

Article

Phylogeny and Systematics of Astigmata with Description of Lycoglyphidae fam. nov. and a Comprehensive Identification Key to Acaroidea [†]

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Abstract

Astigmata is a diverse lineage of mites with significant ecological, medical, and economic importance, yet higher-level relationships within the group remain contentious due to incongruent morphological and molecular data. Here, we integrate multigene data with comparative morphology and ecological traits to reassess phylogenetic relationships, with a focus on the newly described family Lycoglyphidae fam. nov. associated with puffball fungi. Phylogenetic analyses recover Lycoglyphidae within a well-supported cluster—the AR cluster—comprising Acaridae *sensu novo*, Rhizoglyphidae *sensu novo*, and several additional related lineages. Within this framework, previously unrecognized lineages such as Pontoppidaniidae (intertidal seaweed habitats) and Cerophagidae (bee-associated) are supported as monophyletic, showing ecological conservatism. Our phylogeny indicates that mating position is phylogenetically structured, with retroconjugate mating prevalent in the AR cluster (except Histiotomatoidea) and many other lineages, while proconjugate mating is present only in two lineages, Hemisarcoptidae+Glycyphagidae and Rosensteiniidae+Aeroglyphidae. Finally, to facilitate identification and future research, we provide a taxonomic description of new taxa (Lycoglyphidae with *Lycoglyphus* gen. nov., *Obelacarus* gen. nov., and *Viedebantia*) and a comprehensive key to the families and genera of Acaroidea based on both adults and deutonymphs. Our results clarify some higher-level relationships within Astigmata, indicate the importance of integrating molecular, morphological, and ecological evidence, and provide a practical resource for identification and comparative studies.



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This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.**Keywords:** astigmatid mites; Acaroidea; puffball fungi; systematic; morphology; multigene phylogenetics; adults heteromorphyc deutonymphs

1. Introduction

The hyporder Astigmata is a species-rich and ecologically diverse lineage of acariform mites that includes numerous taxa of economic and medical importance, such as stored-product mites (e.g., *Acarus*, *Tyrophagus* and *Glycyphagus*), pyroglyphid house dust mites (*Dermatophagoides*), and parasitic skin mites of mammals (*Sarcoptes* and *Psoroptes*). The majority of this diversity is concentrated in a monophyletic lineage ancestrally characterized by reduced gnathosomal development in phoretic deutonymphs [1] (hereafter

non-schizoglyphid Astigmata), whereas early derivative lineages—Schizoglyphidae (Cretaceous to recent) and Levantoglyphidae (Cretaceous)—retain a well-developed gnathosoma in the deutonymphal stage and are represented by only a few known species [2–4].

The origin and early evolution of non-schizoglyphid Astigmata remain poorly understood. One influential hypothesis proposes the highly derived superfamily Histiostomatoidea as the earliest diverging lineage of this group [5]. In contrast, paleontological evidence based on phoretic deutonymphs of Schizoglyphidae and Levantoglyphidae suggests that the generalized morphological patterns seen in several extant lineages, including those traditionally placed in Acaroidea, may approximate the ancestral condition [2–4]. Consistent with this uncertainty, some molecular phylogenetic analyses recover Acaroidea as paraphyletic, either with Histiostomatoidea nested within it [6–9] or with Histiostomatoidea positioned in the middle portion of the astigmatid tree as sister to Acaroidea [10,11]. These results suggest that the current boundaries of major groups of Astigmata, such as Acaroidea, may be artificial and that its diagnostic characters require reassessment.

Astigmata exhibit extraordinary ecological versatility, much of which is associated with evolution of intimate symbiotic relationships with both invertebrates and vertebrates, including parasitism, mutualism, and commensalism, as well as dispersal via phoresy. Their life cycles are correspondingly plastic and can follow three alternative developmental trajectories depending on the ecological context: (i) omission of the deutonymphal stage and direct molting to feeding stages under abundant resource conditions [3]; (ii) production of a heteromorphic phoretic deutonymph through metamorphosis when resources decline and dispersal becomes advantageous [3]; or (iii) complete developmental arrest in a quiescent cyst-like deutonymph under adverse conditions that favor survival in the absence of food and with low probabilities of successful dispersal [3,6,12–43]. Since the mid-20th century, it has been recognized that this flexibility is rooted in a paedomorphic origin of Astigmata from oribatid soil mites [44–46]. Paedomorphosis likely streamlined morphological development and accelerated life cycles, facilitating the exploitation of ephemeral habitats, such as decaying fungi, plant debris, dung, phytotelmata, and carrion. In these systems, feeding stages can rapidly exploit short-lived resources, whereas heteromorphic deutonymphs provide an efficient mechanism for dispersal to newly available habitats via phoresy.

This functional duality between feeding stages and deutonymphs has profoundly shaped astigmatan systematics. Historically, characters of heteromorphic deutonymphs have played a disproportionate role in classification, reflecting their frequent occurrence as phoretic associates of hosts and, consequently, their greater availability in collections. By contrast, feeding stages of free-living taxa often inhabit concealed or transient microhabitats and are underrepresented in the material that is available for study. Although the morphology-based systematics of Astigmata has been comprehensively revised and synthesized in several influential works [1,5] and remains widely used, these classifications have been influenced by host associations and long-standing difficulties in polarizing character states and identifying robust apomorphies. In this lineage, which has been streamlined via paedomorphosis, diagnostic characters are often not constant; instead, they may exhibit character-state reversals or independent reductions, making morphological classification extremely challenging [6].

Over the past several decades, an extensive body of molecular phylogenetic research has accumulated, ranging from analyses based on single nuclear markers [47–50] to multilocus datasets [6,7,10,51–53], mitochondrial genes [8,9,11,54–61], ultraconserved elements [62], and, more recently, genome-scale data [37,63–67]. These studies provide independent tests of morphology-based hypotheses and have frequently revealed incongruences at the (sub)family and higher levels within Astigmata. At the same time, molecular

phylogenies are themselves subject to important limitations, including incomplete taxon sampling, misidentification of terminals, limited phylogenetic signal, a priori rooting, and susceptibility to long-branch attraction. In particular, genome-scale analyses based on very sparse taxon representation have occasionally inferred implausible deep relationships, such as placing Astigmata as sister to Oribatida [62,65,68], whereas multilocus or even single-locus studies with denser sampling more consistently recover the expected placement of the group [6,7,10,52].

Within this broader context, the phylogenetic position and systematic placement of several acaroid lineages remain problematic. Here, we describe Lycoglyphidae, a new family that is biologically associated with puffball fungi (Lycoperdaceae), whose feeding stages involve consumption of fungal spores and whose deutonymphs disperse phoretically on beetles that are associated with these fungi. The family is supported by molecular evidence and exhibits a conspicuous character state—two setae on the chelicerae—that may represent a plesiomorphic condition shared with early derivative Oribatida, the ancestors of Astigmata. Lycoglyphidae comprises three genera: *Lycoglyphus* gen. nov. (eastern Palaearctic), *Obelacarus* gen. nov. (Nearctic), and *Viedebanttia* Oudemans (widespread), the latter previously placed in Acaridae [69,70]. By integrating molecular data with comparative morphology and life-history traits, we aim to clarify the phylogenetic placement of Lycoglyphidae and to reassess higher-level relationships within Astigmata, particularly the circumscription of Acaroidea and allied lineages. Furthermore, to summarize these findings in the context of relationships within the superfamily Acaroidea, we provide identification keys to families and genera based on both adult and deutonymphal characters.

2. Materials and Methods

Specimens were collected from fungal hosts in the field by the authors and from beetles associated with the fungi. Additional deutonymphs were collected from beetle specimens in museum collections.

The terminology of idiosomal chaetotaxy follows Griffiths et al. [71], and the terminology of the leg chaetotaxy follows those of Grandjean [72] and Griffiths [31] with a correction of coxal setation by Norton [46]. The terminology of the spermatheca follows those of Witaliński et al. [73] and Klimov and OConnor [16]. The gnathosomal morphology follows Grandjean [74]; for appendages, the chaetotaxy and solenidiotaxy follow Grandjean [75] for palps. All measurements are given in micrometers (µm). In keys and text, we use the morphology of Griffiths [71] instead of OConnor [5]. The comparison of these two morphologies is shown in Table 1.

Table 1. Homologies of idiosomal and leg setae and solenidia based on OConnor (2009) [5] and Griffiths (1977) [71].

Name	OConnor (2009)	Name	Griffiths (1977)
Idiosoma			
rostral setae	ro	internal vertical setae	vi
lamellar setae	le	external vertical setae	ve
interlamellar setae	in	internal scapular setae	si
exobothridial setae	ex	external scapular setae	se
-	elc I	supracoxal setae of leg I	scx
gastronotic setae, c-row	c1-3, cp		c1-3, cp
gastronotic setae, d-row	d1-2		d1-2
gastronotic setae, e-row	e1-2		e1-2
gastronotic setae, f-row	f1-2		f1-2
gastronotic setae, h-row	h1-3		h1-3
paraproctal setae	p1-3	pseudanal setae	ps1-3

Table 1. Cont.

