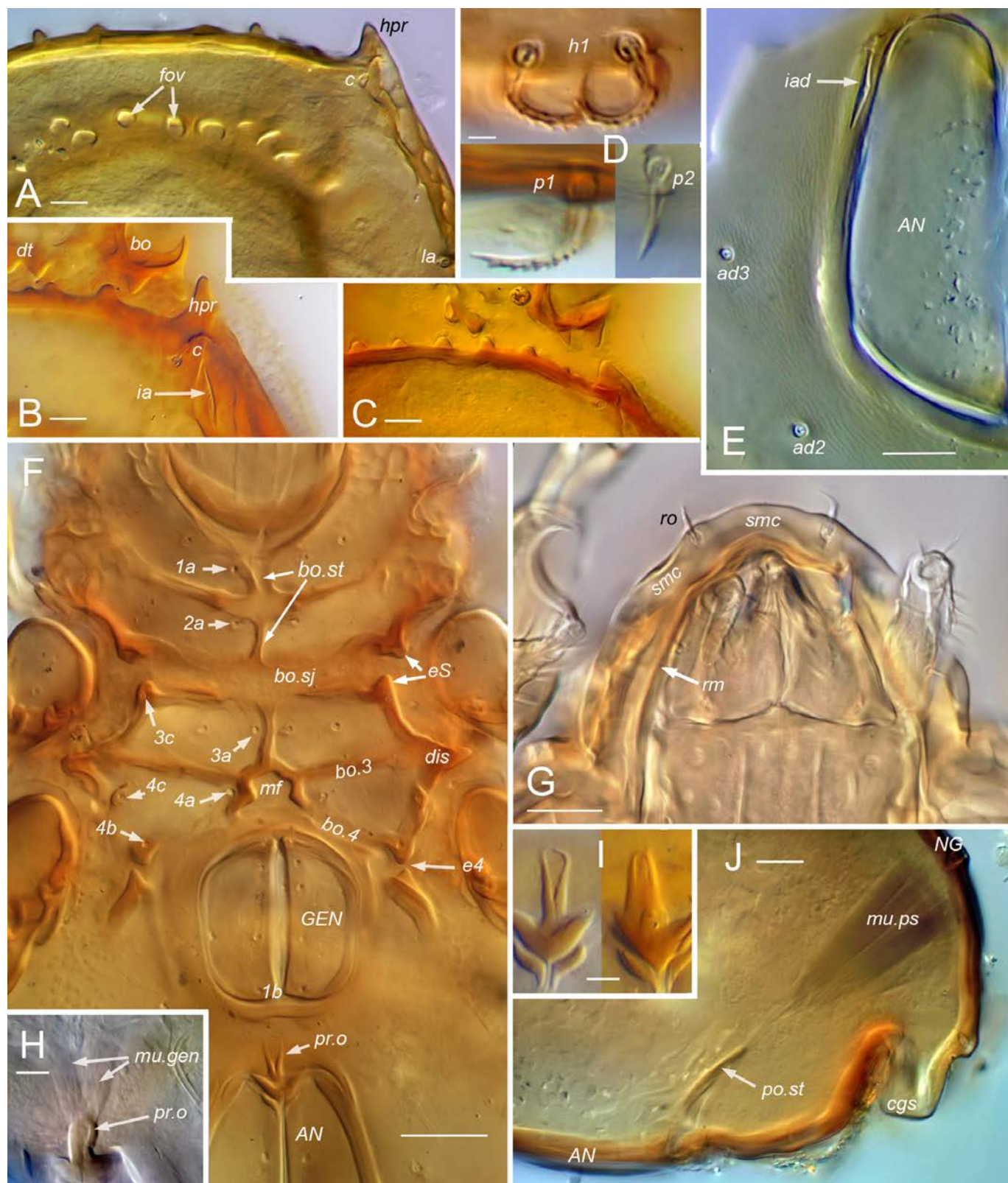
**Legs** (Figs 4–5) — Femora I, II similar in form: with abrupt transition from proximal stalk to bulb, junction at nearly right-angle; femur I ~2.5, II ~2.0 times longer than high in lateral view, stalk occupying ~0.4 femoral length; stalk of femur II slightly broader than that of I. All femora with porose area, mostly on adaxial face of bulb. Tibia I with bulb markedly swollen, only ~1.2 times longer than high. Tarsus I abruptly tapered in distal half, but without distinct projecting mid-dorsal bulge. Tarsus II without noticeable proximal stalk, depth similar to that of tibia in lateral view. Seta *d* of femora short, flame-shaped, similar in structure to dorsal body setae (pigmented, barbed, with conspicuous cerotegument nodule at base; Fig. 5D). Seta *l'* of genu and tibia I not conspicuously enlarged.

## Juveniles

Figures 6–7

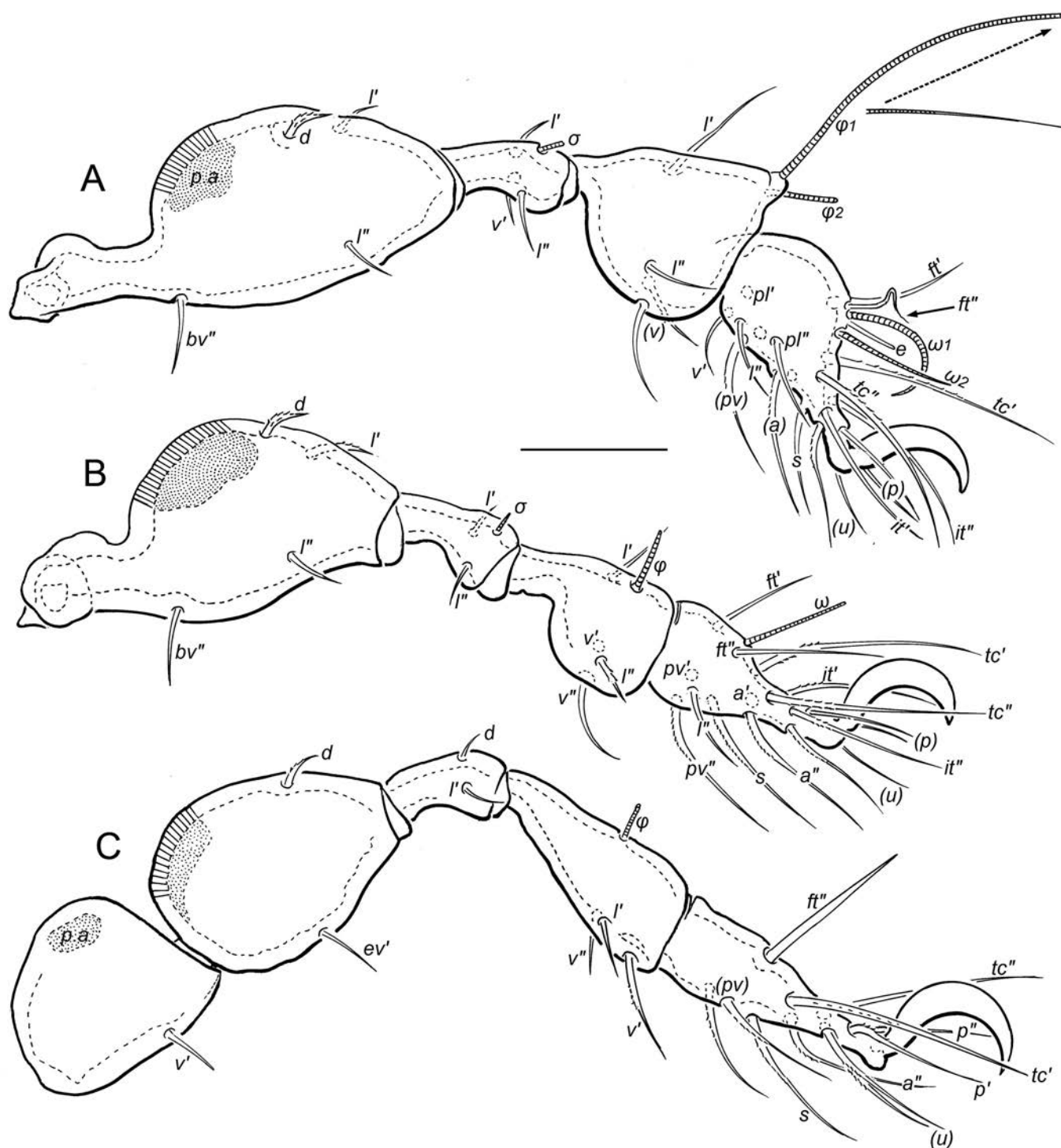
(Larva known only from exuvial scalp)

Length (without setae) and maximum width of protonymph 230 x 98 µm (*n* = 1); deutonymph 230–289 x 107–142 µm (*n* = 9); tritonymph 284–353 x 147–181 µm (*n* = 7). Bothridial seta (Figs 6A, 7H) straight, elongated, nearly as long as prodorsum, gradually thickening distally but without distinct head, slightly lanceolate with angular tip; distinctly squamose in distal half. Setae *in*, *ex*, *le* minute, hardly extending beyond basal cerotegument nodule; *ro* about twice as long but inconspicuous, curved ventrad. Seta *le* inserted on weak tubercle, slightly longer than wide; *ro* inserted on truncate rostral projection appearing like anterior part of submarginal crest of adult (Figs 6B, 7F). Gastronotic region of larva (based on exuvial scalp; Figs 6A, 7B–C) with setae *c*<sub>1</sub>, *c*<sub>2</sub>, *la*, *lm*, *lp* minute (~3–4 µm), smooth, acicular to nearly baculiform, hardly emerging from basal cerotegument nodule; dorsocentral setae closely paired (mutual distance 10–13 µm), *da* (~8–9 µm) and *dm* (~11–12 µm) slightly arched, with strong barbs on outer curvature, *dp* (~24–26 µm) weakly clavate, strongly squamose;



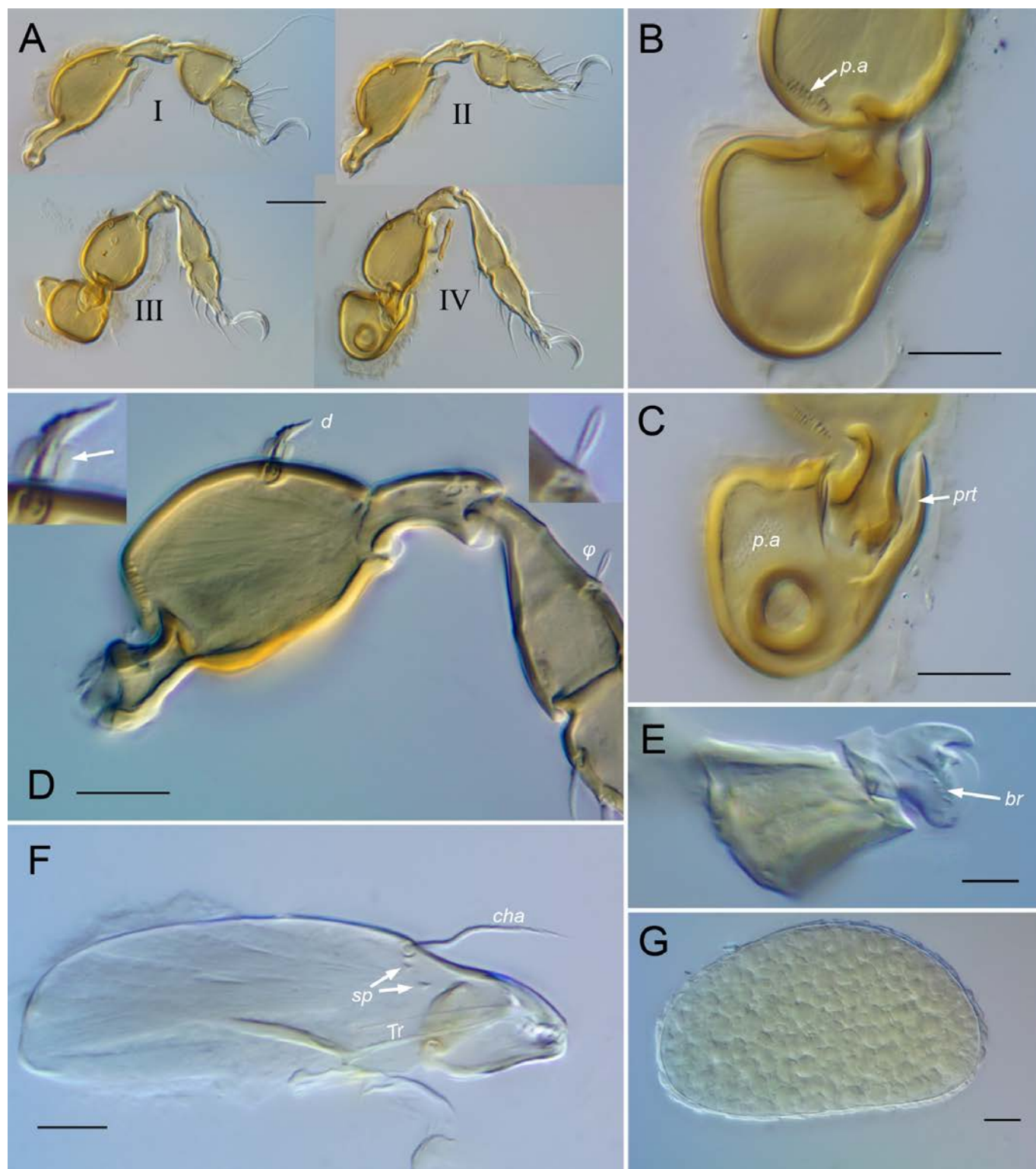
**Figure 3** *Caleremaeus retractus* (Banks), transmitted-light micrographs of near-topotypical adults: A – anterior region of separated notogaster; B – right sejugal region, dorsal view; C – same, different specimen; D – notogastral setae, as labeled; E – adanal region and anal plate (no setae in focus); F – partial venter (setae seen only as alveolus due to focus limitations); G – rostrum and subcapitulum, ventral view; H – preanal organ and associated muscles (no clearing); I – two variants of same, with strong clearing; J – sagittal section of posterior hysterosoma. Scale bars: 20  $\mu$ m (F); 10  $\mu$ m (A-C, E, G, J); 5  $\mu$ m (H, I); 2  $\mu$ m (D).



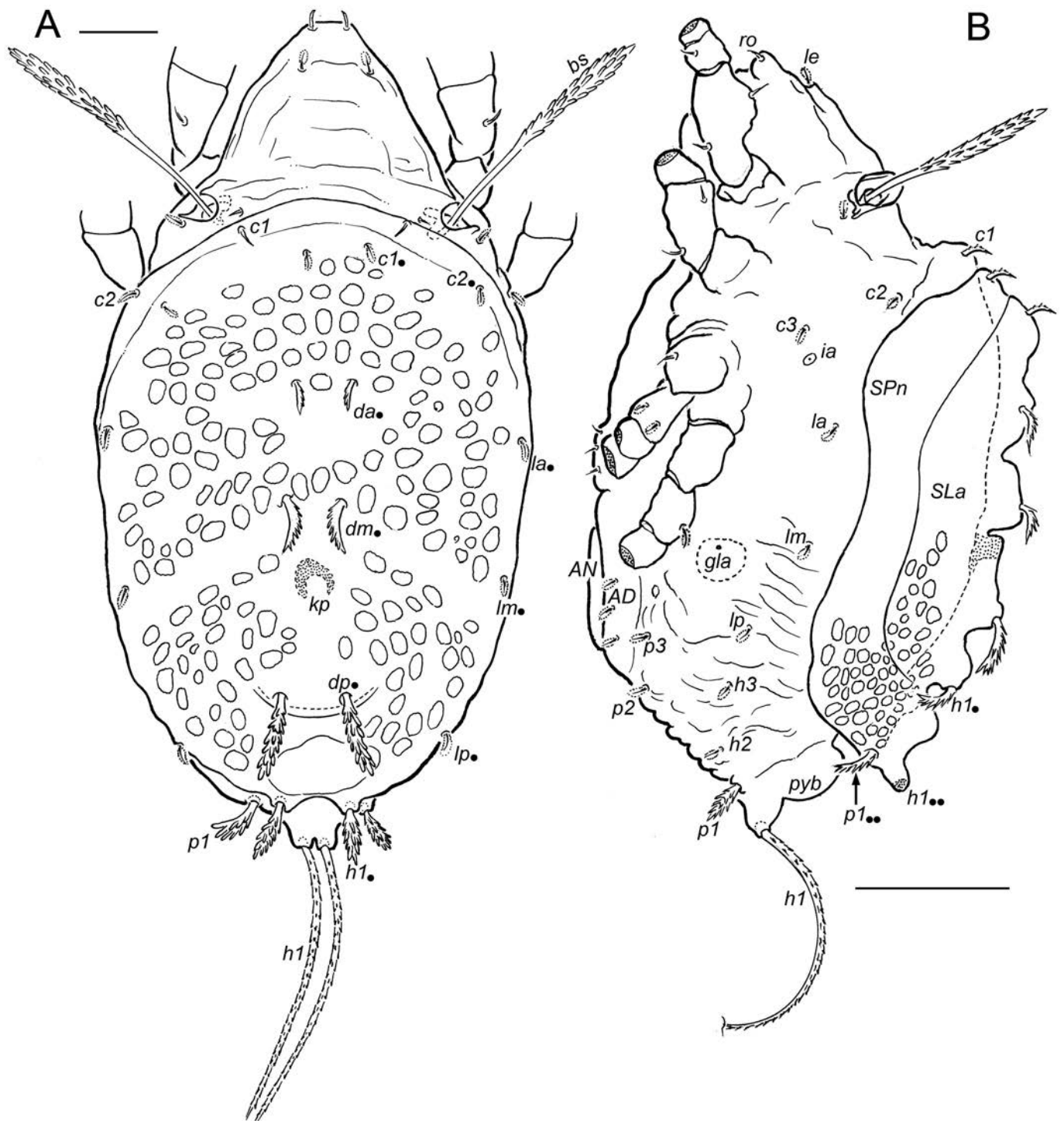


**Figure 4** *Caleremaeus retractus* (Banks), legs of adult (abaxial aspect, trochanter omitted from I, II): A – leg I; B – leg II; C – leg IV. Scale bar: 20  $\mu$ m.