Name	OConnor (2009)	Name	Griffiths (1977)
adanal setae	<i>ad</i> _{1–3}		<i>ad</i> _{1–3}
coxal setae	<i>1a, 3a, 4a, 4b</i>		<i>1a, 3a, 4a, 4b</i>
genital setae	<i>g</i>		<i>g</i>
Legs			
ventral setae of trochanters I–II	<i>v'</i>		<i>pR</i>
ventral setae of trochanters III–IV	<i>v'</i>		<i>sR</i>
basiventral setae of femora	<i>bv''</i>		<i>vF</i>
anterior lateral setae of genua	<i>l'</i>		<i>cG</i>
posterior lateral setae of genua	<i>l''</i>		<i>mG</i>
anterior lateral setae of genua	<i>l'</i>		<i>nG</i>
ventral setae of tibia I–II	<i>v'</i>		<i>gT</i>
ventral setae of tibia III–IV	<i>v'</i>		<i>kT</i>
-	<i>c''</i>		<i>hT</i>
posterior anterolateral of tarsus I	<i>a''</i>		<i>aa</i>
anterior fastigial of tarsi	<i>ft'</i>		<i>ba</i>
posterior fastigial setae of tarsi	<i>ft''</i>		<i>d</i>
anterior primiventral setae of tarsi I–II	<i>pv'</i>		<i>wa</i>
posterior primiventral setae of tarsi I–II	<i>pv''</i>		<i>ra</i>
anterior primiventral setae of tarsi III–IV	<i>pv'</i>		<i>w</i>
posterior primiventral setae of tarsi III–IV	<i>pv''</i>		<i>r</i>
anterior anterolateral setae of tarsi	<i>a'</i>		<i>la</i>
anterior tectal setae of tarsi	<i>tc'</i>		<i>f</i>
posterior tectal setae of tarsi	<i>tc''</i>		<i>e</i>
anterior unguinal setae of tarsi	<i>u'</i>		<i>v</i>
posterior unguinal of tarsi	<i>u''</i>		<i>u</i>
anterior proral setae of tarsi	<i>p'</i>		<i>q</i>
posterior proral setae of tarsi	<i>p''</i>		<i>p</i>
basiventral setae of femur IV	<i>ev'</i>		<i>wF</i>
subunguinal setae of tarsi	<i>s</i>		<i>s</i>
anterior solenidion of genua	<i>σ'</i>		<i>σ'</i>
posterior solenidion of genua	<i>σ''</i>		<i>σ''</i>
solenidion of tibia	<i>φ</i>		<i>φ</i>
solenidion of tarsi I–II	<i>ω</i>		<i>ω</i>
famulus of tarsi I–II	<i>ε</i>		<i>ε</i>

Images were obtained using a Nikon Eclipse E800 microscope (Japan) equipped with DIC optics and a Tucsen Discovery CH30 digital camera (China), as well as a Zeiss Axio Imager.A2 microscope (German) with differential interference contrast (DIC optics) and an Axiocam 305 color camera (German). Image stacks from multiple focal planes were assembled in Helicon Focus 7.6.4 Pro (algorithm B, rarely A), followed by manual retouching to restore fine details from individual focal planes. Composite images were further edited in Adobe Photoshop 22.2.0. Line drawings were produced in Photoshop using microphotographs as the background.

Phylogenetic analysis was conducted in IQ-TREE v.3.0.1 [76–79] using a 619-taxon six-gene densely sampled dataset with the following command line: `iq-tree 3-p Astigmata_6genes.nex -nt 12 -m MFP+MERGE -rcluster 10 -alrt 1000 -bb 1000 -safe`. Briefly, phylogenetic analyses were conducted on a dataset of six genes, including two ribosomal RNA genes (18S and 28S) and four protein-coding genes (EF1α, SRP54, HSP70, and COX1). Gene partitions were defined corresponding to each locus, and ModelFinder within IQ-TREE v3.0.1 was used to select the best-fitting substitution model for each partition and to merge partitions when appropriate (-m MFP+MERGE). Nucleotide genes (18S, 28S) and amino acid genes (EF1A, SRP54, HSP70 and COX1) were automatically recognized by IQ-TREE. Following model selection and partition merging, IQ-TREE used a three-partition scheme: TIM2+F+R7 for 18S, GTR+F+I+R8 for 28S, and Q.INSECT+R6/I for all protein-

coding genes. This partition scheme was then used in the downstream maximum likelihood phylogenetic analysis with 1000 ultrafast bootstrap replicates and SH-aLRT branch tests to assess node support. Our dataset included a total of 6861 sites (aligned) across six initial gene partitions: 18S (1675 nt), 28S (3379 nt), EF1A (363 aa), SRP54 (456 aa), HSP70 (569 aa), and COX1 (419 aa). Missing data across the dataset was low (6.1%). This analysis, along with GenBank accession IDs and sequencing details, will be described in detail elsewhere.

Specimen depositories are as follows:

CNC—Canadian National Collection, Ottawa, Ontario, Canada.

OSAL—The Acarology Laboratory, The Ohio State University, Columbus, Ohio, USA.

UMMZ—Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, USA.

USNMNH—United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (mite collection housed with Systematic Entomology Laboratory, US Department of Agriculture, Beltsville, Maryland, USA).

ZISP—Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

3. Results

3.1. Molecular Phylogenetic Analysis

Our phylogenetic tree recovered Astigmata as an internal lineage within Oribatida *sensu stricto*, forming a well-supported sister relationship with the infraorder Desmonomata (Nothrina + Brachypylina) (SH-aLRT/ultrafast bootstrap = 99/100; Figure 1). Within Astigmata, several major lineages previously recognized based on morphology were recovered, including the superfamilies Schizoglyphoidea, Hemisarcoptoidea, Hypoderatoidea, and Psoroptidia—an unranked lineage composed largely of vertebrate parasites and including the superfamilies Pterolichoidea and Analgoidea (including Sarcoptoidea). These lineages occupied their expected positions in the tree (Figure 1).

The previously unresolved lineage Heterocoptidae (incertae sedis) was robustly resolved as sister to Psoroptidia, with maximal support. In contrast, the superfamilies Glycyphagoidea, Acaroidea, and Histiostomatoidea showed substantial rearrangements. Specifically, (i) Glycyphagidae was recovered as closely related to Hemisarcoptoidea, whereas other glycyphagoid lineages were placed elsewhere in the tree; (ii) within a large clade here termed the AR cluster, Acaroidea was broadly redefined to include only one former core family, Acaridae, which itself was split into several well-supported independent lineages—Rhizoglyphidae *sensu novo*, Acaridae *sensu novo*, Pontoppidaniidae, Cerophagidae, Horstiidae, and Lycoglyphidae fam. nov.—while additional families were also placed within the AR cluster (Histiostomatidae, Chortoglyphidae, Echimyopodidae, and Canestriniidae); and (iii) a distinct group of families clustered around Psoroptidae, including Lardoglyphidae, Aeroglyphidae, Rosensteiniidae, Hypoderatidae, and Heterocoptidae (Figure 1).

The economically important family Acaridae *sensu novo* comprised the tribes Acarini, Tyrophagini, and Acotyledonini; while the family Rhizoglyphidae *sensu novo* largely corresponds to the traditional morphology-based concept, with the exclusion of Acotyledonini (Figure 1).

Mapping the two character states associated with mating position revealed that proconjugate (parallel) mating originated independently in three monophyletic clades: (i) Hemisarcoptoidea + Glycyphagidae, (ii) Histiostomatidae, and (iii) Aeroglyphidae + Rosensteiniidae. In contrast, all other non-schizoglyphid Astigmata exhibited retroconjugate (reverse) mating (Figure 1).

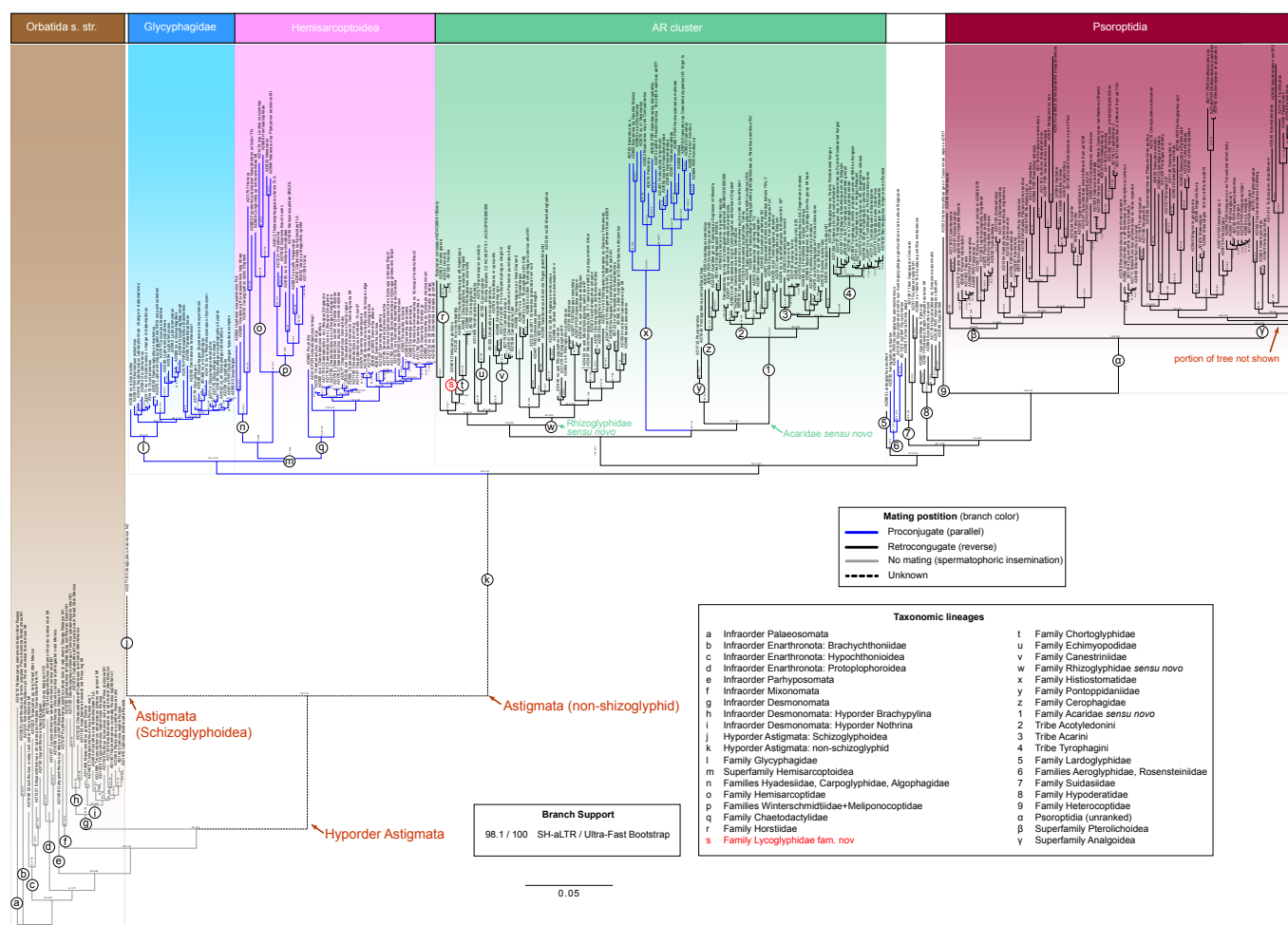


Figure 1. Maximum likelihood tree of astigmatid mites (Astigmata) and outgroups (Oribatida s. str.) inferred in IQ-TREE. The input phylogenetic matrix had 619 taxa and alignments of six genes (6861 sites total aligned): 18S (1675 nt), 28S (3379 nt), EF1A (363 aa), SRP54 (456 aa), HSP70 (569 aa), and COX1 (419 aa). Missing data: 6.1%. Following model selection and partition merging (-m MFP+MERGE), IQ-TREE used a three-partition scheme: TIM2+F+R7 for 18S, GTR+F+I+R8 for 28S, and Q.INSECT+R6/I for all protein-coding genes. This partition scheme was then used in the downstream maximum likelihood phylogenetic analysis with 1000 ultrafast bootstrap replicates and SH-aLRT branch tests to assess node support. A high-resolution tree is also available in Supplementary Materials (Figure S1).

3.2. GenBank Sequence Misidentification

We conducted the following analyses for three suspect and critical GenBank sequences.

For “*Rhizoglyphus robini*” (NC_038058.1; mitochondrial genome) [80], a COX1 search (BLASTx using translation Table 5) returned the closest matches to *Sancassania* (amino acid identity 98.6–99.8%), followed by *Aleuroglyphus* and numerous *Tyrophagus* sequences (95.7–96.3%), consistent with phylogenetic expectations (*Acaridae sensu novo*). We therefore classify this sequence as *Sancassania* cf. *berlesei* (closest COX1 match: 99.8% amino acid identity to *Sancassania berlesei*, YP_009050190.1).

“*Cosmoglyphus oudemansi*” (JBNXMS010000000) is represented by a whole-genome shotgun assembly. Because this assembly contains only nucleotide sequences, we extracted the 18S rRNA gene and conducted a BLAST (nt) (2.17.0) search, which returned six closest matches to *Sancassania* (nucleotide identity 97.7–99.4%). A 96.5% match to *Cosmoglyphus* sp. AD702 (JQ000105.1) was also recovered, as expected given the close phylogenetic relationship between these genera. To further validate these similarity-based BLAST results, we recovered our five standard nuclear genes from this genome and performed a

phylogeny-based identification. This analysis placed the sequence unambiguously within *Sancassania*, among several accurately identified species. We therefore classify this genomic sequence as *Sancassania* (closest 18S rRNA match: 99.4% nucleotide identity to *Sancassania berlesei*, GQ864331.1).

“*Rhizoglyphus* sp.” SJD-2001 (AF287236.1) [48] is represented by a single 18S rRNA sequence. As above, we conducted a BLAST (nt) search, which returned *Cosmoglyphus* sp. as the closest match (99.7% nucleotide identity), followed by numerous sequences belonging to Acaridae *sensu novo* (e.g., *Acarus*, *Tyrophagus* and *Sancassania*). In contrast, true *Rhizoglyphus* is expected to cluster with Rhizoglyphidae *sensu novo*. We therefore classify this sequence as *Cosmoglyphus* sp. (closest 18S rRNA match: 99.7% nucleotide identity to *Cosmoglyphus* sp. AD702, JQ000105.1).

3.3. Systematics

Order Sarcoptiformes Reuter, 1909.

Suborder Oribatida van der Hammen, 1968.

Hyporder Astigmata Canestrini, 1891.

Superfamily Acaroidea Latreille, 1802.

Family Lycoglyphidae fam. nov.

Type genus *Lycoglyphus* gen. nov.

urn:lsid:zoobank.org:act:1B40EBDE-5904-494B-A2F5-5C5E5687E1FF

Diagnosis. Adults. Chelicerae chelate with few teeth and with two setae, *cha* and *chb*; *cha* large, lanceolate, situated anterior to *chb*. Palp reflexed inward, bearing two (*sup* and *cm*) or three (*a*, *sup* and *cm*) setae, terminal solenidion ω and terminal eupathidium *ul''* and *ul'*; palp tarsus has a rounded lateral protrusion with lanceolate *cm*. Subcapitulum without ventral external ridges and with setae *h* and *elcp*. Idiosomal cuticle smooth. Grandjean's organ with one (sometimes with additional tongue-shaped outgrowth) trunk and numerous small spines. Supracoxal setae pinnate. Prodorsal shield vestigial (*Lycoglyphus* and *Obelacarus*) or well developed (*Viedebanttia*), not divided. Setae *ve* present (short or vestigial in *Viedebanttia*). All idiosomal and coxal setae smooth, thin, and filiform. Setae *si*, *se*, *c*₁, *c*₂, *c*_p, *c*₃, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃, *ps*₁, *ps*₂, *ps*₃ present. Anterior coxal apodemes I–IV and posterior coxal apodemes II present. Female oviporus longitudinal with genital valves fused to body anteriorly, free posteriorly. Epigynal apodeme absent. Genital papillae conoidal associated with genital opening. Opisthosoma rounded posteriorly, without opisthosomal shield or sclerotization. Anus positioned near posterior margin of body. Males with para-anal suckers. Legs ventrally positioned. Pretarsi with short strong condylophores. Pretarsal ambulacrum not greatly expanded. Empodial claws present on all legs, simple. Males with sucker-like setae *d* and *e* on tarsus IV. Otherwise, all tarsi with long filiform setae *d*, *f* and short spiniform *e*. Unguinal setae *u*, *v* larger and stouter than proral setae *p*, *q*, or absent. Setae *aa* I, *ba* II present. Tarsus I with solenidion ω_2 basal to ω_1 . Genu I with two solenidion (σ'' and σ'), ratio of the lengths of which differs among genera. Heteromorphic males present, with enlarged leg III with vestigial ambulacrum, rudimentary condylophores and not enlarged claw, spiniform setae *e*, *r*, *w*, *s*, filiform *d*, *f* and rudimentary *v* and *q*, without an enlarged seta similar in form to empodial claw.

Heteromorphic deutonymph. Gnathosoma short, with filiform setae *cm*, *sup* and alveoli *h*. Palps separated, with two segments. Body ovoid, smoothly punctate. Propodosoma not overhanging gnathosoma anteriorly. Setae *vi* present on dorsal propodosoma, *ve* present (*Lycoglyphus*, *Obelacarus*) or absent (*Viedebanttia*). Propodosomal ocelli absent. Hysterosoma with 11 pairs of simple filiform setae on hysterosomal shield (*c*₁, *c*₂, *c*_p, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃). Sejugal furrow present. Coxal setae *1a* and *3a* present (conoidal or filiform). Coxal apodemes I and anterior apodemes II not extending to level of coxal

apodemes III. Coxal apodemes II end freely; III–IV fused medially. Attachment organ with anterior and median suckers (ad_3 and ad_{1+2}) well developed and setae ps_1 and ps_2 in the form of conoids. All segments of legs free. Legs III–IV posteriorly or laterally directed in repose. Pretarsi without membranous ambulacra, empodia arising from tarsal apices. Empodial claw present on all legs. Setae nG III present. Setae aa I, wa I and ba II present. Solenidion ω_2 I present.

Genera included: *Lycoglyphus* gen. nov.; *Obelacarus* gen. nov.; *Viedebanttia* Oudemans, 1929.

Remarks. Lycoglyphidae fam. nov. shares several characteristics with Acaroidea [5,49]: chelicerae are chelate, the subcapitulum and palps with completed chaetome, idiosoma with cuticle smooth, dorsal and paraproctal chaetome complete, female oviporus in the form of an inverted V, internally with strongly folded pseudovipositor, male with paranal suckers and with modified suckerlike setae on tarsus IV, all legs with free segments and complete chaetome, empodial claws present, and pretarsal ambulacrum not greatly expanded. Lycoglyphidae and Bulacaridae share the presence of two cheliceral setae (cha and chb).

Lycoglyphidae differs from Bulacaridae in the lanceolate shape and terminal arrangement cha (vs. filiform, situated in basal part of fixed digit); lateral protrusion on palpal tarsi present (vs. lateral protrusion absent); lanceolate cm (vs. filiform); setae ve present (vs. absent); Grandjean's organ well developed (vs. absent); supracoxal setae scx pinnate (vs. slender, barbed at their terminal half); prodorsal shield vestigial or distinct, whole (vs. divided into paired parallel sclerites); dorsal setae smooth, filiform (vs. dorsal setae lanceolate, barbed and curved); setae $4a$ filiform (vs. lanceolate); epigynal apodeme absent (vs. present); setae aa I present (vs. absent); solenidion ω_1 situated near ε (vs. far from ε); two solenidia σ I (vs. one σ I).