$h_1$  similar to  $dp$  but shorter ( $\sim 15\text{--}17\text{ }\mu\text{m}$ ). Setal pair  $h_1$  closely parallel, greatly elongated,  $\sim 130\text{--}150\text{ }\mu\text{m}$  in tritonymph (length relative to body length  $\sim 0.3$  in proto-,  $0.4\text{--}0.5$  in deuto-, tritonymph); uniformly narrow except slightly tapered distally, with small but conspicuous



**Figure 5** *Caleremaeus retractus* (Banks), transmitted-light micrographs of near-topotypical adults: A – legs I-IV, abaxial view (trochanters I, II not shown); B – trochanter and base of femur IV, mid-depth focus; C – same, deeper focus; D – partial leg III, with enlarged femoral seta *d* (upper left insert, arrow to basal cerotegument nodule) and tibial solenidion  $\phi$  (upper right insert); E – left gena and rutellum, ventral view (removed from subcapitulum); F – chelicera, adaxial view; G – egg removed from oviduct. Scale bars: 20  $\mu$ m (A, G); 10  $\mu$ m (B-D, F); 5  $\mu$ m (E).



**Figure 6** *Caleremaes retractus* (Banks), juveniles: A – protonymph, dorsal view; B – deutonymph, lateral view, with smaller setae omitted from larval (SLa) and protonymphal (SPn) scalps. Dots indicate that seta is on exuvial scalp (one for larval, two for protonymphal). Scale bars: 50  $\mu$ m (B); 10  $\mu$ m (A).



barbs throughout. Nymphal seta  $p_1$  subclavate seen face-on but slightly flattened and cupped, strongly squamose on upper curvature (~20  $\mu\text{m}$  in tritonymph); other gastronotic setae minute, simple, (4–8  $\mu\text{m}$  in tritonymph), hardly emerging from basal cerotegument nodule (Fig. 7I–K). Ventral setae simple, acuminate, without cerotegument nodule; in tritonymph, epimeral setae 6–9  $\mu\text{m}$ , genital and aggenital setae ~4  $\mu\text{m}$ ,  $ad$  setae 6–7  $\mu\text{m}$ ,  $an$  4–5  $\mu\text{m}$ . Genital seta ontogeny variable: deutonymph with two or three pairs, tritonymph with four or five, valves sometimes with asymmetrical complement. Lateral setae of legs generally short, inconspicuous;  $l'$  of tibia I hardly reaching distally to end of segment (Fig. 7M); seta  $d$  of tibia I with cilia and velum-like coating indistinct (Fig. 7L). Exuvial scalps conspicuously reticulated due to fovea-like excavations on underside (Fig. 6A–B, 7A–C, E); seta  $h_1$  consistently broken from nymphal exuviae.

## Comparisons

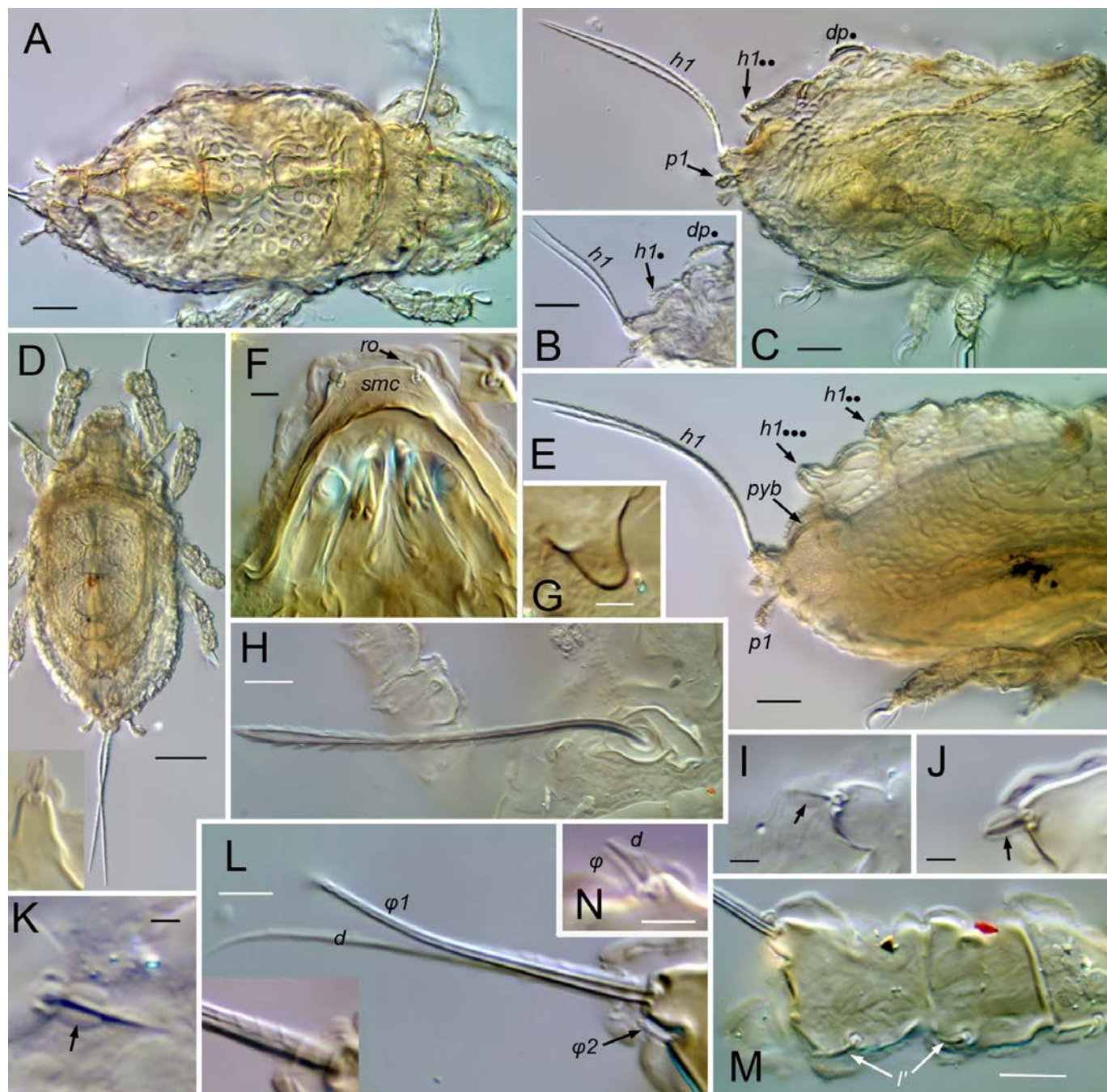
Adults of *Caleremaeus retractus* are similar to those of *C. monilipes* (cf. Weigmann 2006, Miko and Travé 1996) and *C. divisus* in having a distinct lamella and tutorium and lamellar seta inserted on a strong cusp, traits that are absent from *C. arboricolus* and *C. nasutus*. According to the crude illustration of *C. divisus*, the cusp stops well short of the rostral margin, while reaching or surpassing it in *C. monilipes* and *C. retractus*; also, the anterior notogastral tubercles of *C. divisus* were drawn as far larger than those of other species, equal in size to the humeral process (Mihelčič 1952).

Adults of *Caleremaeus retractus* are distinguishable from those of *C. monilipes* (Cm) by: (1) having a less sculptured prodorsum, including weakly-developed lamella (stronger in Cm); (2) having nearly erect setae  $in$ , the pair separated by 4–5 times setal length ( $in$  slightly larger, curved mediad and separated by less than three times setal length in Cm); (3) lacking additional distinct knots or small tubercles along epimeral groove 2 and along the anterior edge of the sejugal groove between tubercle pair  $Sa$  (present in Cm); (4) having a modest humeral process that rarely reaches anteriorly to overlap bothridial tubercles (larger humeral process, overlapping with bothridial tubercle in Cm); (5) being smaller, with adult total length 306–340  $\mu\text{m}$  (373–475  $\mu\text{m}$  in Cm). Nymphs are distinguishable by: (1) the narrow, elongate form and closely parallel orientation of setae  $h_1$  in nymphs (distinctly clavate and divergent in Cm; Fig. 18C); (2) having generally smaller, less conspicuous leg setae (generally larger in Cm; cf. setae  $l'$  in Figs 7M, 18D); having smooth, small, inconspicuous seta  $ro$  (larger, conspicuous, with several strong barbs, projecting distinctly forward beyond rostral margin in Cm; Fig. 18D, see also Michael 1882).

## Possible species group

As noted in the Introduction, morphometric and genetic evidence suggests that European records of *Caleremaeus monilipes* represent a complex of species (Krisper *et al.* 2017) that ultimately may be considered the ‘monilipes’ species-group. The same may be true of the most similar North American species, *C. retractus*.

At an early stage of this study, we identified specimens of *C. retractus* from many locations in eastern North America, including the states of Alabama, Arkansas, Florida, Georgia, Louisiana, Illinois, Indiana, Mississippi, New Hampshire, New York, Vermont, Virginia and West Virginia, as well as the Canadian province of Quebec. Adults of these specimens are presently indistinguishable from those at the type location in North Carolina, except perhaps for a propensity of New York adults to have one or two small knots across epimeral groove 2 from seta  $2a$  (Fig. 18E). But juveniles suggest that more than one species is involved. In addition to the near-topotypical material from Durham Co., North Carolina, we have juveniles from Florida and from New York (Onondaga Co.). The Florida nymphs are identical to the near-topotypes, but New York juveniles are easily distinguished by their shorter, straighter pygidial setae (Fig. 18G;  $h_1$ ), larger seta  $l'$  on tibia and genu I, and tibia I seta  $d$  with more distinct barbs and velum-like coating. As with near-topotypes, setae  $h_1$  of the New York population are adjacent,



**Figure 7** *Caleremaeus retractus* (Banks), transmitted-light micrographs of near-topotypical juveniles: A – protonymph, dorsal view (setae  $h_1$  incomplete); B – same, lateral view of posterior hysterosoma; C – deutonymph, lateral view of hysterosoma; D – tritonymph, dorsal view (insert = right lamellar seta and cusp); E – same, lateral view of hysterosoma; F – tritonymph, ventral view of prodorsal margin and partial gnathosoma (upper right insert = enlarged seta  $ro$ ); G – gastronomic cornicle of tritonymph (scalps removed); H – bothridial seta of deutonymph; I – gastronotal seta  $lm$  from tritonymph (arrow to basal cerotegument nodule); J – same, but seta  $h_2$ ; K – same, but seta  $p_2$ ; L – dorsodistal process of tibia I, tritonymph, distal to left ( $\phi_1$  rising out of focus; insert = opposite side of seta  $d$ , showing faint barbs); M – tibia, genu and distal part of femur I from tritonymph, adaxial view; N – coupled seta  $d$  and solenidion on tibia II (distal to left). Dots in B, C, E indicate that labeled seta (or its insertion) is on exuvial scalp of larva (.), protonymph (..) or deutonymph (...). Scale bars: 50  $\mu$ m (D); 20  $\mu$ m (A-C, E); 10  $\mu$ m (M); 5  $\mu$ m (F-H, L, N); 2  $\mu$ m (I-K).

parallel and consistently broken from exuviae, unlike those of *C. monilipes* and *C. arboricolus* in which they are divergent and retained on exuviae.

The differences could represent geographic variation in these setae, but without further

knowledge of juveniles from other locations, and especially without genetic data, we have no basis for judgement. At present, we prefer to assign specimens with the adult traits of *C. retractus* to a 'retractus' species group unless juveniles are known and correspond with the near-topotypes.

### *Caleremaeus arboricolus* n. sp.

Zoobank: CF4D144D-15F3-467B-94DF-67104DB0C404

**Etymology** — The Latin species epithet 'arboricolus' is an adjective referring to the microhabitat (tree bark) of this species.

**Material examined** — Holotype adult and 35 adult paratypes from: USA, New York, Onondaga Co.; Syracuse, Oakwood Cemetery (43° 01.9' N, 76° 07.9' W); 10.ix.2008; R.A. Norton and D.A. Saunders, col., from mixed lichens on boles of living trees (washed and sieved). Ten adult paratypes from same location, but 24.vi.2019. One larva and 16 nymphs (non-type) from same two collections. Holotype and three paratypes deposited in USNM; five paratypes in CNC; remainder in RNC. Other material (all adults; in CNC and RNC) as follows. *USA: Alabama:* Baldwin Co., Bon Secours National Wildlife Refuge, Jeff Friend Trail (30° 14.6' N, 87° 47.21' W), 6.iii.1994, V. Behan-Pelletier, col., 9 from lichens on horizontal tree trunk. *Maine:* Penobscot Co., Orono, University of Maine Experimental Forest, x.1987, C. Stubbs col., 19 from lichens on red maple (*Acer rubrum* Linn.) trunk. *New Jersey:* Middlesex Co., New Brunswick, 1978, J. Walker col., 1 (no other data). *New York:* Essex Co., Newcomb, Huntington Wildlife Forest, H. Root, col., vii-viii-2002, 11 from lichens on sugar maple (*Acer saccharum* Marshall) [as *Caleremaeus* sp. 1 in Root *et al.* 2007]; Onondaga Co., LaFayette Experiment Station (SUNY-ESF), 19.vii.1973, J.R. Philips col., 1 from regurgitated Great Horned Owl pellet in hardwood forest. *Tennessee:* Anderson Co., Great Smoky Mountain National Park, Indian Gap, 5200' (elev.), 18.vi.1957, W.R.M. Mason col. *Virginia:* Page Co., Shenandoah National Park, Stony Mountain Trail, Skyland area, 4000' elev., 14.viii.1986, E.E. Lindquist col., 1 from lichen mats on tree trunks and rocks. *Canada: Ontario:* Leeds-Grenville Co., Near Otter Lake (34° 34.87' N, 76° 19.77' W), 23.vii.2003, J. Chen, V. Behan-Pelletier, J. Johnson col., 15 from cedar twigs (4m from ground), 5 from juniper twigs (<1m from ground).

**Diagnosis** — *Caleremaeus* species with adults having total length 311–353 µm. Prodorsum without distinct distal cusps; lamellar setae inserted on transverse ridge, each on slightly projecting tubercle; lamella represented by only indistinct apparent vestige; tutorium weakly developed; enantiophysis *eA* absent; oblique row of 2–3 knots in place of typical dorsosejugal tubercle. Notogastral setae conspicuous, erect, mostly thick and squamose, some with coating but without basal cerotegument nodule. Epimeral groove 2 usually without bordering tubercles or knots; ventrosejugal groove with only small, somewhat irregular and variable enantiophysis *eS*. Females and males consistently with five pairs of genital setae. Leg femora each with saccule. *Nymphs* with bothridial seta having squamose, flattened head, similar to that of adult; gastronomic seta *h*<sub>1</sub> thick, straight, squamose, pair distinctly diverging; exuvial scalps not reticulated in transmitted light.

### Adult

Figures 8–11

**Dimensions** — Total length (n = 20) 311–353 µm (mean 332); maximum width 174–216 µm (mean 195). Female (n = 10) length 328–353 µm (mean 342), maximum width 174–216 µm (mean 204); male (n = 10) length 311–333 µm (mean 322), maximum width 181–191 µm (mean 185).

**Integument, setae** — Cerotegument excrescences ranging from dome-like to near-spherical nodules on short, thick stalk (Fig. 10B). Excrescences mostly 4–5 µm diameter on notogaster, closely spaced (mostly less than their diameter apart); dark, dense band of smaller excrescences (2 µm) around posterior and lateral notogastral margin; prodorsum and ventral plate with



inconspicuous, small (1–2  $\mu\text{m}$ ) domes interspersed with dense, minute granules (Fig. 10C). Setae of various forms, but without conspicuous basal cerotegument nodule; some with pigmented coating (possibly cerotegument; e.g. Fig. 9J–K).

**Prodorsum** — Central region foveate, with closely spaced circular depressions, mostly 6–8  $\mu\text{m}$  diameter; foveation distinct between strong anterior transverse ridge and weakly-defined transverse ridge at level of acetabulum I (Fig. 9A). Lamella apparently vestigial, represented only by short, thin longitudinal carina. Without projecting cusp; setal pair *le* inserted on strong transverse ridge, each on distinct lateral tubercle (Fig. 9B–C). Interbothridial region with 2–3 knots (rarely one) in oblique transverse row on either side of central sigilla (Fig. 9E), sometimes with weakly-defined ridge parallel to row, between it and seta *in* (Fig. 8A). Submarginal crest ending anteriorly at seta *ro*; area between crest and rostral margin smooth, not scrobiculate (Fig. 9G). Rostral bulge moderately developed, without embossed pattern on ventral face (Fig. 9H). Tutorium weakly developed, gradually effacing both anteriorly and posteriorly; prodorsal enantiophysis absent. Lateral face highly sculptured (Fig. 9G); with several small tubercles or knots between bothridium and acetabulum I; with scalloped concentric carina or series of several short oblique ridges immediately anterior to parietal wall of acetabulum I. Variably foveate between pedotectum I and acetabulum II. With short transverse ridge above pedotectum I. Bothridium with anterior wall weakly foveate; posterior wall usually with one strong tooth (sometimes two) and 1–2 additional weak teeth or knots (Fig. 9D–E). Bothridial seta (50–60  $\mu\text{m}$ ; Fig. 9D–F) flattened, with clavate outline seen face-on, distally rounded or slightly acute; head strongly pigmented, vaguely squamose, with low, narrow, blunt scales or mounds in linear, slightly radiating pattern; stalk smooth, not noticeably pigmented. Setae *in* and *le* short, distinctly barbed, pigmented and with isotropic coating; *in* (~12–15  $\mu\text{m}$ ), acuminate, *le* (15–25  $\mu\text{m}$ ) isodiametric to slightly clavate (Fig. 9B–C). Seta *ro* (20–27  $\mu\text{m}$ ) unpigmented, uncoated, with weak, inconspicuous barbs. Seta *ex* simple, minute (4–5  $\mu\text{m}$ ); vestige *exv* posteroventral to *ex*, separated by at least one alveolar width (Fig. 9I).