Lycoglyphidae can be distinguished from Acaridae by the combination of the following characters, including: two cheliceral setae (vs. one only cha); palp tarsi with large rounded lateral protrusion on which the lanceolate setae cm are situated (vs. without lateral protrusion, cm typically filiform); Grandjean's organ with numerous small spines (vs. usually smooth).

Lycoglyphidae can be distinguished from Gaudiellidae and Suidasiidae by asymmetrical tarsal setae e and f — e spiniform, f —filiform (vs. setae e and f filiform, similar in length).

Lycoglyphidae can be distinguished from Glycacaridae by prodorsal shield entire, not being in the form of pair of parallel sclerites, vestigial (vs. being in the form of pair of well-developed parallel sclerites); smooth dorsal setae (vs. elongate and heavily barbed); smooth cuticle (vs. cuticle with small triangular microtrichae).

Lycoglyphidae can be differentiated from most Lardoglyphidae by simple empodial claws in both sexes (vs. bifurcate in females and sometimes males).

Lycoglyphidae can be differentiated from Scatoglyphidae by the anus situated near posterior margin of body (vs. anus positioned directly behind genital opening, displaced from the posterior edge of the body by a distance greater than the length of the anus); well-developed rounded para-anal suckers in males (vs. vestigial or absent in males).

Heteromorphic deutonymphs of Lycoglyphidae are difficult to distinguish from Acaridae due to the great morphological diversity of the latter. Lycoglyphidae, like some Acaridae, have two-segmented palps, setae cm , sup are present on the gnathosoma, leg setae aa I, wa I–II, hT I–II, gT I–II, ba II, nG III are present, and one solenidion is present on genu I. Heteromorphic deutonymphs of *Viedebanttia* clearly distinguished from all others by their long tibiae I–II (much longer than the corresponding genua) (tibia I–II no longer than genua in other genera of new family).

Heteromorphic deutonymphs of Lycoglyphidae differ from Suidasiidae and Largoglyphidae by presence of empodial claw on leg IV (vs. absent). Deutonymphs of Lycoglyphidae differ from Gaudiellidae by having coxal apodemes III–IV fused medially and coxal fields III–IV closed (vs. coxal apodemes III–IV ending freely and coxal fields III–IV open).

Biology. Species of this family are closely associated with puffball fungi of the genus *Lycoperdon* and *Apioperdon* (Agaricales and Lycoperdaceae). Adult mites and other feeding stages live inside old sporocarps of their fungal hosts, where they feed on fungal spores. Phoretic deutonymphs of *Lycoglyphus* and *Obelacarus* disperse on endomychid beetles (Coleoptera and Endomychidae), whose larvae are biologically associated with the same fungal host and feed on fungal spores in puffballs (genus *Lycoperdina* Latreille, 1807) [81]. In some cases, mite species of two genera (*Lycoglyphus* and *Viedebanttia*) co-occur within the same host specimen. In contrast, deutonymphs of *Viedebanttia* are mostly phoretic on unspecialized hosts (e.g., Carabidae, Formicidae and Myriapoda). Although this type of phoresy is largely a “one-way ticket” for the mites, who frequently fail to survive or reach a suitable sporocarp, it can nonetheless be ecologically significant for the fungus. Mites carrying spores are more likely to deposit them in habitats suitable for germination than spores dispersed passively by wind, thereby enhancing the fungus’s probability of successful colonization, even if the mites themselves perish. An additional reason why *Viedebanttia* is found phoretic on a wide range of unspecialized hosts is that this genus is not exclusively restricted to puffballs but may also occur in other common fungal hosts, such as *Daldinia* (Xylariales and Hypoxylaceae). This broader habitat preference likely explains why *Viedebanttia* exhibits less host specificity in phoretic associations than *Lycoglyphus* and *Obelacarus*.

Lycoglyphus gen. nov.

Type species: *Lycoglyphus kurosai* sp. nov.; monotypic.

urn:lsid:zoobank.org:act:12619B10-7AF8-4AF0-8561-2BD422D15F5A

Diagnosis. Adult. Central trunk of supracoxal setae *scx* lanceolate with numerous lateral processes. Grandjean’s organ with one pointed trunk and numerous small spines. Prodorsal shield vestigial. Seta *ve* well developed, located on the same transverse line as *vi*. Posterior coxal apodeme II absent, and sclerite present. Unguinal setae *u* and *v* vestigial. Solenidia ϕ I–II reach the apices of their respective tarsi without ambulacra. Solenidion σ'' I longer than σ' . Solenidion σ III absent. Inseminatory canal of spermatheca with relatively large diameter. Paired sclerites of efferent ducts elongated, with very short stem.

Heteromorphic deutonymph. Seta *ve* present. Ratio hysterosomal shield/prodorsal shield length = 1.9–2.1. Coxal fields I closed. Coxal setae *1a* and *3a* filiform. External conoidal setae *ps*₂ of attachment organ slightly posterior to median sucker *ad*₁₊₂. Tibiae I–II similar in length or only slightly longer than corresponding genua. Seta *aa* I weakly spiniform, short (no longer than ω_3). Setae *e* I–II cylindrical with sucker-like apex, different in form from simply foliate seta *f*. Setae *d* I–II shorter than *e* I–II. Seta *ba* II shorter than ω_1 II. Setae *p* and *q* I–IV small spiniform. Seta *f* IV slightly longer than leg IV. Solenidion σ III absent.

Etymology. The generic name *Lycoglyphus* is a contraction of *Lycoperdon* (the fungal host) and the Greek verb γλύφω (*glýphō*, “to carve, engrave, or gnaw out”), alluding to the mite’s life-history and trophic association with puffball fungi. Gender masculine.

Remarks. The differences between the three genera of Lycoglyphidae fam. nov. are presented in the key below.

Lycoglyphus kurosai sp. nov.

Unnamed acarid mite—Kurosa, 2000 [82]: 940, fig. 27.

urn:lsid:zoobank.org:act:4276E81C-24A1-438C-A5E9-95B3F1C7DD80

Figures 2–11



Figure 2. *Lycoglyphus kurosai* sp. nov. and gen. nov., female, holotype, dorsal view.

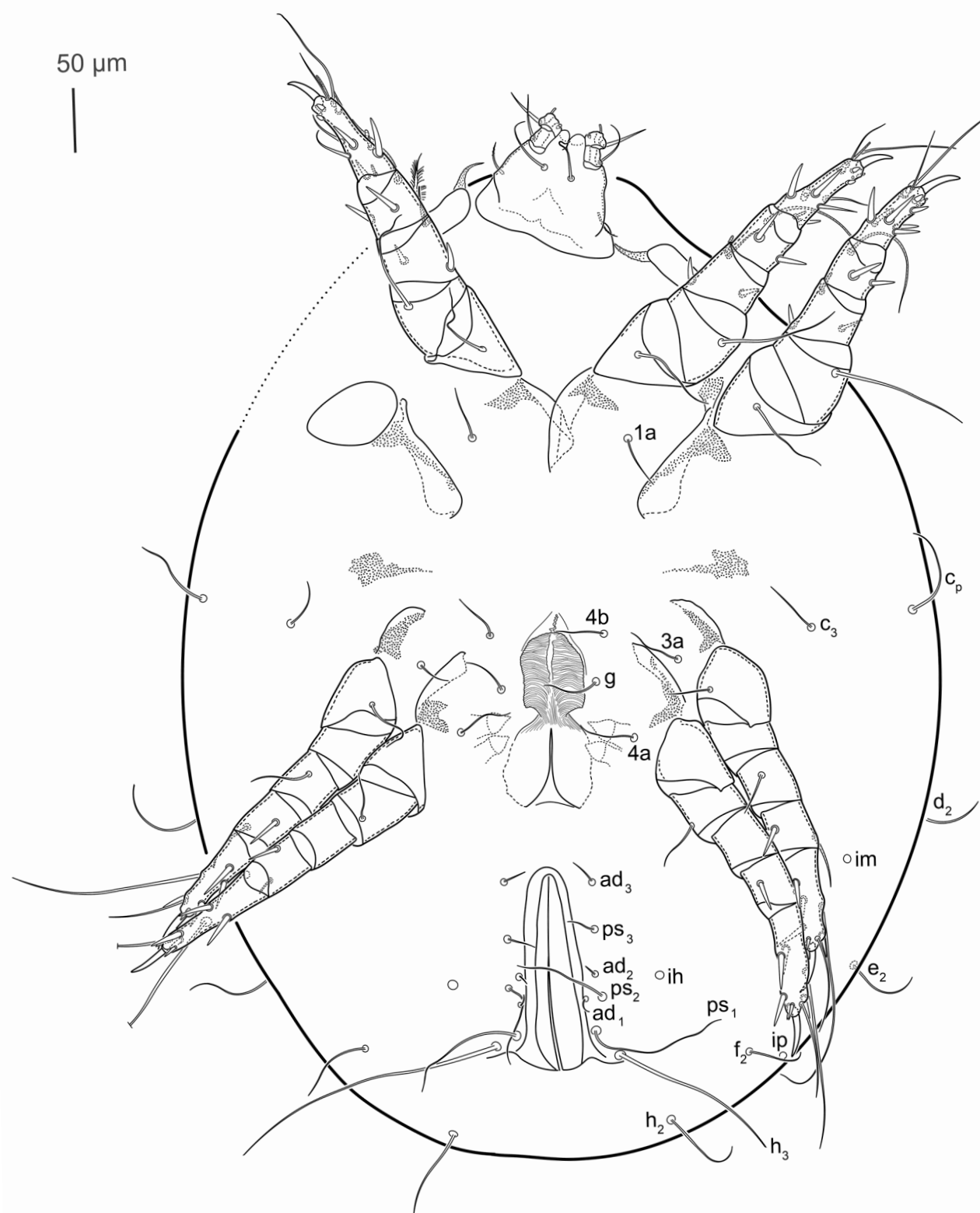


Figure 3. *Lycoglyphus kurosai* sp. nov. and gen. nov., female, holotype, ventral view.