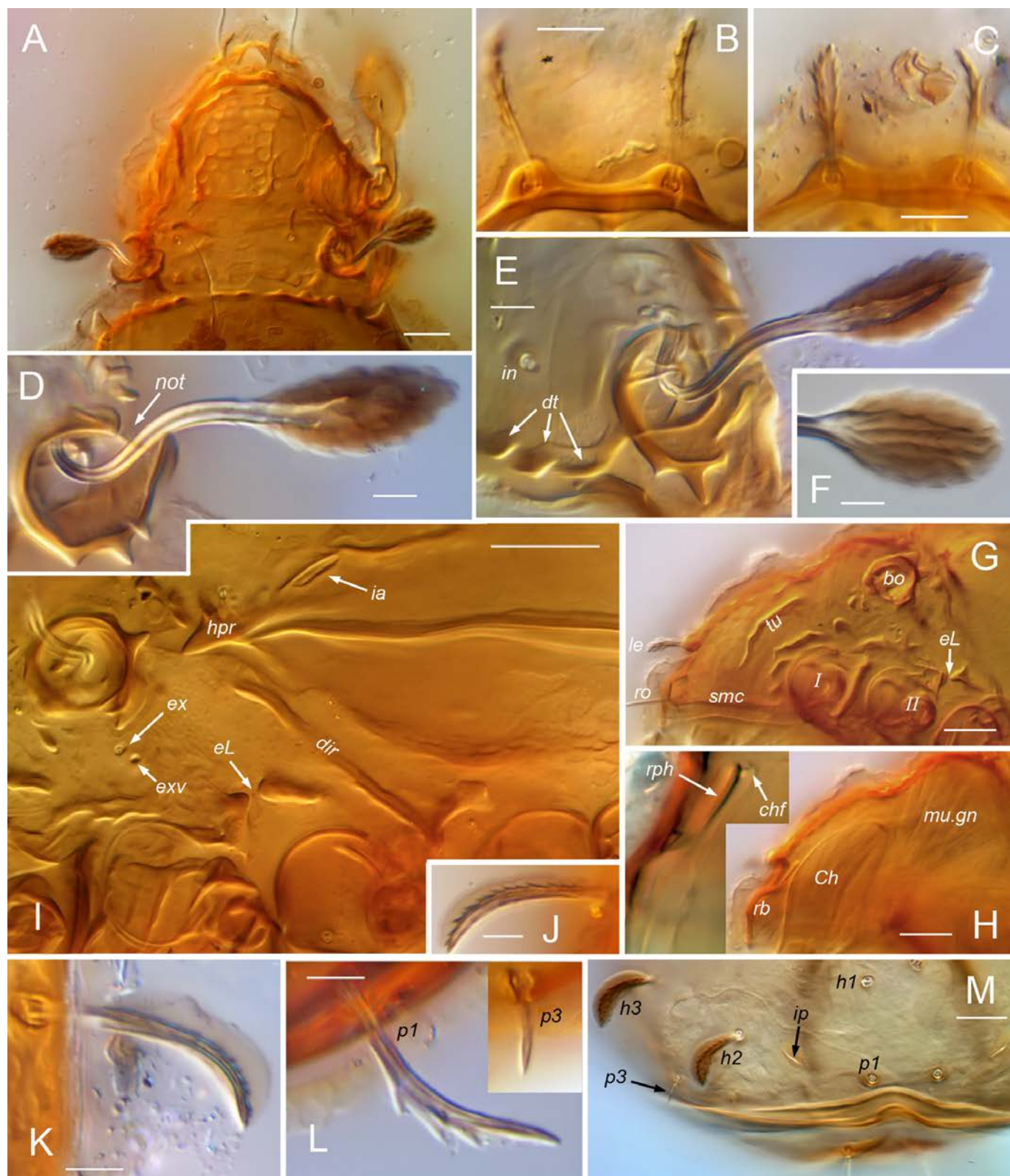
**Notogaster** — With 6–12 knots on anterior margin, mostly 5–7  $\mu\text{m}$  diameter, often weakly defined (Figs 8A, 9A); humeral process relatively small, not projecting beyond anterior margin. About 12–15 strongly defined foveae (5–8  $\mu\text{m}$  diameter) in transverse sulcus; otherwise without fovea or foveolae. Posterior bulge rather evenly tapered posteriorly; each lateral margin of bulge with nearly linear series of 8–15 knots or short ridges (Figs 8A, 10A). Setae of several types: *lp*, *h<sub>3</sub>*, *h<sub>2</sub>* (25–30  $\mu\text{m}$ ) lightly pigmented, flattened, subclavate seen face-on, somewhat cupped and curved, with numerous conspicuous barbs on outer face and pigmented coating of variable thickness (Fig. 9J–K); *h<sub>1</sub>* similar but strongly curved mediad, mutual distance of pair equal to setal length or less; *la*, *lm* similar to *lp* but narrower, shorter (20–22  $\mu\text{m}$ ); seta *c* (12–15  $\mu\text{m}$ ) not broadened or only slightly so, and with little or no coating; *p*-row not broadened and without coating, *p<sub>1</sub>* (~25  $\mu\text{m}$ ) usually with strong, sharp point and few but strong barbs, *p<sub>2</sub>*, *p<sub>3</sub>* very short (8–9  $\mu\text{m}$ ), spiniform, smooth or with 1–2 small barbs (Fig. 9L).

**Venter and lateral podosoma** — Epimere I foveate laterally; other epimeres without depressed features other than epimeral grooves and medial fossa on epimere IV, though strongly marked internal muscle sigilla often give reticulate impression in transmitted light (Fig. 8B). Development of coxisternal knots and tubercles somewhat variable: usually with several minute knots anterolateral to seta *2a* and 2–3 others opposing them on epimere I across shallow epimeral groove 2; usually with small tubercle bearing seta *3c* opposing 1–2 others across sejugal groove (comprising enantiophysis *eS*); knot or small tubercle sometimes present closely anterolateral to seta *4c*; epimeral groove 4 with relatively small aggenital enantiophysis (*e4*) but without other tubercles or knots. Lateral region of epimeres III, IV without distinct coaptive ridge associated with leg trochanters. Without discrete discidium, but with distinct discoidal ridge reaching anterodorsally to sejugal groove (Fig. 9; *dir*), sometimes appearing like discidium in optical projection (Fig. 8B). Ventral setae simple, acicular, each inserting on small, low but distinct basal tubercle. Coxisternal setae 15–20  $\mu\text{m}$ . Both genders consistently with five pairs of short (7–9  $\mu\text{m}$ ) genital setae; anal setae similar (10–12  $\mu\text{m}$ ). Adanal setae slightly longer: *ad<sub>1</sub>* (18–20  $\mu\text{m}$ ) posteriorly positioned, slightly shorter than mutual distance



**Gnathosoma** — Subcapitulum without foveae, hypostomal ( $h$ ,  $\sim 15\ \mu\text{m}$ ) and genal ( $a$ ,  $m$ ,





**Figure 9** *Caleremaeus arboricolus* n. sp., transmitted-light micrographs of adult: A – anterior third, dorsal view; B – transverse ridge and setae *le*; C – same, different specimen; D – bothridium and seta *bs*; E – posterolateral area of prodorsum, dorsal view; F – head of bothridial seta; G – prodorsum, lateral view; H – same, deep focus optical section (insert on left = enlarged base of rostral bulge and rostrophragma); I – middle third of body, lateral view; J – notogastral seta *h*<sub>2</sub>; K – notogastral seta *lp*; L – notogastral setae *p*<sub>1</sub> and *p*<sub>3</sub>; M – posterior view (setae *h*<sub>1</sub>, *p*<sub>1</sub> broken from alveolus). Scale bars: 20 μm (A, G–I, M); 10 μm (B, C); 5 μm (D–F, J–L).

15–17, 20–25  $\mu\text{m}$  respectively) setae attenuate. Chelicera 75–80  $\mu\text{m}$  long; without spicules; setae *cha* (~20  $\mu\text{m}$ ), *chb* (~15  $\mu\text{m}$ ) attenuate, barbed.

**Legs** — Femur I elongated, 4–4.5 times longer than maximum height in lateral view, with gradual transition between stalk and bulb, at distinctly oblique angle (Fig. 11A). Femur II (Fig. 11H) differently shaped: length only slightly more than twice height, with very short stalk, distinctly broader than that of femur I. All femora lacking surficial porose area but with short, broad saccule opening through short slit on proximal wall of bulb; saccule shape variable – simple, sausage-shaped or with irregular width (Fig. 11G–J). Trochanters III, IV with normal adaxial porose area. Genua and tibiae often with irregular dorsal contour due to several transverse ridges; genu and tibia I with enlarged seta *l'*, that of genu surpassing distal end of segment, that of tibia equal or greater than maximum tibia height (Fig. 11E). Tarsus I with slight projection mid-dorsally, bearing solenidia, famulus and seta *ft''*. Femoral seta *d* normal, acute, straight to slightly curved, without basal cerotegument nodule (Fig. 11H).

## Juveniles

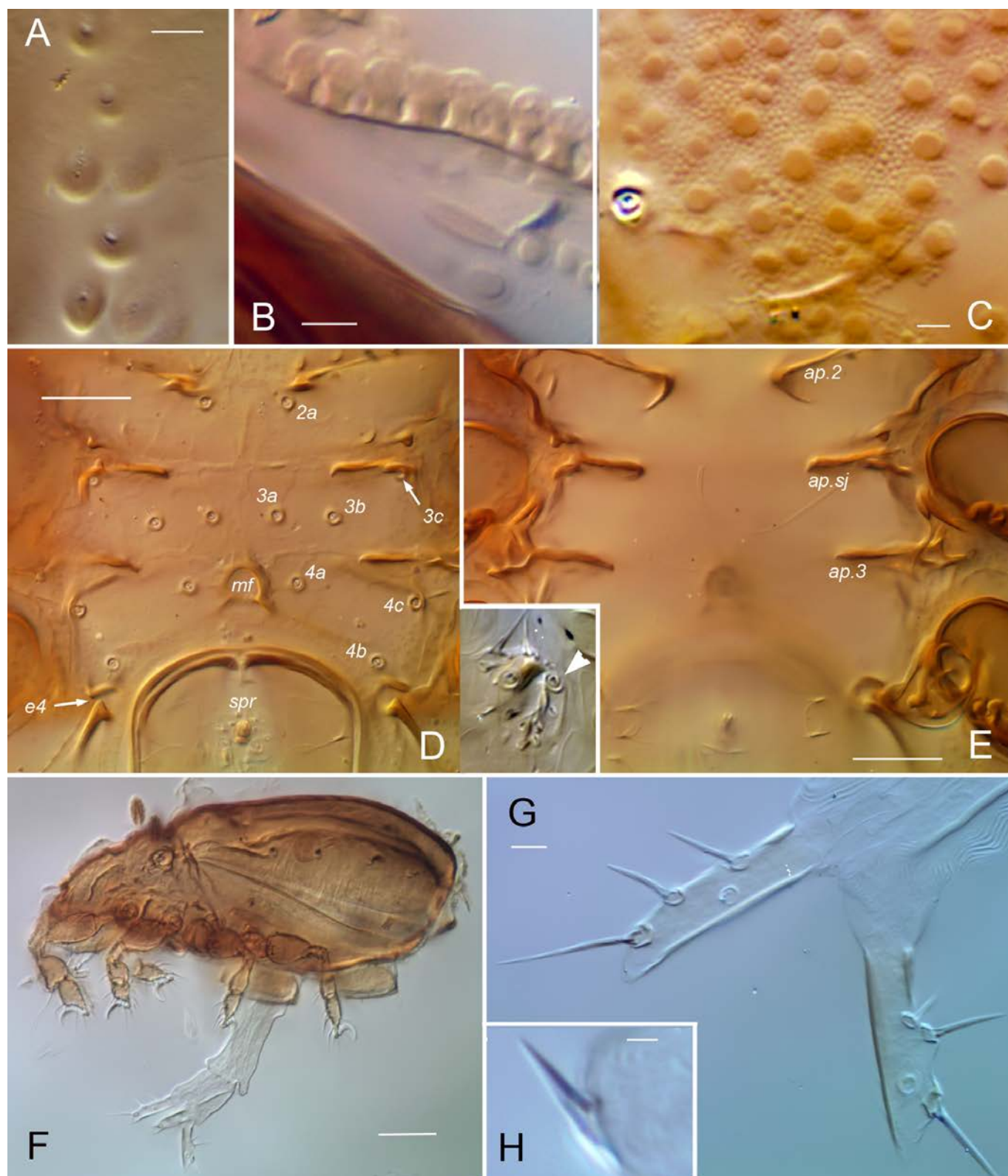
Figure 12

Length (without setae) and maximum width of larva (La) 196 x 92  $\mu\text{m}$  (n = 1); protonymph 220 x 99  $\mu\text{m}$  (n = 1); deutonymph 252–284 x 123–137  $\mu\text{m}$  (n = 4); tritonymph (Tn) 294–319 x 157–167  $\mu\text{m}$  (n = 2). Setae without conspicuous basal cerotegument nodule, but many with clear, basal isotropic sleeve, most conspicuous in small setae (e.g. Fig. 12A, *lp*). Bothridial seta similar to that of adult: with distinct flattened head, clavate seen face-on, vaguely squamose (Fig. 12J). Seta *ro* conspicuous, projecting forward (~17  $\mu\text{m}$  in La, 25  $\mu\text{m}$  in Tn), longer than mutual distance of pair, acicular, weakly barbed, with inconspicuous coating near base; setae *le*, *in* and *ex* minute (~5  $\mu\text{m}$  in La, ~7  $\mu\text{m}$  in Tn), baculiform to acute, thickened by nearly complete isotropic coating, *le* of nymphs inserted on small tubercles. Larva with setae *c*<sub>2</sub>, *c*<sub>3</sub> and dorsolateral series small, smooth, baculiform to acute, not or hardly emerging from clear sleeve (Fig. 12A; *lp*). Middle row pigmented, with length and roughness increasing posteriorly, basal coating less conspicuous or apparently absent (Fig. 12A): *c*<sub>1</sub> (~5  $\mu\text{m}$ ), *da* (~12  $\mu\text{m}$ ) and *dm* (~15  $\mu\text{m}$ ) blunt, with one to several coarse barbs; *dp* (~25  $\mu\text{m}$ ) coarsely squamose with acute tip, slightly longer than mutual distance of pair; seta *h*<sub>1</sub> (~20  $\mu\text{m}$ ) directed straight posteriorly or slightly diverging, shorter than mutual distance, broadest and coarsely squamose in middle. Setae *h*<sub>2</sub> (attenuate, ~15  $\mu\text{m}$ ) and *h*<sub>3</sub> (acicular, ~5  $\mu\text{m}$ ) inserted close to paraprocts. Nymphs with gastronal setae in *c*- and *l*-series small (8–12  $\mu\text{m}$  in Tn), simple, baculiform to slightly tapered, extending little beyond coating. Nymphs with *h*<sub>1</sub> large (~80  $\mu\text{m}$  in Tn), distinctly diverging, pigmented, slightly broadened and squamose in middle, distally blunt, setae and supporting posterior lobe upturned in deuto- and tritonymph but not protonymph (Fig. 12C); *h*<sub>2</sub>, *h*<sub>3</sub> (25–30  $\mu\text{m}$  in Tn) pigmented, coarsely barbed to squamose. Seta *p*<sub>1</sub> (30–40  $\mu\text{m}$  in Tn) broadened and squamose in middle, distally blunt; *p*<sub>2</sub> (~15  $\mu\text{m}$  in Tn) simple, acicular to acuminate. Ventral setae simple, acuminate to attenuate, with coating in basal half; in Tn epimeral setae 10–15  $\mu\text{m}$ , genital and aggenital setae 8–10  $\mu\text{m}$ , *ad* setae 10–12  $\mu\text{m}$ , *an* 4–5  $\mu\text{m}$ . Genital seta ontogeny consistently 1-2-4-5 (protonymph to adult). Ventral cuticle with microgranulate cerotegument, small excrescences often arranged in short lines (Fig. 12H). Ventral setae and those of basal leg segments short, simple, with full isotropic coating, sometimes displaced during preparation (Fig. 12H, K). Lateral setae on legs well developed, conspicuous; *l'* of tibia I enlarged, coarsely barbed to squamose, extending distally well beyond end of segment (Fig. 12J); seta *d* of tibia I with distinct barbs and velum-like coating (Fig. 12I). Exuvial scalps not reticulated, ornamented only with surface plication (Fig. 12A); seta *h*<sub>1</sub> consistently retained on all exuviae.