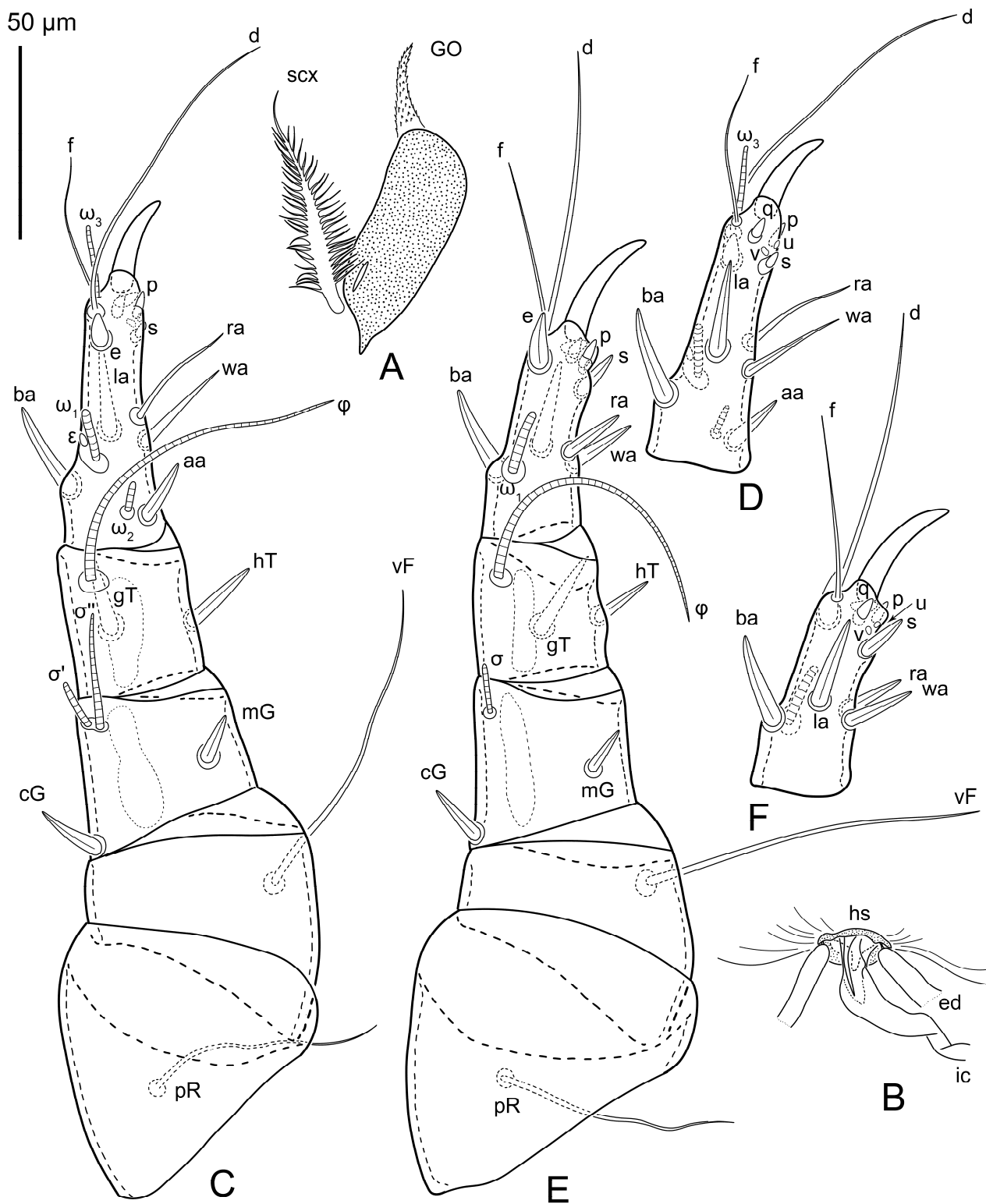


Figure 4. *Lycoglyphus kurosai* sp. nov. and gen. nov., female, holotype: (A)—supracoxal shield, supracoxal seta and Grandjean's organ; (B)—spermatheca; (C)—leg I, posterior view; (D)—tarsus I, anterior view; (E)—leg II, posterior view; (F)—tarsus II, anterior view.

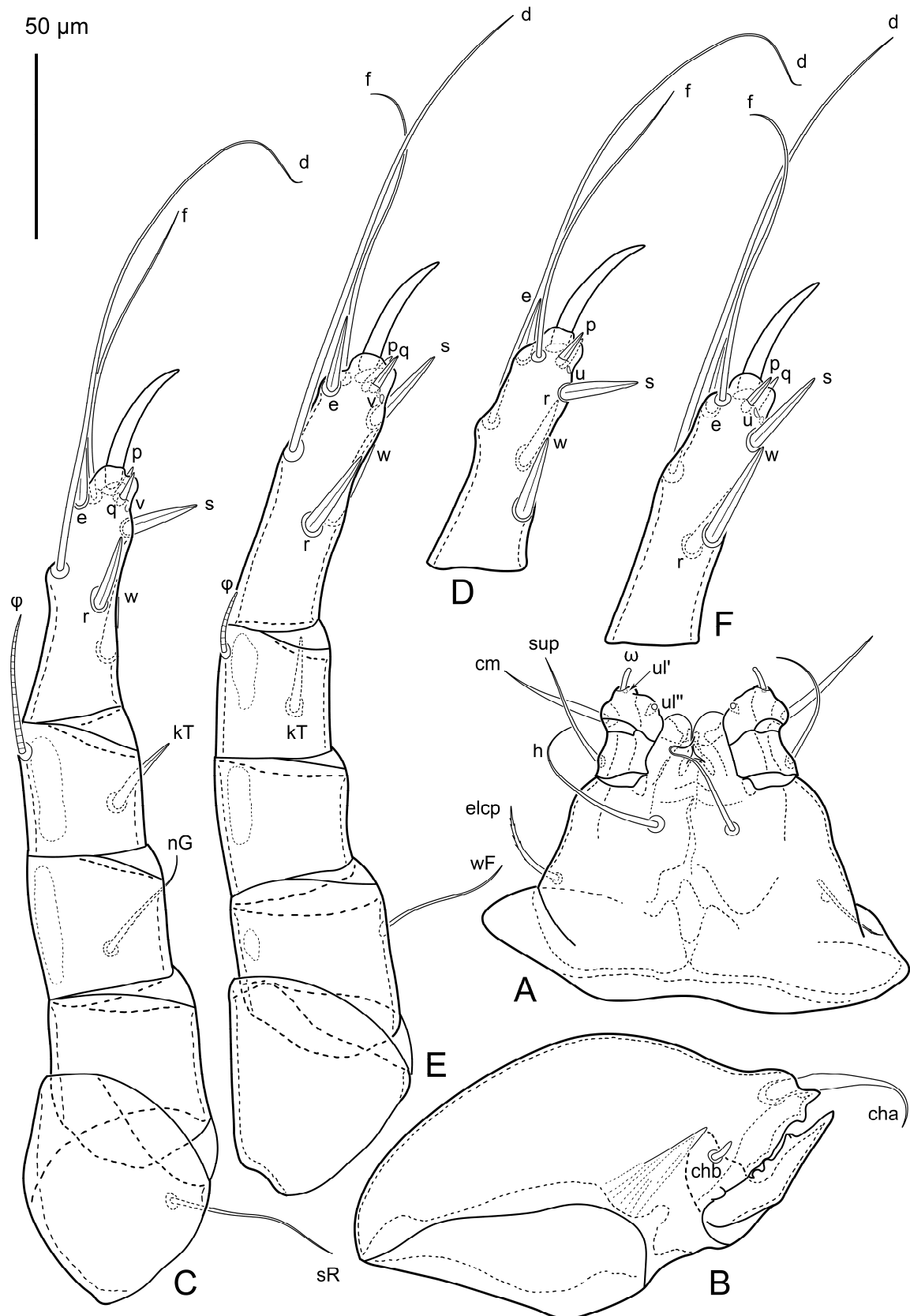


Figure 5. *Lycoglyphus kurosai* sp. nov. and gen. nov., female, holotype: (A)—subcapitulum; (B)—chelicera; (C)—leg III, posterior view; (D)—tarsus III, anterior view; (E)—leg IV, posterior view; (F)—tarsus IV, anterior view.

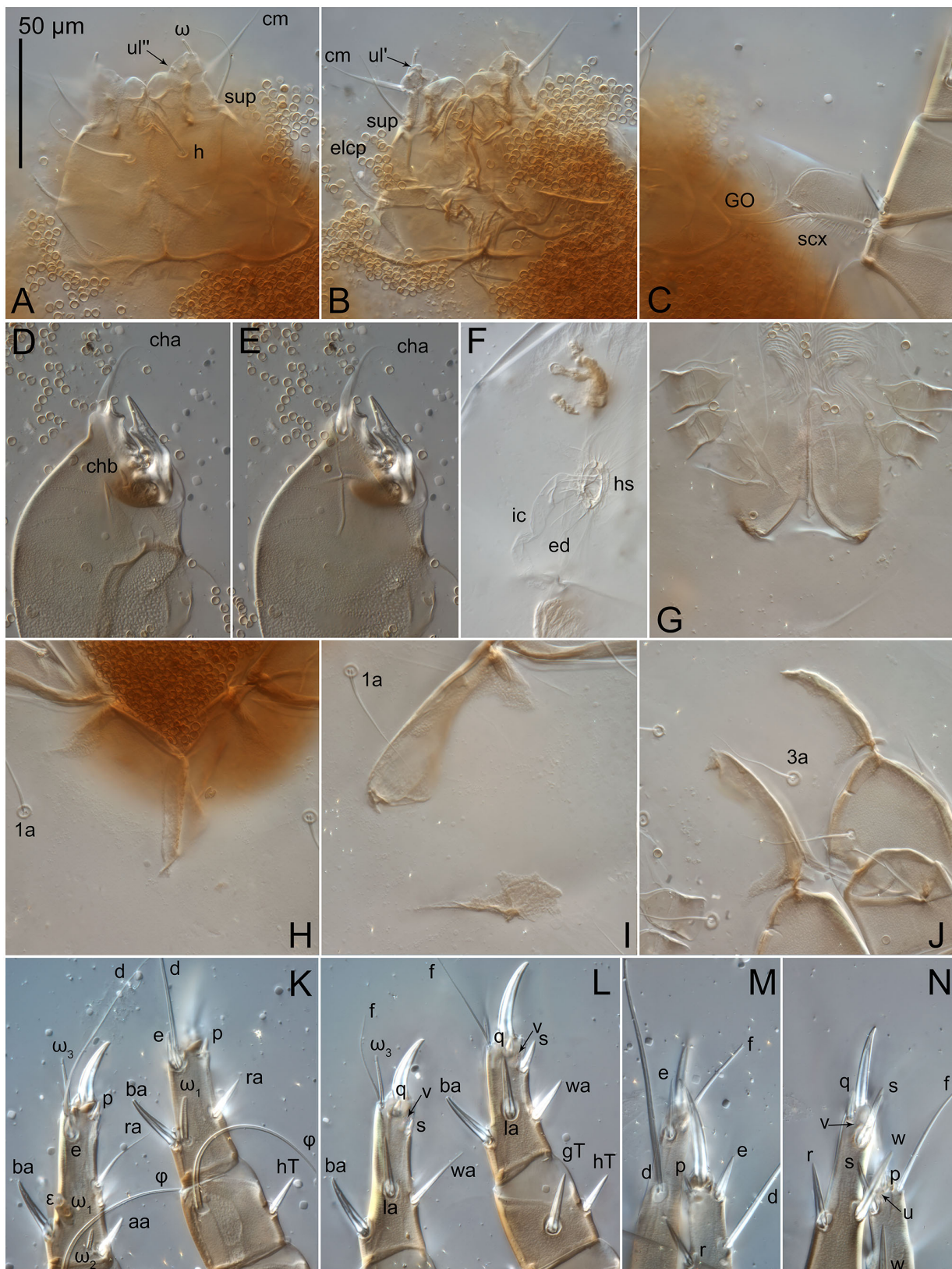


Figure 6. *Lycoglyphus kurosai* sp. nov. and gen. nov., female, holotype, DIC images: (A,B)—subcapitulum; (C)—supracoxal shield, supracoxal seta and Grandjean's organ; (D,E)—chelicera; (F)—spermatheca; (G)—genital opening; (H)—apodemes I; (I)—apodemes II; (J)—apodemes III and IV; (K)—tarsi I and II, posterior view; (L)—tarsi I and II, anterior view; (M)—tarsi III and IV, posterior view; (N)—tarsi III and IV, anterior view.

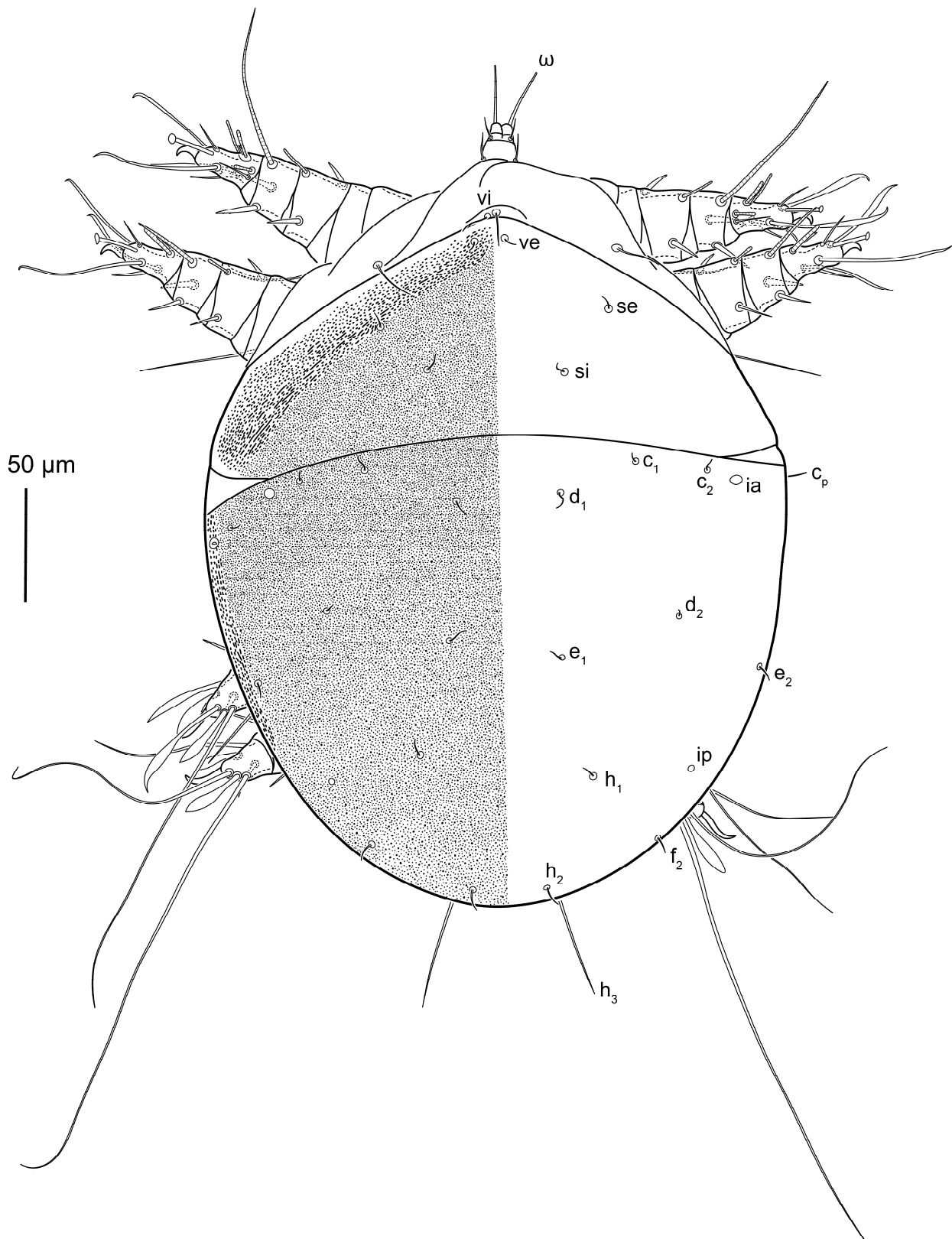


Figure 7. *Lycoglyphus kurosai* sp. nov. and gen. nov., phoretic deutonymph, dorsal view.

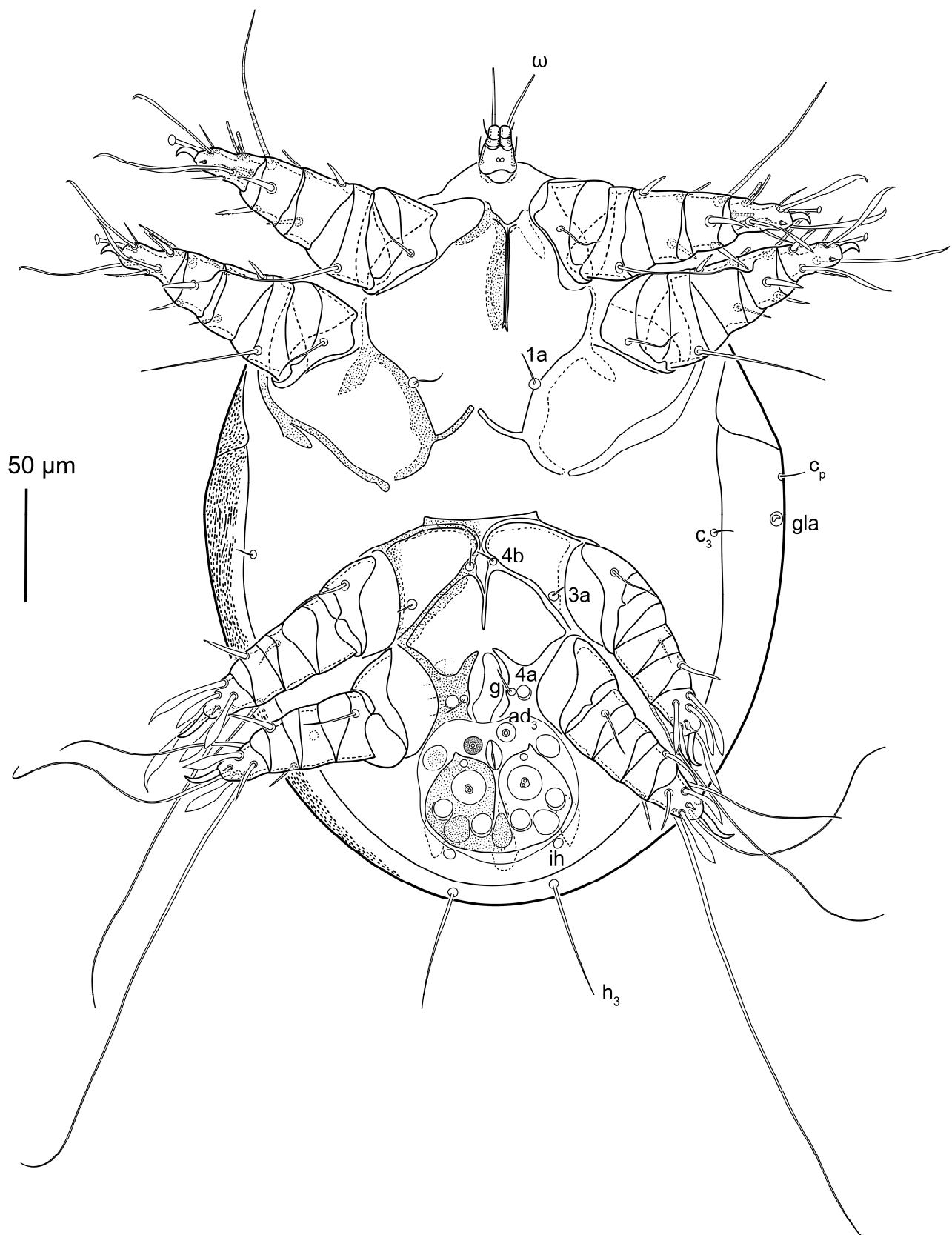


Figure 8. *Lycoglyphus kurosai* sp. nov. and gen. nov., phoretic deutonymph, ventral view.