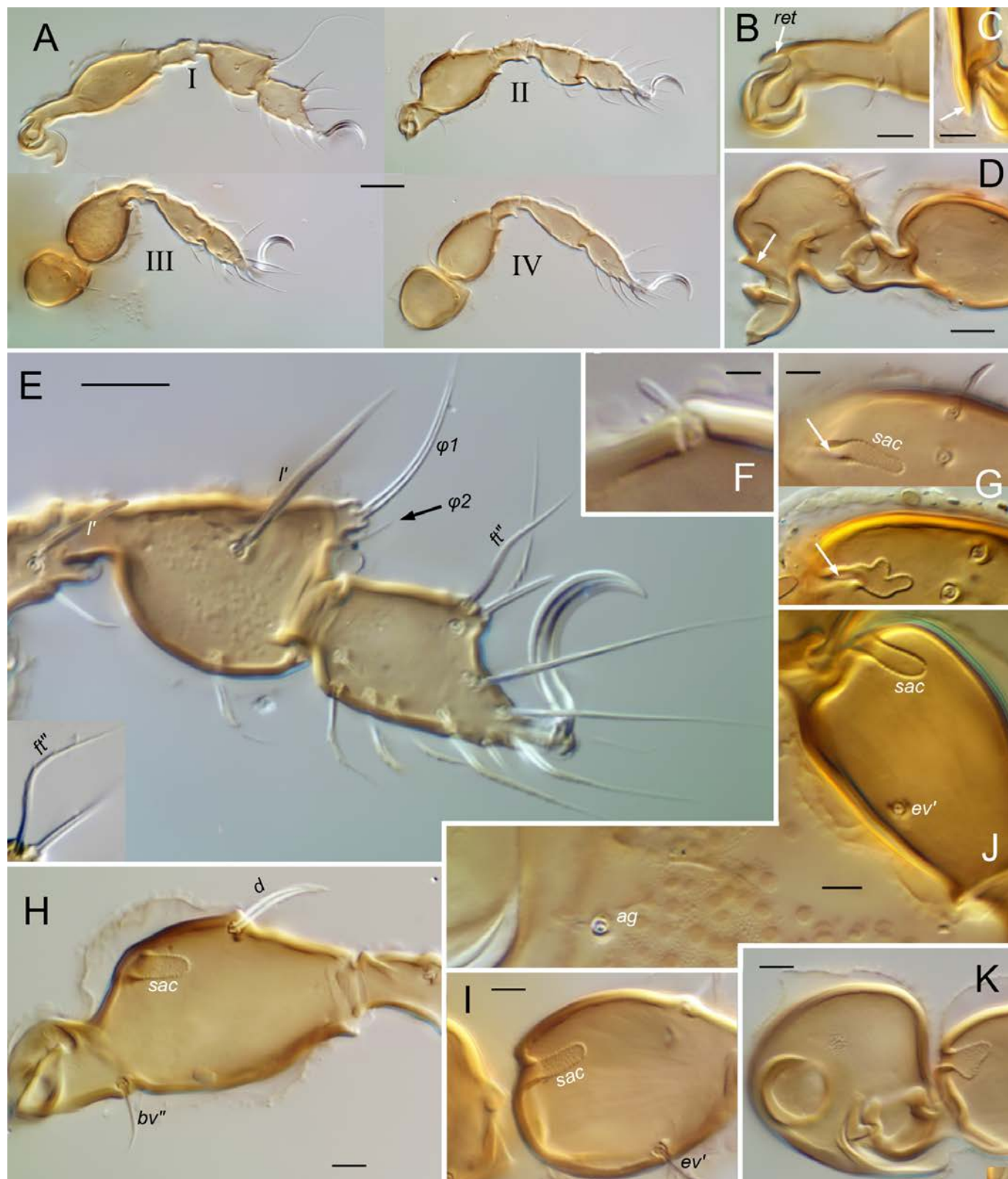
## Comparisons

Adults of *C. arboricolus* are distinguishable from those of all described extant *Caleremaeus* species in: having a prodorsum lacking enantiophysis *eA* and having the dorsosejugal tubercle



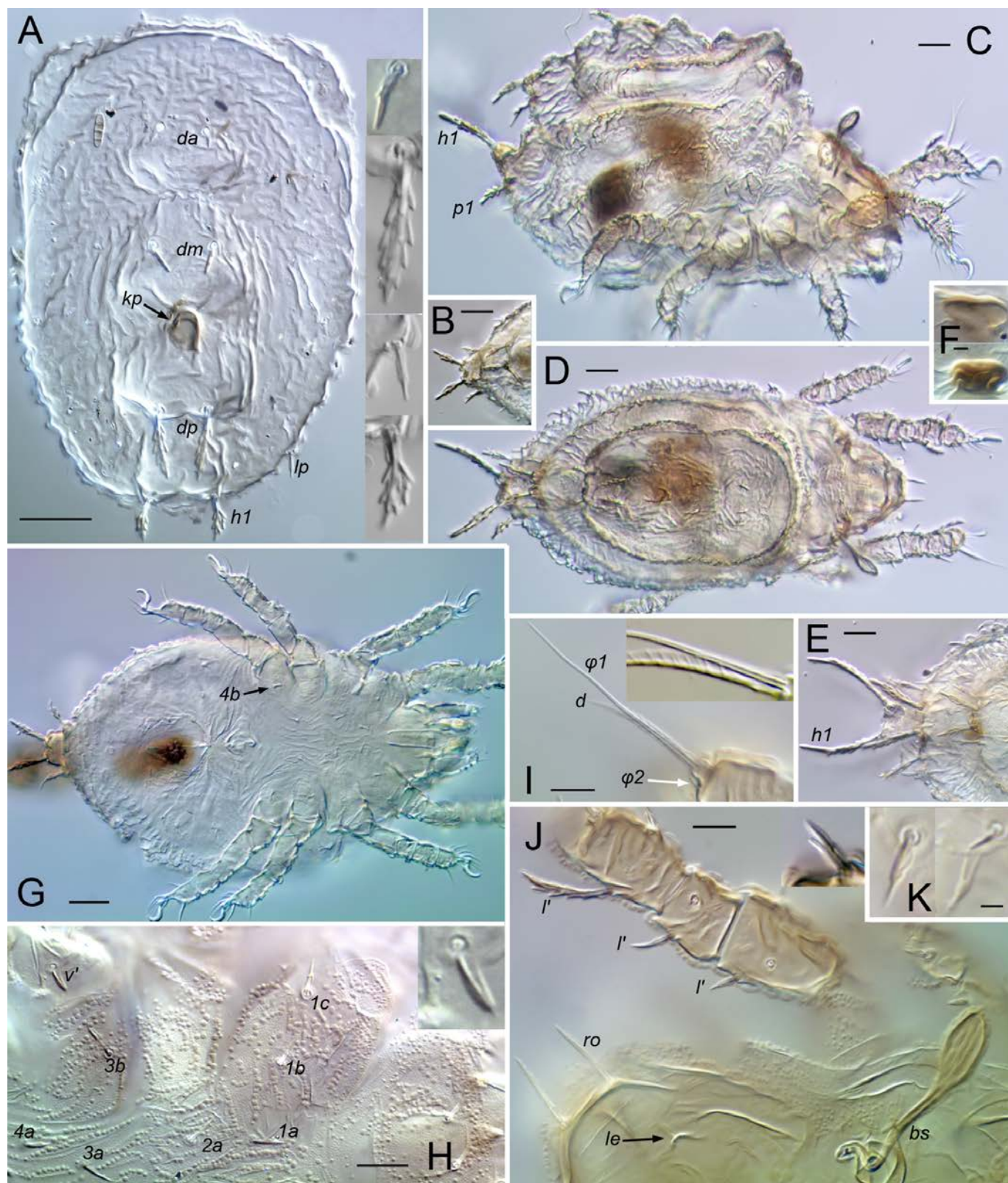


**Figure 10** *Caleremaeus arboricolus* n. sp., transmitted-light micrographs of adult: A – part of series of knots at margin of posterior notogastral bulge; B – detached notogastral cerotegument (optical cross-section); C – ventral plate cerotegument (face-on) near seta *ag*; D – coxisternum of male, surface focus (insert lower right = spermatopositor, arrowhead on largest alveolus); E – same, deeper focus; F – female with mostly extended ovipositor; G – distal part of ovipositor, showing ventral lobe (right) and one (of pair) dorsal lobe (left); H – coronal seta of ovipositor. Scale bars: 50 µm (F); 20 µm (D, E); 5 µm (A, B, G); 2 µm (C, H).



**Figure 11** *Caleremaeus arboricolus* n. sp., transmitted-light micrographs of adult: A – legs I-IV, abaxial view (trochanter II not shown); B – base of femur I, abaxial; C – same, ventral view (arrow to partial retroectum); D – trochanter III, ventral view (arrow to partial retroectum), with base of femur (twisted); E – tibia and tarsus I, adaxial view (lower left insert =  $\phi_1$  and base of solenidion  $\phi_2$  of different specimen); F – solenidion  $\phi$  of tibia II; G – proximodorsal part of two femora I, showing variants of femur I saccule (arrow to stigma); H – femur II and partial genu, abaxial view; I – femur III, abaxial view; J – aggenital region and abaxial view of femur IV; K – trochanter and base of femur IV, abaxial view. Scale bars: 20  $\mu$ m (A); 10  $\mu$ m (B-E); 5  $\mu$ m (G-K); 2  $\mu$ m (F).





**Figure 12** *Caleremaeus arboricolus* n. sp., transmitted-light micrographs of juveniles: A – exuvial scalp of larva, with inserts (top to bottom) of enlarged setae *da*, *dp*, *lp*, *h1*; B – protonymph, pygidial region, dorsal view; C – deutonymph, lateral view; D – same, dorsal view; E – tritonymph, pygidial region; F – exuvial scale attachments, lateral view, with sclerotized pocket in underside of larval scalp (*kp*) on top, detached and nested cornicle *k* of proto- and deutonymph from same specimen on bottom; G – protonymph, ventral view; H – partial coxisternum of deutonymph, ventral view, anterior to right (insert = trochanter III seta *v'*); I – dorsodistal tubercle of tibia I of deutonymph (lower) and tritonymph (upper: partial, better showing barbs and velum of seta *d*); J – deutonymph, dorsal view of partial prodorsum and leg I (insert: coupled seta *d* and solenidion of tibia II); K – femur I seta *bv''* of deutonymph, intact (left) and with isotropic external layer separated from birefringent core (right). Scale bars: 20  $\mu$ m (A-E, G); 10  $\mu$ m (H-J); 2  $\mu$ m (F, K).



(*dt*) represented instead by a linear series of usually three knots; having a notogaster with a series of knots outlining the posterior bulge and setae that are conspicuous, squamose (except  $p_2, p_3$ ); and saccules on leg femora instead of porose areas.

The most similar described species is *C. gleso*, which is known only from Baltic amber. Based on Sellnick's (1931) description and sketchy dorsal illustration of an adult, *C. gleso* shares with *C. arboricolus* the absence of distinct prodorsal cusps extending forward from a transverse ridge and notogastral setae that are clavate, at least in part. *C. gleso* differs from *C. arboricolus* in having: a prodorsum with larger, more clavate lamellar setae; a more sculptured central prodorsum (perhaps with more defined lamellae); and a depression on either side of the transverse sulcus. The notogaster was described as having foveate anterior and posterior bulges, but the sclerotized cuticle of these structures is smooth in all known extant species. Considering the difficulties of observing small amber inclusions, Sellnick may have mistaken the round cerotegument excrescences for 'pits', but this can be confirmed only if the species is rediscovered.

### *Caleremaeus nasutus* n. sp.

Zoobank: 38F837A3-7D6C-4D2C-B339-D4183DA29EBB

**Etymology** — The Latin species epithet 'nasutus' is an adjective referring to the large nose-like anterior lobe of the prodorsum.

**Material examined** — Holotype and 13 paratype adults from: USA, Alabama, Randolph Co., State Route 48, ca. 1 km east of Woodland (33° 22.8' N, 85° 23.4' W), 3.xii.1980, R.A. Norton col., from litter layer in young shortleaf pine (*Pinus echinata* Mill.) and mixed-oak (*Quercus* spp.) forest. Other material: Another 75 paratype adults are from Alabama, Lee Co., near Auburn, 7.xi.1975 (collector unknown), from litter in loblolly pine (*Pinus taeda* Linn.) forest. Holotype and 10 paratypes deposited in USNM; 15 paratypes in CNC, remainder in RNC.

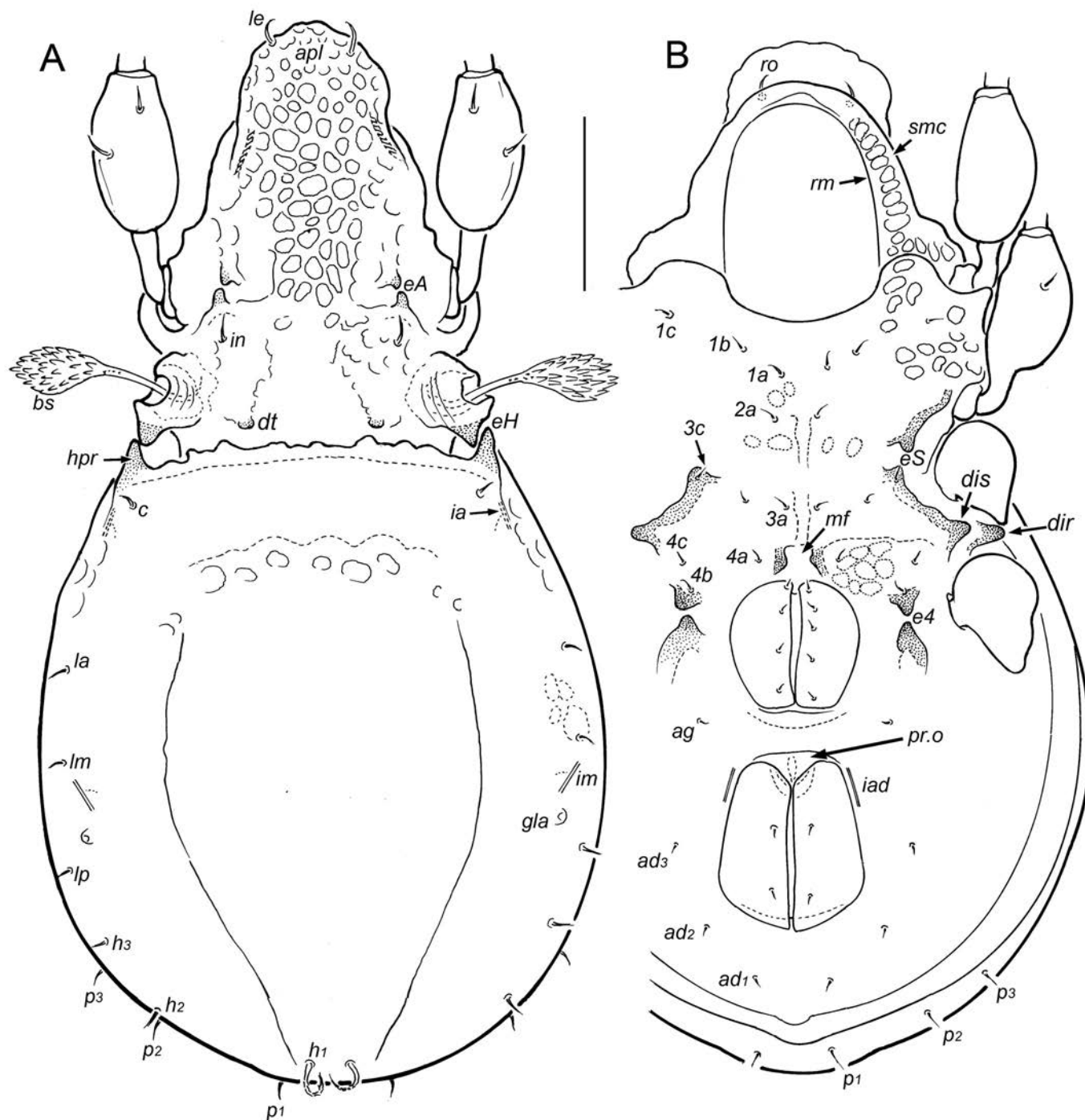
**Diagnosis** — *Caleremaeus* species with adults having total length 284–348 µm. Prodorsum without cusp or distinct lamella; lamellar setae inserted on large, hollow, tongue-shaped anterior lobe; tutorium weakly developed, enantiophysis *eA* present; usually with single small pair of dorsosejugal tubercles. Notogastral setae small (mostly ~10–15 µm), most barbed and curled beyond basal cerotegument nodule. Epimeral groove 2 without bordering tubercles or knots; ventrosejugal groove with only simple enantiophysis *eS*. Genital setation variable; females usually with five, males with 4–6 setae on each plate. Leg femora each with porose area. Juveniles unknown.

### Adult

Figures 13–17

**Dimensions** — Total length of 20 paratypes 284–348 µm (mean 326); maximum width 162–196 µm (mean 180). Female ( $n = 10$ ) length 336–348 µm (mean 342), maximum width 186–196 µm (mean 191); male ( $n = 10$ ) length 284–323 µm (mean 309), width 162–181 µm (mean 169).