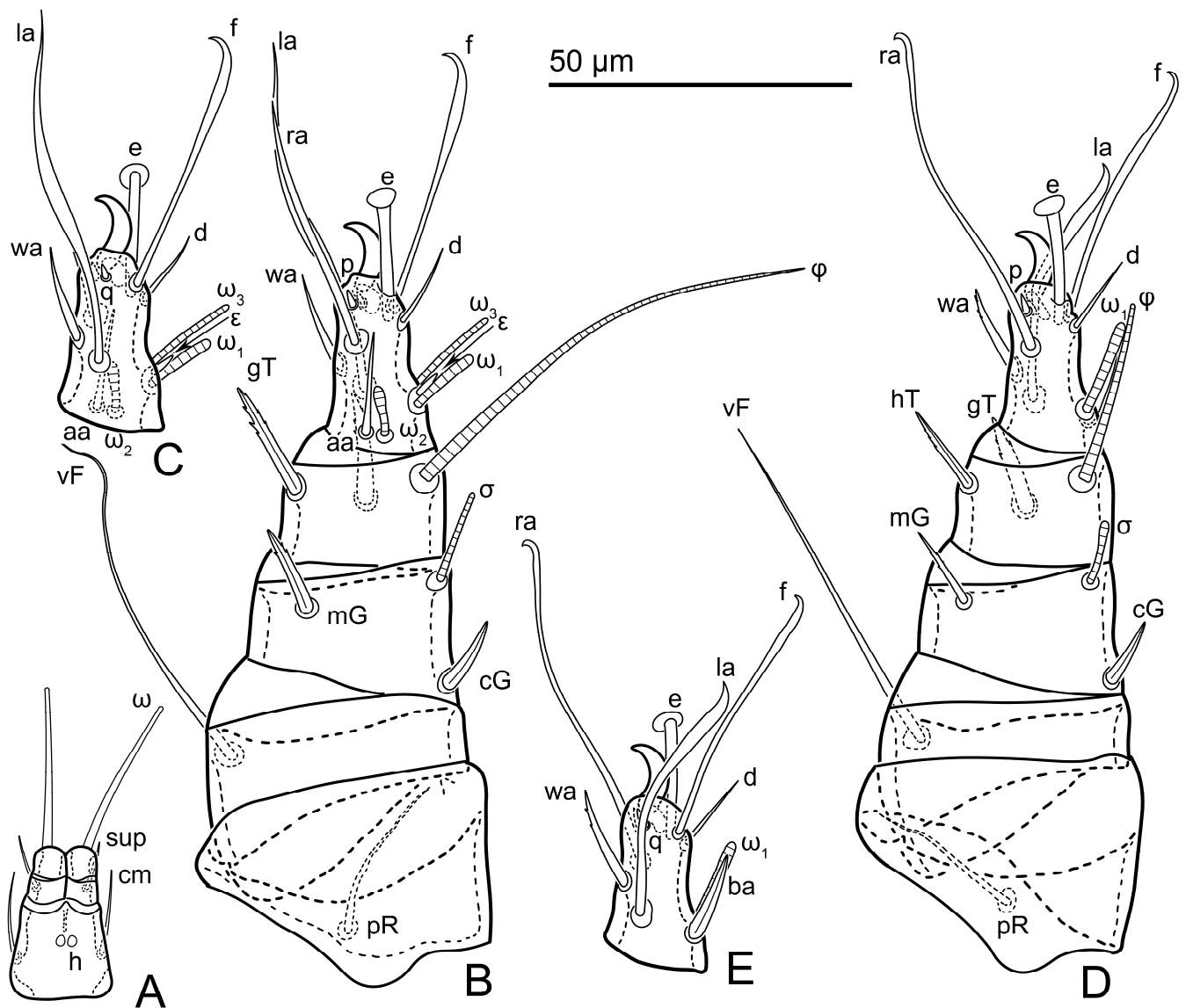


Figure 9. *Lycoglyphus kurosai* sp. nov. and gen. nov., phoretic deutonymph: (A)—gnathosoma, ventral view; (B)—leg I, posterior view; (C)—tarsus I, anterior view; (D)—leg II, posterior view; (E)—tarsus II, anterior view.

Material. Holotype: female—RUSSIA: Primorsky Krai, Ussuriysky District, Kaimanovka, ex *Lycoperdon* sp. (Agaricales: Lycoperdaceae), 21 Jun 1998 (ZISP). Paratypes: 13 HDN—same data; 5 HDN—same data, ex *Lycoperdina koltzei* Reitter (Coleoptera, Endomychidae) from *Lycoperdon* sp., 21 Jun 1998 (ZISP).

Description. Female (n = 1) (Figures 2–6). Idiosoma (Figures 2 and 3) oval, saccular, 800×610 , 1.3 times longer than wide. Idiosomal cuticle smooth.

Gnathosoma (Figure 5A,B and Figure 6A,B,D,E): subcapitulum (Figures 5A and 6A,B) wide, 77×110 , evenly punctated; subcapitular setae (*h*) long, widened basally; palpal supracoxal seta *elcp* present, weakly barbed; palps wide; lateral dorsal palp tibial setae (*sup*) filiform; palp tibial setae (*a*) absent; dorsal palp tarsal seta (*cm*) lanceolate, its base located on a large rounded lateral protrusion of palp tarsus; terminal palp tarsal solenidion ω short; terminal eupathidium *ul'''* small, dome-shaped; terminal eupathidium *ul'* small, rounded. Chelicera (Figures 5B and 6D,E) with two setae: *cha* large, lanceolate, situated distally on fixed digit, *chb* short, and spiniform. Fixed digit of chelicera with one tooth; movable digit with three teeth (anterior double).

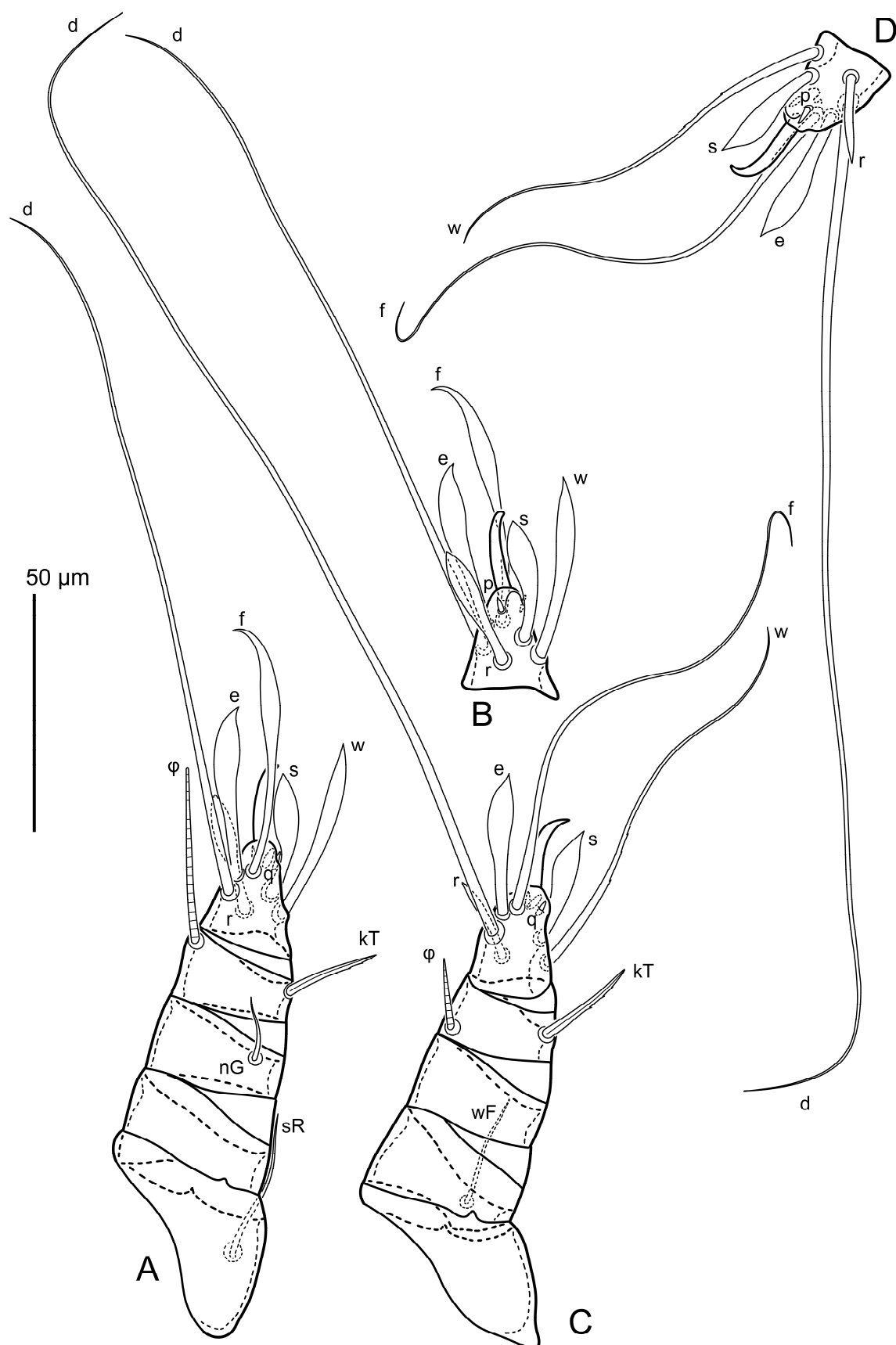


Figure 10. *Lycoglyphus kurosai* sp. nov. and gen. nov., phoretic deutonymph: (A)—leg III, posterior view; (B)—tarsus III, anterior view; (C)—leg IV, posterior view; (D)—tarsus IV, anterior view.