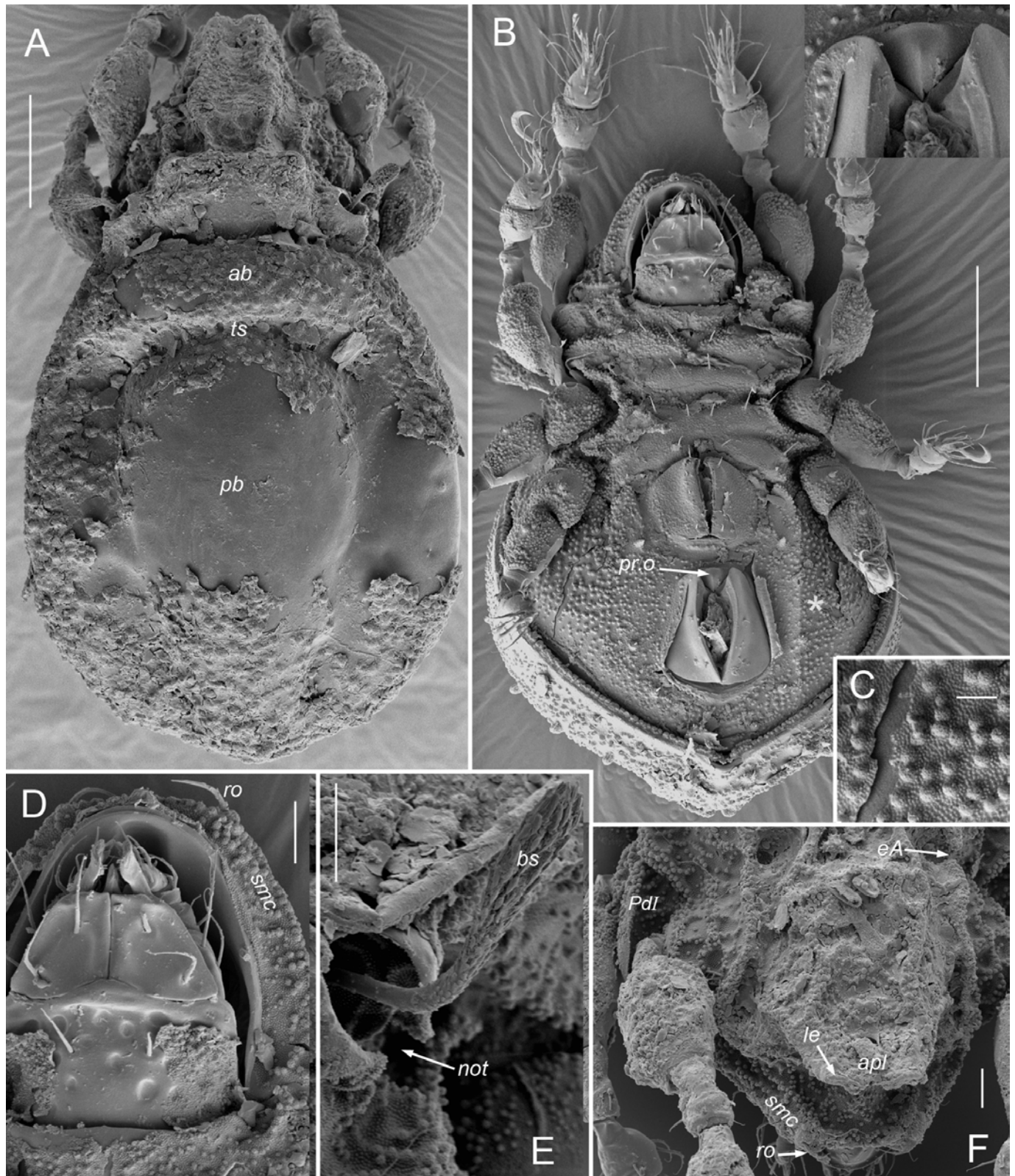
**Integument, setae** — Cerotegument excrescences mostly in form of dome- to mushroom-shaped or near-spherical excrescences, but partly irregular in form (Figs 14, 16A, B, H); largest on notogaster (mostly 3–5 µm diameter), smallest (1–2 µm) on venter where microgranules cover and fill intervening space (Fig. 14C–D). Dorsal setae (except *bs*) short, inconspicuous, acute to acuminate; basal third hyaline, birefringent, smooth, straight, surrounded by distinct and usually shaded cerotegument nodule; distal region isotropic, pigmented, curved to curled, with minute barbs on outer curvature (Fig. 16A, B, D), sometimes pulled away during preparations (Fig. 16C). Ventral setae (except adanal series) simple, nearly straight, without pigment or distinct basal cerotegument nodule.



**Figure 13** *Caleremaeus nasutus* n. sp., adult: A – dorsal view (legs mostly omitted); B – ventral view (legs omitted). Scale bar: 50  $\mu$ m.

**Prodorsum** — Surface foveate (depressions mostly 7–9  $\mu$ m diameter) except posteromedial region (above sigilla for cheliceral retractor muscles) smooth. Without lamella or cusp; setal pair *le* inserting on large, hollow, tongue-shaped anterior lobe (Figs 14F, 15E; *apl*) that conspicuously overhangs rostrum; lobe distally rounded in dorsal view (Figs 13A, 15A) or medially indented (Figs 14A, 15B). Tutorium weakly developed, but enantiophysis *eA* present





**Figure 14** *Caleremaeus nasutus* n. sp., scanning electron micrographs of adult: A – dorsal view cerotegument broken from central region of notogaster; B – ventral view, with enlargement of preanal region in upper right (\* indicates location of C); C – fractured cerotegument on ventral plate; D – subcapitulum and surrounding region, ventral view; E – bothridial region, anterior view; F – proterosoma, anterior view. Scale bars: 50 µm (A, B); 10 µm (D-F); 2 µm (C).



(Fig. 15A, E); lamella absent or represented by vaguely defined short longitudinal ridge medial to *eA* (Figs 14A, 15A, C). Rostral bulge inconspicuous under large prodorsal lobe; embossed pattern present (Fig. 15F–H). Submarginal crest complete anteriorly, between setal pair *ro* (Figs 13B, 14F); cuticle scrobiculate between crest and rostral margin (Fig. 15E). Short longitudinal ridge present laterally, above acetabula I–II. With single pair of small dorsosejugal tubercles. Bothridial seta (60–65 µm) with head strongly squamose (Figs 13A, 14E); bothridial wall foveate anteriorly (Fig. 15E), posteriorly with one strong tooth-like tubercle and with (Fig. 15C) or without second smaller adjacent (more medial) tubercle. Seta *le* short (13–18 µm), acuminate, slightly curved, pigmented and with minute barbs beyond basal nodule, inserted near anterior contour of prodorsal lobe with mutual distance at least three times length; *ro* similar in shape, with similar mutual distance; *in* similar but slightly shorter (11–13 µm); seta *ex* minute (~2 µm), vestige *exv* ventral or posteroventral to *ex*, nearly touching (Fig. 15E).

**Notogaster** — Anterior margin varying from irregular, with vaguely defined small tubercles and knots, to having half-dozen distinct, tooth-like tubercles; humeral process (~10 µm) usually overlapping main tubercle of bothridium. Transverse sulcus with about 10–12 foveae of different size (5–8 µm diameter); foveae also present anterolaterally, between *hpr* and seta *la* (Fig. 13A). Without series of knots along margin of posterior bulge. Setae distinctly bent or curled upon leaving basal cerotegument nodule; *p*<sub>2</sub>, *p*<sub>3</sub> (~6 µm) unpigmented, fine, simple, acuminate; all others pigmented, with small coarse barbs and acuminate tip: *c* (8–10 µm), *la-lp*, *h*<sub>2</sub>, *h*<sub>3</sub> (11–14 µm; Fig. 16B–D), *h*<sub>1</sub> (14–17 µm; Fig. 16A).

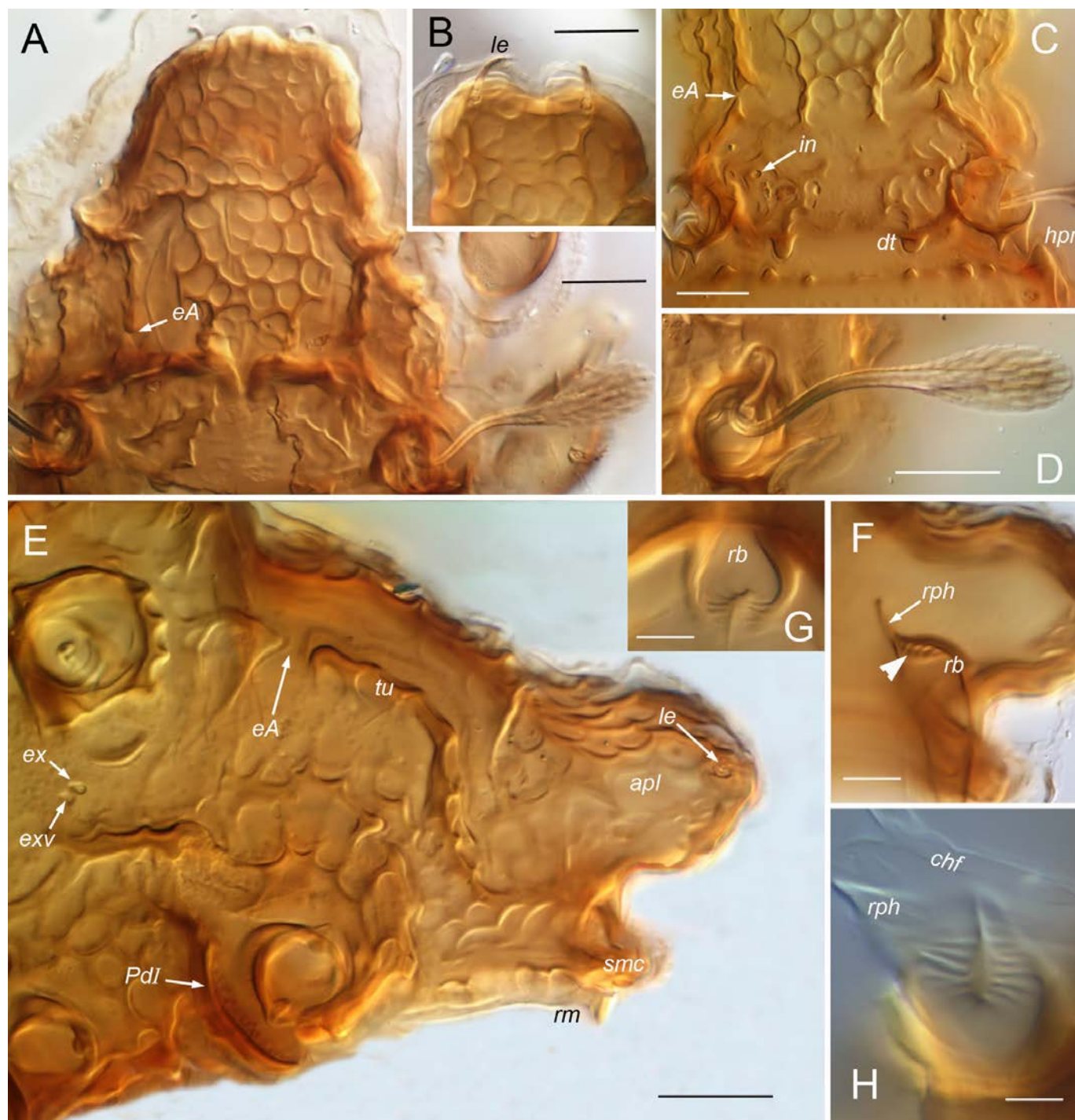
**Venter and lateral podosoma** — Foveate in acetabular region and lateral parts of coxisternum, and sometimes in single transverse row behind smooth mentotectum. Coxisternum without tubercles or knots along epimeral groove 2; enantiophyses *eS* of modest size, each tubercle simple in form; *e4* strongly developed (Fig. 16H); medial fossa with small pair of projections on inner margin (Fig. 16E). Discidium well-developed, usually appearing connected to posterior tubercle of *eS* by coaptive ridge, but rarely to anterior tubercle of *e4*. Enantiophysis *eL* and discidial ridge well defined (Fig. 16F); latter with distinct projection at ventral end, appearing like second discidium in ventral view (Figs 13B, 16E). Epimeral setae acuminate to attenuate (11–15 µm). Genital setation variable, 4–6 setae on each plate: of 10 females examined, seven symmetrical with 5/5 setae, three asymmetrical with 5/6; of 11 males examined, four symmetrical with 4/4, five with 5/5 and one each asymmetrical with 4/5, 4/6. Anogenital setae acicular; aggenital, genital and anal seate (5–8 µm) simple, adanal setae (10–13 µm) with basal nodule. Lyrifissure *iad* 8–10 µm. Apophysis of preanal organ tubular (Fig. 16G). Outline of ventral plate slightly bulging posteriorly, between setal pair *ad*<sub>1</sub>.

**Gnathosoma** — Subcapitulum foveolate, hypostomal (*h*, ~14 µm) and genal (*a*, *m*, 12–13 µm) setae attenuate. Chelicera (Fig. 17D) ~75–80 µm long; without spicules; setae *cha* (~23 µm), *chb* (~15 µm) attenuate, barbed.

**Legs** — Femur I ~2.7 times longer than maximum height in lateral view, with sharp, nearly right-angle transition between stalk and bulb (Fig. 17A). Femur II (Fig. 17B) similar, but slightly shorter (~2.5); stalk occupying about third length of femur I, about quarter that of femur II. All femora with porose area, mostly on adaxial face of bulb. Tibia I ~1.3 times longer than high in lateral view. Tarsus I abruptly tapering in distal half, but without distinct projecting mid-dorsal bulge (Fig. 17C). Tarsus II without noticeable proximal stalk, depth similar to that of tibia in lateral view. Seta *d* of femora short, flame-shaped (Fig. 17B), similar in structure to dorsal body setae (pigmented, barbed, with conspicuous cerotegument nodule at base). Seta *l'* of genu and tibia I not conspicuously enlarged.

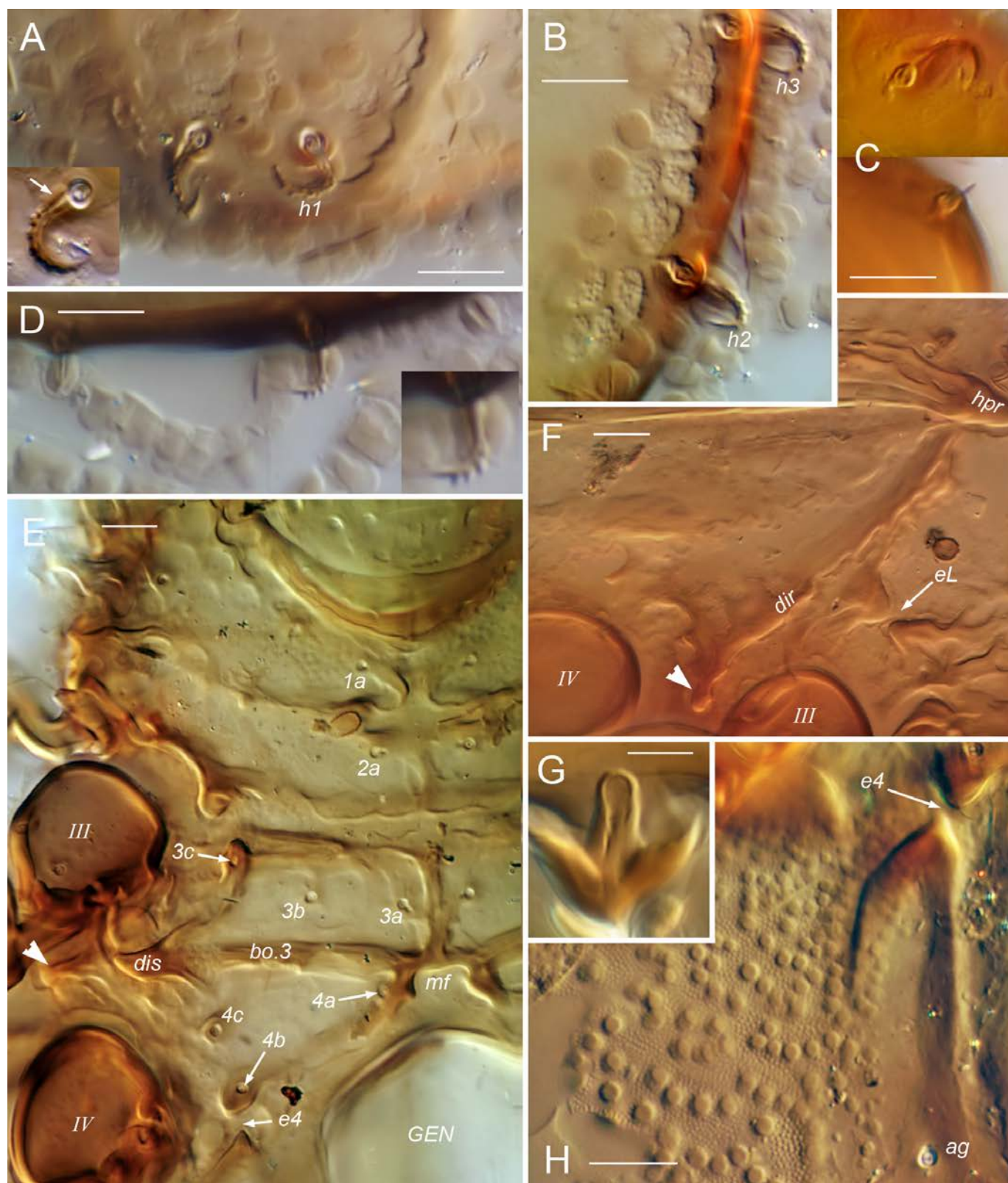
## Comparisons

Adults of *C. nasutus* are unique among described *Caleremaeus* species in having a prodorsum with a large, tongue-shaped anterior lobe, bearing the lamellar setae. Otherwise, they share several features with *C. monilipes* and *C. retractus*, including the presence of enantiophysis *eA*, the presence of an embossed pattern on the ventral face of the rostral lobe and rostrrophragma,



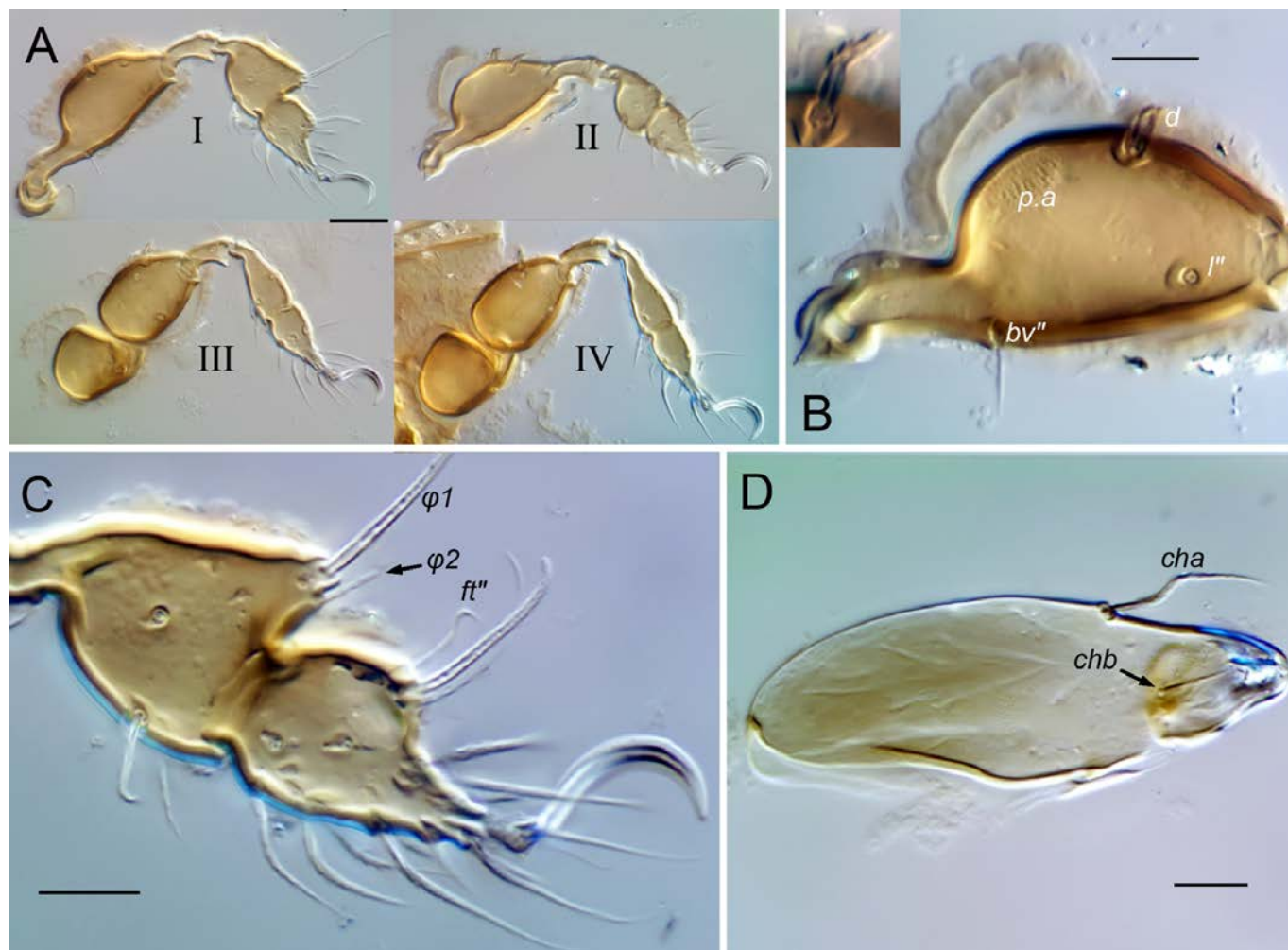
**Figure 15** *Caleremaeus nasutus* n. sp., transmitted-light micrographs of adult: A – prodorsum, dorsal view; B – anterior prodorsal lobe, different specimen; C – posterior prodorsum and sejugal region, dorsal view; D – bothridial seta; E – prodorsum, lateral view (gnathosoma removed); F – optical section of E, focused near midline; G – optical section of rostrum, anterior to top, dorsal view, focused on embossed figure on inner face of rostral bulge; H – same, different specimen, anterodorsal view of dissected fragment (rostrum broken on left). Scale bars: 20  $\mu$ m (A-E); 10  $\mu$ m (F-H).





**Figure 16** *Caleremaeus nasutus* n. sp., transmitted-light micrographs of adult: A – end of posterior notogastral bulge, region of setal pair  $h_1$ , dorsal view (insert =  $h_1$  from another specimen, arrow to basal cerotegument nodule); B – posterolateral contour of notogaster, dorsal view; C – notogastral seta  $la$ , entire (above) and with isotropic outer layer removed leaving only birefringent core; D – posterior contour of notogaster, ventral view (left  $p_1$  and  $p_2$  lost, leaving only basal cerotegument nodule; insert = enlarged  $p_1$ ); E – coxisternum, ventral view (arrowhead on projection at end of discoidal ridge); F – region above legs III-IV, lateral view (arrowhead as for F); G – preanal organ, optical section; H – region of aggenital enantiophysis. Scale bars: 10  $\mu$ m (A-F, H); 5  $\mu$ m (G).





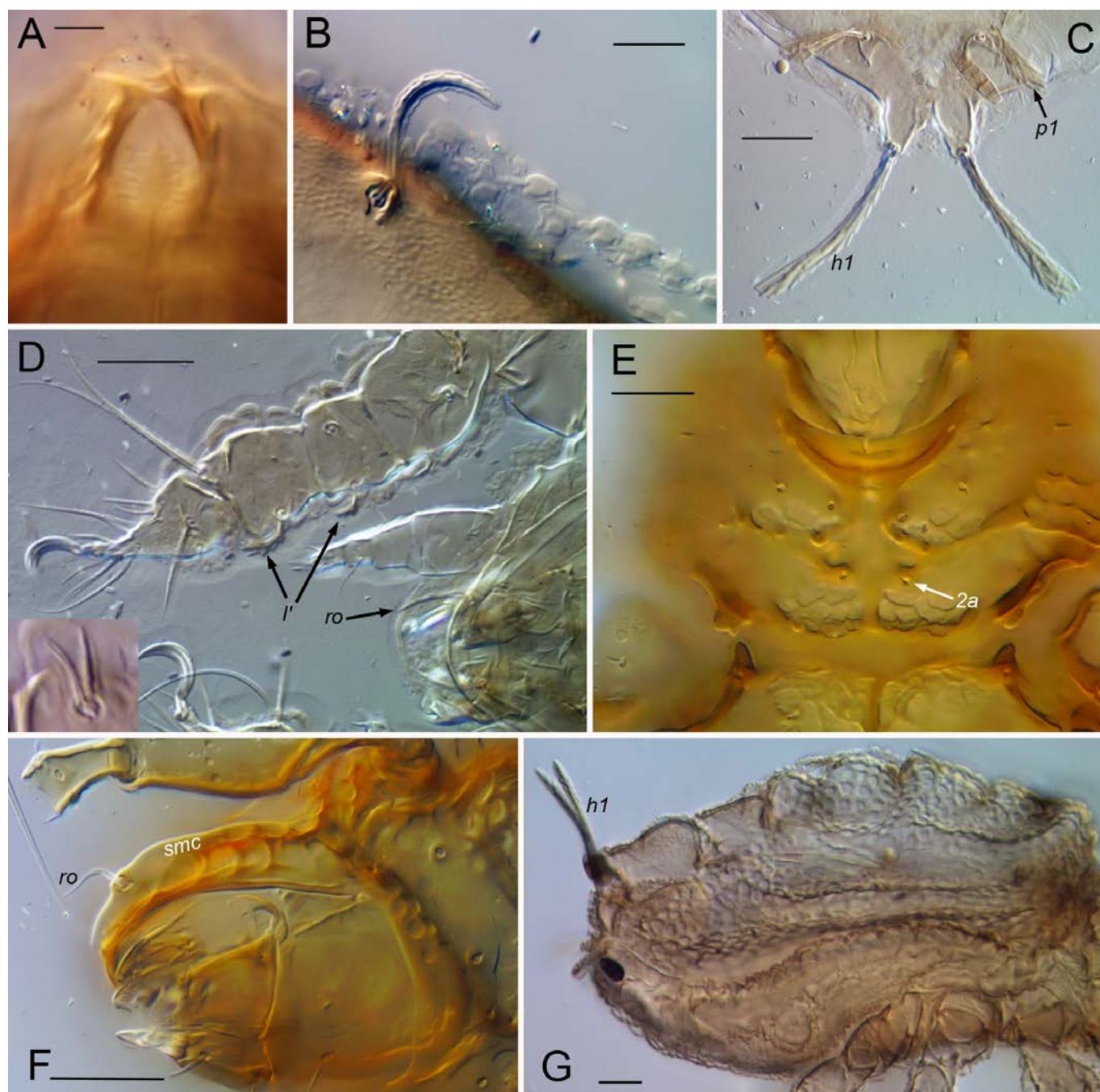
**Figure 17** *Caleremaeus nasutus* n. sp., transmitted-light micrographs of adult: A – legs I-IV, abaxial view (trochanter II not shown); B – femur II (cerotegument mostly separated; insert = seta *d* of femur I); C – tibia and tarsus I; D – chelicera, abaxial view. Scale bars: 20  $\mu$ m (A); 10  $\mu$ m (B-D).

and ridges laterally on epimeres III-IV that outline depressions coapted to the respective trochanters. The form of dorsal setae (with basal cerotegument nodule and pigmented, barbed distal portion) is shared with *C. retractus*, but not *C. monilipes*.

### Notes on biology

**Reproduction** — Gravid females of *Caleremaeus* species in this study carried a maximum of two eggs (one in each oviduct) but a single egg was most common. Eggs are slightly flattened unilaterally, about 1.8 times longer than broad (Fig. 5G). Females were more abundant than males, but all species seem bisexual; males accounted for about one-third to one-half of adults in our samples. This is consistent with data for *C. monilipes* presented by Seniczak and Seniczak (2019) but Grandjean (1941) reported a slight male bias (1: 0.8) for this species.

**Food** — Overall, species of *Caleremaeus* appear to be opportunistic feeders on fungi and decaying plant organic matter, as is typical of oribatid mites (Schneider *et al.* 2004). Based on very limited and unquantified information, adults and juveniles of both *C. retractus* (Fig. 19A–E) and *C. arboricolus* (Fig. 19F–H) ingest diverse fungal material—both hyphae and spores—and it dominated most boli and pellets we observed. Most other material was not

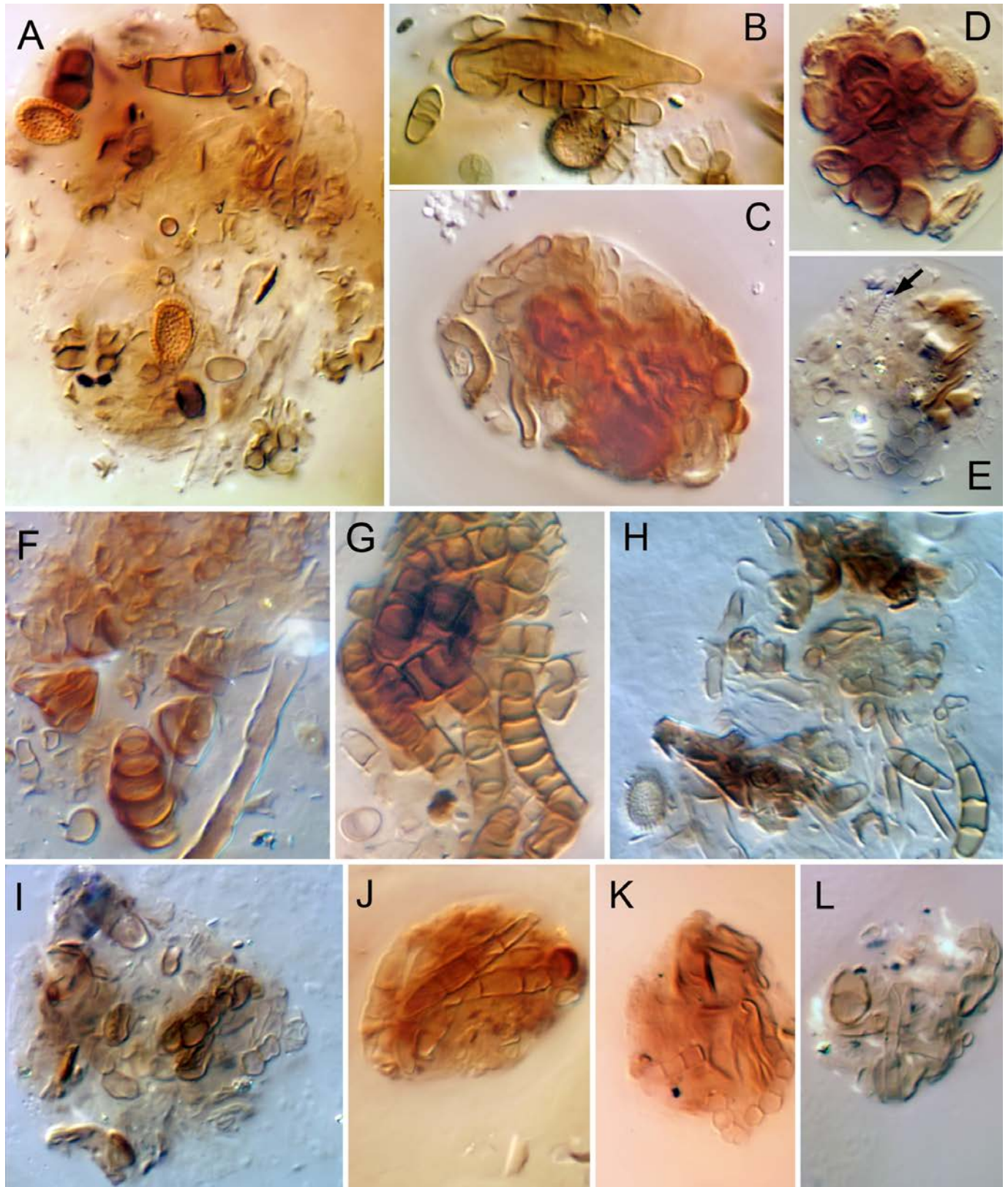


**Figure 18** Transmitted-light micrographs of *C. monilipes* (A-D) and *Caleremaeus* 'retractus' group from New York (E-G): A – adult (from Sweden), rostral bulge, deep focus to show embossed pattern; B – adult (from Spain), seta  $h_2$  and nearby cerotegument; C – deutonymph (from Sweden), pygidial region, ventral view of flattened specimen; D – same, leg I and rostral region, dorsal view (lower left insert: tibia II coupled seta  $d$  and solenidion); E – anterior part of coxisternum; F – anterior third, ventrolateral view; G – deutonymph, hysterosoma, lateral view. Scale bars: 20  $\mu\text{m}$  (C-G); 10  $\mu\text{m}$  (A, B).

identified but appeared to comprise fragments of plant-based organic matter. Boli and pellets in adults of *C. nasutus* (Fig. 19I–L) were generally like those of other species.

Despite its wide distribution, little has been written on the feeding biology of *C. monilipes*. Skubała and Maslak 2010 regarded *C. monilipes* as a xylophage, but neither of the two cited references (Luxton 1972; Schatz 1983) made such a claim. Fischer *et al.* (2010) found *C. monilipes* adults from tree trunks to have stable-isotope signatures more in line with those of





**Figure 19** Food boluses and fecal pellets from within specimens of *Caleremaeus retracts* (A-E), *C. arboricolus* (F-H) and *C. nasutus* n. sp. (I-L): A – food bolus in adult; B – part of different bolus in same adult; C – fecal pellet in different adult; D – same, different adult; E – fecal pellet in tritonymph (arrow on spiral thickening of plant tracheid cell); F – food bolus in adult; G – food bolus in deutonymph; H – food bolus in protonymph; I – food bolus in adult; J, K, L – fecal pellet in three different adults. Scale bar: 10  $\mu$ m (all to same scale).



soil-dwelling species, rather than lichen feeders; they speculated that they eat algae or other resources available on bark.

**Habitat associations** — Collectively, *Caleremaeus* species clearly show some affinity for above-ground microhabitats, primarily in forests. *Caleremaeus nasutus* and *C. retractus* (*sensu stricto*) have not been found outside soil microhabitats, but this may be due to a lack of appropriate sampling where these mites occur. Based on material in the CNC and RNC, members of the ‘retractus’ group have been collected from diverse non-soil substrates, including arboreal and saxicolous lichens and mosses, bark of both coniferous and deciduous trees (including cankered bark of chestnut trees), rotting wood of logs and tree-holes and decaying woody fungal sporocarps, in addition to soil-litter. *Caleremaeus arboricolus* is consistently associated with arboreal microhabitats, including bark, twigs and lichens; the single non-arboreal collection was from a regurgitated owl-pellet lying on the soil surface. The similar *C. gleso*, known only as a Baltic amber fossil, was almost certainly arboreal since trees were the source of original resin-flows. While little is known of *C. divisus*, it has been reported only from arboricolous moss.

There are scattered reports of *Caleremaeus monilipes* being collected in low to moderate density from forest soil-litter (e.g. Moraza and Peña 2005), but the original collection was from decaying wood (Michael 1882) and woody substrates seem to be the primary microhabitat, particularly logs in early stages of decomposition (Siira-Pietikainen *et al.* 2008; Skubala and Maslak 2010 and included references; Seniczak and Seniczak 2019; Seniczak *et al.* 2019) or rot-holes in standing trees (Skubala and Gurgul 2011; Taylor and Ranius 2014). Other works suggest less fidelity to dead woody substrates. Travé (1963) considered it a predominantly saxicolous species that could also be found on trees. Subías (1977) considered it a muscicole, found with similar frequency on rocks and low on tree trunks; Fischer *et al.* (2010) also noted the lower-trunk affiliation. By contrast, Arroyo *et al.* (2013) found moderate numbers in oak-canopy mosses, and Seniczak and Seniczak (2019) reported an abundance on oak-trunk moss above 1.5 m, but absence from lower regions. Moss substrates also were indicated by Schweizer (1957) and Bonnet *et al.* (1975). Odd reports (at least some clearly related to transported substrates) include discoveries in nests of mice, birds and ants (Lebedeva and Poltavskaya 2013; Krawczyk *et al.* 2015; Elo *et al.* 2018). It remains to be determined how much the microhabitat diversity of *C. monilipes* reflects possible cryptic speciation (see Introduction).

## Family-group classification

### Composition

Caleremaeidae Grandjean, 1965b, was monogeneric when proposed, but as many as six other genera have been added since, according to author; these include *Veloppia* and five genera usually grouped as Anderemaeidae (*Anderemaeus*, *Cristeremaeus*, *Epieremulus*, *Luxtoneremaeus*, *Yugaseremaeus*). We believe that none of these additions (or others that have been informally suggested in unpublished internet documents: i.e. *Megeremaeus*, *Caucaseremaeus*; Subías 2019) can be supported in a phylogenetic context, and that the family should remain monogeneric.

The removal of *Veloppia* will be discussed in detail separately (Norton *et al.*, in preparation). Woas (2002) doubted its inclusion in Caleremaeidae and perceived a closer relationship to Hungarobelbidae. With increased knowledge, we view the various adult similarities proposed by Norton (1978) as more widespread and possibly symplesiomorphic, and juvenile traits clearly show that *Veloppia* is not among the plicate eupheredermous groups.

The idea that the southern-hemisphere genus *Anderemaeus* and some other members of Anderemaeidae are confamilial with *Caleremaeus* recently was discussed and rejected by Norton and Ermilov (2019). In summary, inclusion of *Anderemaeus* in Caleremaeidae was first formalized by Woas (2002), but it had roots in earlier studies (Franklin and Woas 1992,

Subías and Arillo 2001). By transferring the type-genus, Woas (2002) effectively subsumed Anderemaeidae within Caleremaeidae *sensu lato*. Subías (2004) followed this proposal but expanded it by including all genera of Anderemaeidae. Woas' proposal was based on three shared traits, paraphrased here: the presence of a lamella-tutorium complex; the presence of the aggenital enantiophysis (*e4*, *U*); and a tubular preanal organ. Norton and Ermilov (2019) considered these to be symplesiomorphies of the relevant taxa, and instead showed that *Anderemaeus*—and therefore its family, Anderemaeidae—are part of a clade of Brachypylina that is more highly derived than *Caleremaeus*. Based largely on the morphology of juveniles, they transferred Anderemaeidae to Gustavioidea.

## Superfamily classification

Grandjean (1965b) proposed Caleremaeidae as part of a reorganization of what he called the 'groupe E restant', i.e. remaining eupheredermous genera that, due to insufficient knowledge, were not treated in his iconic classification of oribatid mites (Grandjean 1954a). He included six of the families in the newly proposed Eremuloidea (= Ameroidea; R10) but left Caleremaeidae, Eremaeidae and Tenuialidae without higher assignment. Since then, Caleremaeidae most often has been included in Oppioidea (e.g., Balogh 1972; Bulanova-Zachvatkina 1975; Marshall *et al.* 1987; Fujikawa 1991; Balogh and Balogh 1992), but as concepts of that superfamily became more restricted, Caleremaeidae was omitted (e.g. Behan-Pelletier 1991).

Subías (2004) deconstructed the traditional Oppioidea and included his broad sense of Caleremaeidae (see above) in a newly recognized Eremelloidea, but none of the other included families is known to be eupheredermous. This classification has been little used by other authors. Informally, in unpublished but frequently-cited online annual updates, Subías (2016 and following) abandoned Eremelloidea and grouped Caleremaeidae *sensu lato* with Eremaeidea. This had been suggested earlier—but not formalized—by Franklin and Woas (1992), though Subías' concept of the latter superfamily seems much broader than theirs. Weigmann (2006) noted that previous classifications of Caleremaeidae were problematic in a phylogenetic context and recognized the monofamilial Caleremaeoidea, though he did not indicate whether his sense of Caleremaeidae was broad or narrow.

Previously (Norton and Behan-Pelletier 2009; Schatz *et al.* 2011), we followed the tentative suggestions of Woas (2002) and included Caleremaeidae in an expanded concept of Ameroidea. It was the most recent of several expansions of the superfamily that began with Grandjean's (1966) addition of Staurobatidae. Curiously, he did not also include Basilobelbidae, despite their having the key traits of aggenital neotrichy and highly reduced proral setae on tarsi II-IV (see Grandjean 1959b, as *Hammation*), but this family was added by Balogh (1972) along with Heterobelbidae. Subsequently, Miko and Travé (1996) added Hungarobelbidae and Woas (2002) added Rhynchoribatidae, Spinozetidae and Oxyameridae. We relied upon the similarities of *Caleremaeus* and *Hungarobelba* noted by Travé (1961) and Miko and Travé (1996) to support adding Caleremaeidae to Ameroidea, but the resulting group of 14 families little resembles Grandjean's (1965b) original concept and even includes some families whose juveniles are not known to be eupheredermous. After our detailed studies of *Caleremaeus* herein, and reconsideration of traits—plus reference to two limited molecular studies—we no longer feel that this transfer to Ameroidea was reasonable; there are three general reasons.

First, the several purported similarities of *Caleremaeus* and *Hungarobelba* are not exclusive enough to be convincing synapomorphies or are not clearly homologous. Paraphrasing from Travé (1961) and Miko and Travé (1996), these are as follows. (1) The two genera share the laterosejugal enantiophysis (*eL*): however, this is found in several other eupheredermous taxa (R4). (2) They share the prodorsal enantiophysis (*eA*) and associated groove, though *eA* can be absent (presumed lost) from species in each genus: but *eA* is even more widespread than *eL* (see R4 and summary in Norton and Ermilov 2019). (3) They share an anteriorly truncate notogaster, with some type of humeral projection: again, this is not exclusive, being shared also by numerous other eupheredermous taxa—i.e. *Veloppia*, Megeremaeidae, Cepheidae—as

well as some disparate apherodermous families such as Anderemaeidae, Autognetidae and Quadropiidae, as well as Spinozetidae (with juveniles unknown). (4) They purportedly share a similar dimorphic type of genital papilla, with the posterior two pairs being more elongated, clavate, and slightly distant from the anterior pair: but these papillae are not perfectly rounded, and their shape can appear slightly different depending on orientation—we found no difference in shape or spacing among the papillae of any *Caleremaeus* species (see also Behan-Pelletier 1991). (5) They share a ridge near the rostral margin that bears seta *ro*: these are differently formed structures—that of *Caleremaeus* is a uniform shelf-like structure that may extend around the front of the rostrum while that of *Hungarobelba* is a much less conspicuous carina that effaces anteriorly; it is not unusual in Brachypylina for a carina (lateral ridge) to be directed anteriorly from acetabulum I, though typically it lies close to or even merges with the rostral margin (e.g. Grandjean 1960, 1962; Behan-Pelletier 1990) rather than reaching seta *ro*. (6) They supposedly share a long famulus on tarsus I: but this is vague, and a matter of degree—that of *Hungarobelba* is indeed unusually long and tapered but so is that of Basilobelbidae (Grandjean 1959b), and a long, tapered famulus is common in Damaeidae; the famulus of *Caleremaeus* is more modest in length and baculiform.

Second, the most distinctive trait of Ameroidea—at least in its original context (Grandjean 1965b, 1966)—that might be considered apomorphic among eupheredermous taxa is aggenital neotrichy, and several of the component families also have a more general ventral neotrichy. *Caleremaeus* exhibits no neotrichy on the body or legs. Other unusual traits of Ameroidea are not universal in the group. Most, but not all families exhibit size regression of proral setae on legs II–IV, where they are small, spiniform and often inconspicuous. In *Caleremaeus* these setae are plesiomorphic: normally formed and conspicuous. *Caleremaeus* also has a rather plesiomorphic form of preanal organ, in which the internalized apodematal extension is a simple, hollow, tubular or caecum-like structure. This does not occur in Ameroidea, but no clearly derived state for the group has been characterized. In its expanded context of 14 families, Ameroidea seems unjustifiable by synapomorphies; it has been defined (Norton and Behan-Pelletier 2009) by a collection of some widespread plesiomorphies and others that are present or absent according to family.

Third, the only existing molecular phylogeny study that includes *Caleremaeus* and members of Ameroidea contradicts the inclusion of Caleremaeidae in Ameroidea. With a focus on relationships among members of Zetorchestoidea, Lienhard *et al.* (2013) examined tree topology for seven eupheredermous families. Their consensus tree, based on a combined data set of mitochondrial (COI) and nuclear (EF-1 $\alpha$ ) genes, showed *Caleremaeus* as the sister-group of *Niphocephus* (Niphocephidae); in turn, this clade was sister-taxon to the families Ctenobelbidae and Damaeolidae, which are unquestioned members of Ameroidea. Numerous eupheredermous families were not represented, and not all branches had high statistical support, but the strong linkage of *Caleremaeus* to Niphocephidae, rather than the ameroid families, seems significant. Like *Caleremaeus* (but unlike Ameroidea), juveniles of Niphocephidae—and other members of Zetorchestoidea (sensu Schatz *et al.* 2011), as well as Neoliodoidea and Plateremaeoidea—have plicate cuticle, a trait that we consider plesiomorphic in Brachypylina.

The only other molecular work that included *Caleremaeus* was based on the 18S ribosomal RNA gene. In a study encompassing representatives of many Brachypylina families, but none in Ameroidea, Schaefer and Caruso (2019; supplemental online material) presented two detailed trees. A maximum likelihood tree included *Caleremaeus* within a clade that contained four species in the family Damaeidae (in the monofamilial Damaeioidea), while in a Bayesian inference tree *Caleremaeus* formed a trichotomy with two different clades of those Damaeidae species. Since no Damaeidae were included in the Lienhard *et al.* (2013) work, direct comparison is not possible.

Faced with a seemingly mosaic distribution of morphological traits among the main eupheredermous taxa (Miko and Travé 1996; Woas 2002), at present we can offer no strong argument for including Caleremaeidae in any of the larger superfamilies. For example, the characteristic topography of the *Caleremaeus* notogaster is approximated in certain



Plateremaeoidea—Pedrocortesellidae (e.g. Hunt 1996, his Fig. 34A)—but no other similarities seem important and differences are many. The prodorsum of at least some *Caleremaeus* species seems most similar to that of Megeremaeidae (Eremaeidea) in having a lamella-tutorium complex, *eA*, *eL*, *eH* and an alveolar vestige of the second exobothridial seta, but most hysterosomal and leg traits differ. The scalp-attachment cornicle of *Caleremaeus* nymphs is seen also in Damaeoidea, but nymphs of the latter are not plicate, and adults differ in many ways.

Therefore, we adopt Weigmann's (2006) monofamilial Caleremaeoidea, but view Caleremaeidae in its strictest sense, i.e. including only *Caleremaeus*. Its diagnosis, as well as that of the family, would be identical to that of the genus, given above. Such a redundant classification has no phylogenetic content, but in this instance it seems preferable to retaining Caleremaeidae in an obviously polyphyletic superfamily, such as Ameroidea in the sense used by Woas (2002), Subías (2004), Norton and Behan-Pelletier (2009) and Schatz *et al.* (2011). Caleremaeoidea joins Neoliodoidea, Plateremaeoidea and Zetorchestoidea in a paraphyletic cluster of superfamilies near the base of Brachypylina phylogeny, characterized by eupheredermous nymphs with plicate cuticle.

## Remarks on morphology and classification

**1. Role and evolution of lamella and tutorium** — It seems likely that the lamella and tutorium appeared early in the evolution of Brachypylina, in a ridge- or rib-like form such as in Megeremaeidae (Aoki and Fujikawa 1971; Behan-Pelletier 1990; see also Woas 2002, Norton and Ermilov 2019). As known for 150 years (Michael and George 1879; Berlese 1896), the two structures play a role in defense by providing a place for coaptation of leg I, the distal parts of which typically lie between them when legs are adducted following disturbance. In more derived oribatid mites they often are highly developed as blade-like projections that overhang the adducted leg from above and below, respectively (Grandjean 1952; Fernandez *et al.* 2013).

Regression also has occurred, with transitions starting from both blade - and ridge-like forms. In some families or genera of the derived, poronotic superfamilies Ceratozetoidea and Oripodoidea, large blade-like lamellae and tutoria have regressed to narrow carina or ridges, or have disappeared. Similarly, in *Caleremaeus monilipes* and *C. divisus* the ridge-like lamella-tutorium complex seems sufficiently developed to provide a coaptive space (see Seniczak and Seniczak 2019, their Fig. 4), while in North American species this complex ranges from partially regressed (*C. retractus*, *C. nasutus*) to being almost entirely lost (*C. arboricolus*). Whether the defensive leg adduction occurs in any *Caleremaeus* species is unknown, as behavior has not been reported.

**2. Rostral bulge** — This bulge is a centrally located convexity in the solid limb of the rostral tectum that appears to accommodate distal elements of the gnathosoma—probably the cheliceral tips—when the mite is in a defensive posture with chelicerae retracted and the subcapitulum elevated. It is a common feature in brachypylina oribatid mites and often it seems 'excavated' on the inner face to make the bulge very thin-walled, though this is not true of *Caleremaeus* species. Also, the pattern of excavation may result in an apparent central tooth projecting into the bulge (Norton and Ermilov 2017). *Caleremaeus* has no such tooth, but a frontal view of some species may give such an impression, since a unique, raised central rib is seen in optical cross-section (Fig. 2L). The rib is the central element of an embossed 'scorpion-like' pattern on the lower surface of the bulge (Figs 2K; 15F–H; 18A) that is present in all examined species except *C. arboricolus*. The central rib is crossed by a symmetrical series of about six raised transverse striae directed perpendicularly from it. The transverse striae are concentrated at the base of the rostral bulge, but the 'tail' of the scorpion appears to continue onto the freely-projecting rostrum, to which the soft cheliceral frame is attached (Fig. 15H; *rph*, *ch.fr*).

**3. Exobothridial seta vestige** — Close to the exobothridial seta in the adult of all examined *Caleremaeus* species is a circular pale spot that in transmitted light looks much

like the alveolus of seta *ex*, except no seta emerges from it. We consider it an alveolar vestige (*exv*) of the second exobothridial seta, a seta that has been lost from all members of Brachypylina. Among Brachypylina, we know of a similar vestige only in adults of Eremaeidae and Megeremaeidae (Behan-Pelletier 1993; as *em*). Though interesting, we interpret this similarity as a symplesiomorphy and therefore not evidence of a phylogenetic relationship among these families. A similar vestige is widespread in the outgroup Nothrina, many members of which also have a single exobothridial seta (e.g. Norton *et al.* 1996), and even in some Enarthronota (Grandjean 1963).

**4. Enantiophyses** — Adults of *Caleremaeus* species are rich in enantiophyses, tubercles that oppose each other across a cuticular groove. The grooves and tubercles seem to function in holding and anchoring an air film that has contact with the stigmata of the apodematal-acetabular tracheal system (Chen *et al.* 2004). It is obvious how such localized plastrons are important for intertidal taxa (e.g. Pfingstl and Krisper 2014), but even for fully terrestrial species they could be important whenever the immediate environment is inundated with water for extended periods of time.

Grandjean (1954b) proposed the term ‘enantiophysis’ in reference to Damaeidae and later (1960) refined his ideas and nomenclature, but the structures are widespread, particularly in early- to middle-derivative eupheredermous families. Grandjean (1960, 1966) doubted that enantiophysis homology among taxa could be established on a general scale, but he did note the widespread taxonomic distribution of two, both of which occur in *Caleremaeus* (Figs 1, 13). These span the important sejugal groove, which encircles the body and in which one of the three pairs of stigmata open. The parastigmatic enantiophysis (*eS* or *S*) spans the groove just below the sejugal stigma, and the humeral enantiophysis (*eH* or *H*) spans it behind the bothridium, from which a tubercle on its posterior wall opposes a humeral projection from the notogaster. Since then, it has become apparent that three other enantiophyses are consistently placed and readily identified.

The laterosejugal enantiophysis (*eL* or *L*) also spans the sejugal groove, but mid-laterally, above the acetabula (Norton 1978). In the literature it has been reported for relatively few taxa—Caleremaeidae, Hungarobelbidae, *Gymnodampia* (Ameridae), *Veloppia*—but it also exists in Megeremaeidae (e.g. Behan-Pelletier 1990, her Fig. 32). Moreover, many descriptions of oribatid mites omit details of the lateral podosoma, so this is certainly an incomplete list. An almost certain independent evolution occurred in some Selenoribatidae, intertidal mites that rely on plastron respiration (Pfingstl 2013, 2015). In this family the anterior tubercle bears the opening of the coxal gland (*z*), which is not true of other taxa and reinforces the idea that this is an independent appearance of *eL*. Grandjean (1968) considered this a parastigmatic enantiophysis but it is distinctly dorsal to the acetabula, whereas in its usual sense *eS* is below them.

Two others are associated with different grooves. The prodorsal (*eA*, or *A*) enantiophysis spans a dorsolateral groove on the prodorsum between the levels of acetabula I and II. If a tutorium exists, its posterior end forms the anterior tubercle of *eA*, with a separate tubercle immediately posterior to the groove. In the absence of a tutorium there can be a separate small tubercle on the anterior side of the groove. This enantiophysis is constant, or nearly so, in some eupheredermous families (Megeremaeidae, Pheroliodidae), but has variable presence in Caleremaeidae, Hungarobelbidae and *Veloppia*. It may be absent from most members of a family, but present in one or more genera, as in Damaeidae (*Tokukobelba*, some *Kunstidamaeus*), Ameridae (*Gymnodampia*) and the apheredermous family Anderemaeidae.

The aggenital enantiophysis (*e4*, *U*, *G*, *co.ag*) spans epimeral groove 4, with the anterior tubercle often bearing seta *4b* (see R5). It is widespread but scattered among the non-poronotic Brachypylina, as summarized by Norton and Ermilov (2019). Among proven eupheredermous taxa it is present in all species of Caleremaeidae and *Veloppia*, some Cepheidae (*Eupterotegaeus*) and some Eutegaeidae (*Neoeutegaeus*); among ‘presumed’ eupheredermous families—i.e. with unknown juveniles but classified in Cepheoidea and Polypterotozetoidea—it seems to be universal in Microtegeidae, Cerocephidae and Nodocephidae. Among apheredermous taxa,

it is typical of Anderemaeidae and is found in one genus each of Otocephaeidae (*Fissicepheus*; Aoki 1967) and Nosybeidae (*Topalia*; Colloff 2019). It is absent from Megeremaeidae and Hungarobelbidae, and is questionable in a few Damaeidae (a tubercle bearing seta *4b* may be hypertrophied, but no posterior tubercle is present (e.g. *Tokukobelba*; Lamos 2016).

**5. Epimeral setation** — Herein (Figs 3F, 8B, 10D, 13B), we follow the modification of Grandjean's (1934) chaetotaxy for epimeral setae proposed by Norton and Franklin (2018; their Remark #15). The fundamental difference is that Grandjean focused on the order of setal appearance on each epimere, while the modification focuses on positional correspondence and therefore probably reflects metameric homology. This modification especially affects the notations for *4a* and *4b*, setae on an epimere that is first formed in the protonymph. Like the many leg IV setae that are delayed to the deutonymph, we feel seta *4a* (= *4b* in the widely used Grandjean chaetotaxy) is also delayed to the deutonymph; when it appears, it is well aligned with larval setae *1a*, *2a* and *3a* on the soft sternal cuticle (Fig. 12H). By contrast, protonymphal seta *4b* (= *4a* in the Grandjean chaetotaxy) is inserted on the paired epimeral sclerite (Fig. 12G; out of view in Fig. 12H), as are larval setae *1b* and *3b*.

**6. Preanal organ** — This sclerotized structure serves for the origin of paired adductor muscles that act on the genital valves (Grandjean 1969). It appears to have evolved from a simple unpaired plate on the anterior wall of the anal vestibule, as in many Nothrina, to become a largely internalized apodeme or apophysis in most Brachypylina. When the anal valves are tightly closed, the base of the organ either may be entirely hidden in the vestibule or it may be partly exposed; this depends on the size of the base and especially whether or not the anterior tectum of the two anal valves fully meet. In *Caleremaeus* species the organ is much like that of Damaeidae (Grandjean 1969, his Fig. 5A; *LF*), though the shape of the internal apophysis differs. The exposed base of the organ is relatively large, subtriangular in ventral view (Figs 8B, 13B, 14B; *pr.o*); the muscles originate on the internalized tubular apophysis and insert directly on the genital plate (Figs 3F, H, I, 16G). Weigmann (2006; his Fig. 121b) illustrated the anal plates of *C. monilipes* as completely covering the preanal organ, but this appears to be an error: in all our specimens of *C. monilipes* the base of the organ is exposed when anal plates are closed.

**7. Leg setation** — *Variation.* The complement of setae and solenidia on legs of both adult and juvenile instars is remarkably consistent in *Caleremaeus*, such that Table 1 expresses the ontogeny in all examined species to the extent that data exist (see R12). No interspecific difference was noted among adults, and a single example relates to ontogeny: seta *l'* of tibia III is tritonymphal in *C. monilipes*, but deutonymphal in the other studied species (Table 1). Noted intraspecific variation includes only the following: (1) in the near-topotypical population of *C. retractus*, genu I seta *v'* was absent from two of nine tritonymphal legs examined; (2) in the topotypical population of *C. arboricolus*, tibia IV seta *l'* was absent from one of eight tritonymphal legs examined; (3) in the same population, tarsal seta *l''* was absent from one of 10 adult legs I examined and (4) tarsal seta *pl'* was absent from one (different) adult leg. The last example presumably is anomalous, since *pl'* is a fundamental, eustasic tarsal seta that forms in the larva. The previous three relate to delays in the formation of amphistasic setae (setae variable among species or populations regarding the instar of first appearance). In examples 1 and 2 the setae presumably would have appeared in the adult, since these setae were present on all adults examined; in example 3, the delay in an adult-forming seta represented a loss by retardation in the concepts of F. Grandjean (see review in Norton 1977).

*Trochanter III.* *Caleremaeus* species are unusual in having both setae of trochanter III—*v'* and *l'*—formed in the deutonymph. The many oribatid mites for which setal development is known exhibit a variety of ontogenies on trochanter III, but usually these setae are formed in successive instars. We know of only four other species with the *Caleremaeus* pattern. Of these, only *Niphocephus nivalis* (Schweizer, 1922) is a member of Brachypylina (Travé 1959); the other three are in the nothrine superfamily Malaconothroidea and include *Mainothrus badius* (Berlese, 1905), *Tyrphonoethrus maior* (Berlese, 1910; as *Trimalaconothrus novus* and denoted



$v'_1, v'_2$ ) and *Allonothrus giganticus* Haq, 1978 (data respectively from Seniczak *et al.* 1998; Knülle 1957 and R.A.N. unpublished).

**Lateral setae.** On femora and tibiae I and II of *Caleremaeus* species, the lateral pseudosymmetrical pair have positions that seem far from being 'paired' (Fig. 4A, B). The adaxial member ( $l'$ ) is high on the inner face, whereas the abaxial member ( $l''$ ) is low on the outer face. On tibiae I and II  $l''$  can easily be mistaken for a ventral seta prior to the tritonymph, when  $v''$  first appears below it. On tibiae III and IV (Fig. 4C), which lack  $l''$ , it is seta  $l'$  that is abaxial and very low on the outer face, but in these instances  $v'$  is already present by the time  $l'$  forms, so the potential confusion is less. In essence, the setal verticil of these segments seems somewhat rotated on the segment, turned clockwise on legs I and II and counterclockwise on III and IV, but the shifts are most obvious in the lateral setae. Wauthy and Fain (1991) referred to such asymmetries—resulting from one member of a pair rising from its ancestral position and the opposite member falling—as 'basculations'. Those noted here are abaxial (=antiaxial) basculations ( $''$  on I/II and  $'$  on III/IV); they are not uncommon in oribatid mites, but they seem unusually strong in *Caleremaeus*.

**Itral setae.** The itral pair ( $it$ ) of tarsal setae are amphistasic, always post-larval, and always appear in the same position between the proral and tectal pairs, which are in contrast eustasic larval setae. But the specifics of this development among oribatid mites are surprisingly diverse, with more than a dozen ontogenetic patterns known (Grandjean (1961a, 1964a; see also Norton and Franklin 2018). The presence and instar of appearance of itral setae vary among taxa, among the four tarsi, and rarely even between members of the pseudosymmetrical pair. The itral ontogeny of *Caleremaeus* is interesting for two reasons. First, the pattern is complex, differing on each leg. Grandjean (1964a) noted this for *C. monilipes* by a formula that indicated first appearance of itral setae on tarsi I–IV: (n3—Ad—[0, Ad]—0). In other words, the itral pair appears in the tritonymph on tarsus I, in the adult on tarsus II, and fails to form on tarsus IV; tarsus III is asymmetrical in this regard, with  $it'$  failing to form but  $it''$  appearing in the adult. The second interesting point is that this complex formula, which is unique among oribatid mites, appears to be a generic trait (though only the adult setation is known in *C. nasutus* and we have no setation data for *C. divisus*; also, see R12).

**8. Nomenclature of posterior gastronotic setae  $h_1$  vs  $p_1$**  — In numerous families of oribatid mites, particularly eupheredermous taxa, the hysterostoma of nymphs terminates in a posterior process, typically with an indistinct pygidial (or caudal) sclerite, on which two pairs of setae insert. One pair usually is closer together than the other and slightly more dorsal, though in some taxa they are at equal height; most often the medial, higher pair is significantly larger. When applying his opisthonotal chaetotaxy to *Porobelba spinosa* (Damaeidae) nymphs, Grandjean (1954c) was uncertain which of these pairs represented  $h_1$  and which was  $p_1$ . This is understandable, given that the pygidial region represents the dorsal part of terminal hysterostomal segments and therefore undergoes the least amount of spreading as segments are added to the caudal bend during anamorphosis (Grandjean 1939). Slightly later, for the similar pygidium of *Polypterozetes* (Polypterozetidae), Grandjean (1959a) clearly labeled the larger, more dorso-medial pair as  $h_1$ .

By contrast, regarding *Caleremaeus monilipes*, Grandjean (1965b; p. 719) specifically and clearly considered the larger, more medial setae on the pygidial sclerite (therein called the 'croupion') to be pair  $p_1$ ; we infer therefore that he considered the smaller, more separated, slightly lower pair to be  $h_1$ . We found no explanation in his writings, but this seeming reversal of his hypothesis on homology is consistent with his labeling of setae in studies of at least three other eupheredermous taxa —*Mongaillardia* (Ameroidea; Grandjean 1961b), *Pheroliodes* (Plateremaeidae; Grandjean 1964b) and *Fosseremus* (Damaeolidae; Grandjean 1965a)—though the medial pair are not enlarged in these groups.

Without noting this apparent contradiction, most subsequent authors appear to have followed the earlier *Polypterozetes*-model in considering the adjacent and usually larger middle pair to belong to segment H (with the notation  $h_1$ ). Some examples relate to Neoliodoidea (Seniczak *et al.* 2018b, *Platylodes*), Plateremaeoidea (Ermilov *et al.* 2010, *Pedrocortesella*,

*Aleurodamaeus*), Damaeoidea (Miko and Mourek 2008, *Kunstidamaeus*), Gustavioidea (Seniczak *et al.* 2018a, *Hafenrefferia*) and *C. monilipes* (Seniczak and Seniczak 2019). We follow this view herein. The slightly more dorsal position of the middle pair in the typical formation argues for their belonging to segment H instead of PS, which is not part of the opisthonotum until the protonymph. This opinion is not universal among recent authors: Weigmann 2002 considered the large medial setae to be  $p_1$  in nymphs of *Eremobelba* (Ameroidea).

**9. Attachment of scalps** — In many oribatid mites whose nymphs carry exuvial scalps there is no obvious attachment mechanism, but some taxa have evolved a structural specialization for this purpose. For example, in the poronotic family Oribatellidae opisthonotal seta *dp* is either structurally modified or it inserts in a sheath-like callosity under the previous exuvium (Grandjean 1953), and in some Tegeribatidae (*Tegeribates*) a small bulge around this same seta forms a convexity in exuvia that nest together (Behan-Pelletier 2017).

The best-known mechanism is that of the Damaeidae, in which a distinct projecting cornicle on the opisthonotum inserts into the cornicle of the previous exuvium, forming a nested attachment structure. The cornicle may be short and simple or elongate and variously curved or twisted, according to species. In his review of this structure in Damaeidae, Ermilov (2012) indicated that it was unique to this family, but in fact there are two other examples. One is *Caleremaeus*, first noted by Grandjean (1965b). As described above (see also Seniczak and Seniczak 2019) its cornicle is a simple papilla, not very different from the simplest damaeid cornicle, e.g., that of some *Damaeus* species (Grandjean 1960). The other is Basilobelbidae, in which nymphal exuvia attach through a nesting ‘stylus’ that is not essentially different from the damaeid cornicle; the truly unique aspect of scalp attachment in this family is the strange mechanism by which the tritonymphal scalp is anteriorly fixed to the adult notogaster (Grandjean 1959b). In the related family Heterobelbidae, which has yet another unique mechanism for attachment of the tritonymphal exuvium to the notogaster, there is no cornicle or other obvious mechanism connecting the scalps themselves (Beck 1962; Okayama 1980).

Caleremaeidae, Damaeidae and Basilobelbidae share a similar apomorphic attachment mechanism, but it seems unlikely that they form a single clade within the eupheredermous taxa. Nor is there a taxon with an obvious precursor to the cornicle-mechanism, though *Eremobelbidae* gives a hint as to how it might have evolved. Weigmann (2002) described a small stalk on the opisthonotum of *Eremobelba* juveniles, which apparently adheres to the previous exuvium. If true, one could envision the stalk becoming hollow, like a cornicle, but it seems more parsimonious to evolve a cornicle from a simple bulge (*cf.* *Tegeribates*, above). Seniczak and Seniczak (2019) considered the cornicles of *Caleremaeus* and Damaeidae to be convergences, and at present we have no strong contradictory evidence.

**10. Ameroidea: nomenclature and content** — Applying the principle of coordinate categories, Marshall *et al.* 1987 recognized that Eremuloidea was not the oldest appropriate name for the superfamily that Grandjean (1965b) proposed to include Amerobelbidae, Ctenobelbidae, Eremulidae, Damaeolidae, Eremobelbidae and Ameridae (adding Staurobatidae in 1966). They considered Amerobelboidea Grandjean, 1954 to be the oldest available name for this group and considered Eremuloidea a junior synonym. But they cited the wrong date for Amerobelbidae, which was a nomen nudum when it first appeared in the literature (Grandjean 1954a) as noted by Schatz *et al.* (2011); it was formally published by Grandjean (1961b). But they also cited an incorrect author and date—Grandjean 1965b—for the family-group name Ameridae. Ameridae was proposed by Bulanova-Zachvatkina (1957) and, since this is the oldest name in the group, Ameroidea is the proper name for Grandjean’s Eremuloidea. The first correct use of Ameroidea seems to have been by Pérez-Iñigo (1997).

**11. Corrections to Norton and Behan-Pelletier (2009)** — In 2009, Caleremaeidae was included in Ameroidea, as noted above. But a more complete knowledge of the family, with its plicate juveniles, raises doubts about this grouping. Stated traits of Ameroidea (p. 457) that are not found in Caleremaeidae include: (1) absence of a tutorium (it is present in most species); (2) absence of a discidium (it is present in some species); (3) genital setation 6 pairs (4–6 can be

present); (4) preanal organ without caecum (the internalized process is hollow, essentially like a caecum); and (5) proral setae of legs short and spiniform (they are normally formed setae). The diagnostic couplet (p. 483, couplet 88) distinguishing Caleremaeidae from Anderemaeidae also is wrong or misleading (*cf.* Norton and Ermilov 2019). The first character should be deleted: as noted above, Caleremaeidae species have ring-like ridges within the bothridium. The character ‘circular depressions between setae *c* and *la*’ refers to the foveae of the transverse sulcus; more important is the absence in Anderemaeidae of the unique notogastral topography (bulges and sulcus) found in Caleremaeidae. Enantiophysis *A* (= *eA*) is said to be absent from Anderemaeidae and present in Caleremaeidae, but in fact it is typical of Anderemaeidae and present or absent in Caleremaeidae. The cheliceral character should be ignored: it does not apply to most taxa currently included in Anderemaeidae.

**12. Discrepancies with Seniczak and Seniczak (2019)** — This important paper, based on material from Norway, redescribed the adult of the type species of *Caleremaeus*, *C. monilipes*, and presented the first complete assessment of ontogeny. However, during our study of *C. monilipes* specimens from Germany, Spain and Sweden, we noted several discrepancies with their results. After reexamination of these issues, Anna Seniczak kindly provided explanations and in some cases corrections (personal communication with R.A.N., 2019).

*Enantiophyses*. Their Fig. 3 shows the absence of enantiophysis *eL*, which is present on all our specimens (and was illustrated but not labeled by Miko and Travé 1996; their Fig. 8C). The specimen illustrated for their Fig. 3 was a light brown (teneral) specimen on which *eL* was not conspicuous, but *eL* clearly is present in the darker, more mature adults among their material. Also, they used some unconventional notations for enantiophyses (see R4); most significant was the use of *Va-Vp* (usually reserved for the ventrosejugal enantiophysis) for the aggenital enantiophysis spanning epimeral groove 4, and *E4a-E4p* for small tubercles on either side of epimeral groove 3.

*Discidium*. They illustrated and labeled a discidium (their Fig. 2; *dis*), whereas Grandjean (1965b) had indicated the absence of a discidium or discoidal ridge in this species. According to A. Seniczak, their darker specimens match the figures of Miko and Travé (1996; their Figs 8C, 13B), which show a low, irregular and vaguely defined elevation in the region between acetabula III and IV. Our specimens also match the latter figures: when viewed from below in transmitted light, the irregular elevation appears darker by projection, but the impression disappears in lateral view. As described above, the development of a discidium or discoidal ridge is variable among species of *Caleremaeus*, and that of *C. monilipes* seems weakest of all.

*Pedotectum I*. All species of *Caleremaeus* have a typical, well-defined pedotectum I in the form of a ‘cupped’ scale that posteroventrally envelops the base of leg I. This is well-shown in their Figs 2 and 4. However, their Fig. 1 is misleading in showing it as an isolated structure, distant from the leg, and their text incorrectly designates it as a propodolateral apophysis (*P*) instead of a pedotectum.

*Leg setation*. There are three discrepancies between their description of leg setation (their Fig. 13 and Table 2) and the results of our studies on *C. monilipes*. Upon reexamination of their material they found the following: only one iter seta, *it''*, develops on tarsus III and only one antelateral seta, *a'*, develops on tarsus IV; both setae *v'* and *l'* form on trochanter III in the deutonymph. Therefore, there is no conflict with our generic description.

*Palp solenidion*. In their Fig. 3C, the palp is illustrated as having solenidion  $\omega$  entirely fused to seta *acm*, but in correspondence they expressed some uncertainty, not having directly distinguished the two components. In all our studied material of *Caleremaeus*, including *C. monilipes*,  $\omega$  is independent from *acm* and lies prone on the tarsal cuticle, where it is inconspicuous. Grandjean (1965b) also noted this independent, prone form in *C. monilipes* (presumably a French population).



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