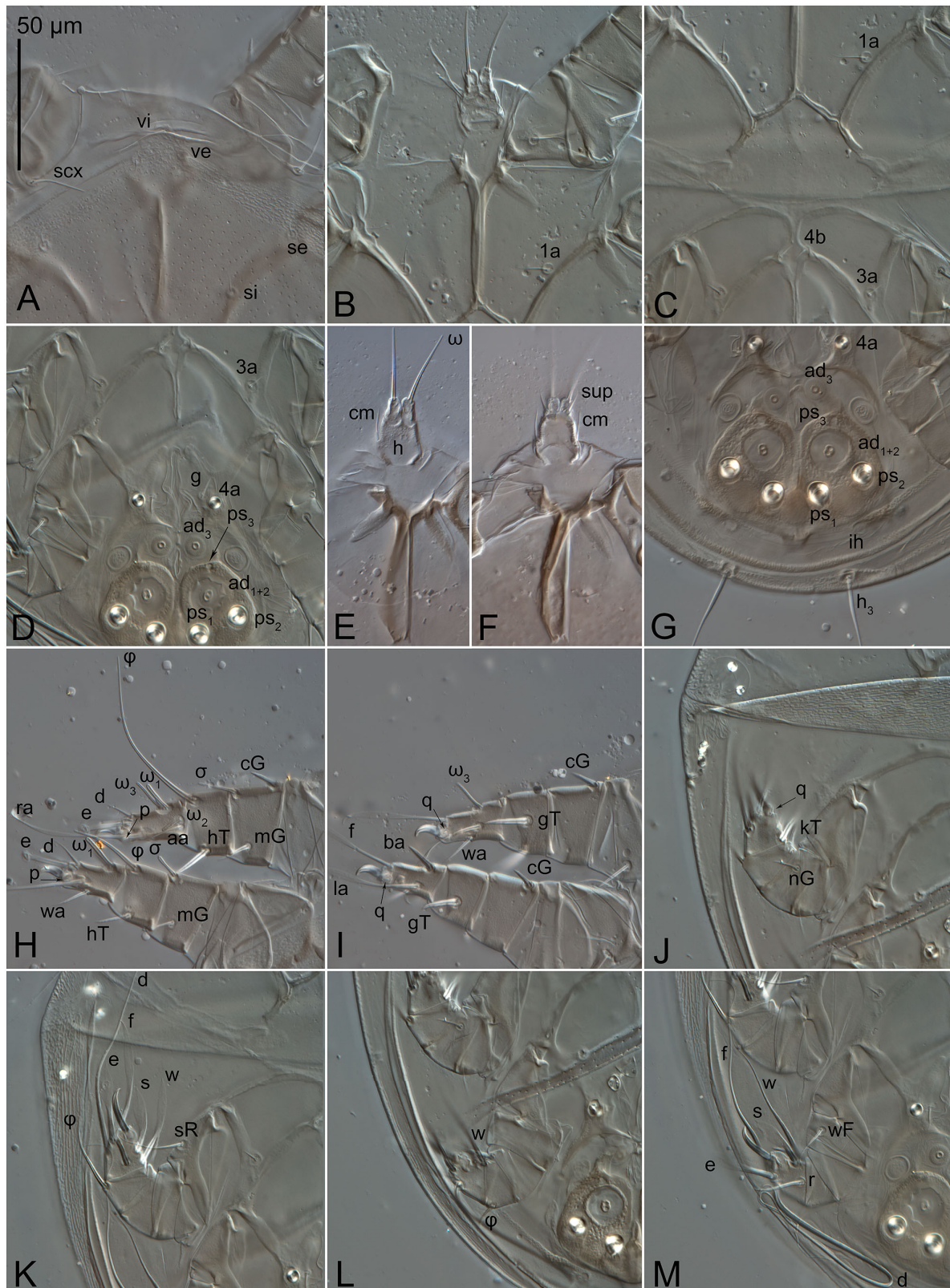


Figure 11. *Lycoglyphus kurosai* sp. nov. and gen. nov., phoretic deutonymph, DIC images: (A)—anterior part of propodosoma, dorsal view; (B)—anterior part of propodosoma, ventral view; (C)—apodemes I–III; (D)—apodemes IV and anal region; (E)—gnathosoma, ventral view; (F)—gnathosoma, dorsal view; (G)—attachment shield; (H)—legs I and II, posterior view; (I)—legs I and II, anterior view; (J)—leg III, dorsal view; (K)—leg III, ventral view; (L)—leg IV, dorsal view; (M)—leg IV, ventral view.

Prodorsal shield vestigial, represented by a short weakly sclerotized area with punctation behind bases of setae *vi*. Grandjean's organ (GO) with one pointed trunk and numerous small spines (Figures 4A and 6C). Supracoxal setae (*scx*) pinnate—its central trunk lanceolate with numerous (24–25) long lateral processes pointed at tip (Figures 4A and 6C). Supracoxal shield oval, punctate, with a small pointed projection near base of *scx*. Idiosomal setae (*vi*, *ve*, *si*, *se*, *c*₁, *c*₂, *c*_p, *c*₃, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃, *ps*₁, *ps*₂, *ps*₃) smooth, filiform, setae *h*₃, *se*, *vi* longer than other setae; *ve* and *si* shorter than other setae. Opisthosomal gland openings between setal bases *e*₁ and *e*₂. Four pairs of fundamental cupules (*ia*, *im*, *ip* and *ih*) present. Ventral idiosoma with four pairs of coxal setae (*1a*, *3a*, *4a* and *4b*) and one pair of genital setae (*g*). Coxal sclerites: I—short, narrow, triangular (Figure 6H); anterior II—narrowly extended along anterior apodeme II, with a slight expansion at base (Figure 6I); posterior apodeme II absent, but present as shapeless sclerite (Figure 6I); III and IV—narrowly extended along apodemes, with a slight expansion at base (Figure 6J). Genital region (Figure 6G) situated between coxal fields III and IV; genital valves form an inverted Y; epigynal apodeme absent. Genital papillae (Figure 6G) wide, with pointed ends. Anal opening ventral, long; distance between ovipore and anal opening less than half length of anal opening. Copulatory tube absent. Inseminatory canal of spermatheca wide, ribbon-like, slightly widened at junction with base of spermatheca (Figures 4B and 6F). Base of spermatheca flat, ring-shaped. Paired efferent ducts (Figures 4B and 6F) elongated, with very short stem (difficult to see). Three pairs adanal (*ad*_{1–3}) setae.

All legs shorter than body; all segments free (Figure 4C–F, Figure 5C–F and Figure 6K–N). Trochanters I–III each with long filiform seta, *pR* I–II, *sR* III; trochanter IV without setae. Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV long, filiform. Genua setation 2-2-1-0; setae *mG* and *cG* I–II spiniform; seta *nG* III filiform. Tibial setation 2-2-1-1; setae *hT* I–II, *gT* I–II and *kT* III–IV spiniform, *hT* slightly shorter than *gT*. Tarsal setation 13-12-10-10; pretarsi consist of slightly curved and long empodial claws attached to short paired condylophores. Tarsus I with setae *ra*, *f* and *d* filiform, *aa*, *ba*, *e*, *wa*, *la* larger spiniform, *s*, *p* and *q* short spiniform, and *u* and *v* represented by very small remnants. Tarsus II with same setae except *ra* spiniform and *s* larger, spiniform, and *aa* absent. Tarsi III and IV with setae *f* and *d* filiform, *r*, *w*, *e* and *s* larger spiniform, *p* and *q* small spiniform, and *u* and *v* represented by very small remnants. Solenidia ω_1 on tarsi I and II cylindrical, with clavate apex, not bent. Solenidium ω_2 on tarsus I shorter than ω_1 , cylindrical, with rounded apex, situated distinctly posterior to ω_1 , beside *aa*. Solenidium ω_3 distal on tarsus I, cylindrical, with rounded tip, longer than ω_1 . Famulus (ϵ) of tarsus I wide, spiniform, with broadly rounded apex. Solenidia ϕ of tibiae I–II elongate, tapering, reaching the apices of their respective tarsi without ambulacra but not protruding beyond apex of empodial claws; solenidia ϕ III–IV tapering, shorter than respective tarsi (without ambulacra), ϕ III reaches level of bases setae *w* and *r*, and ϕ IV not reaching level of these setae. Solenidia σ' and σ'' on genu I elongate, tapering, σ'' longer than σ' , σ'' not quite reaching bases of ϕ I. Solenidium σ on genu II more than 9–10 times longer than its width, with rounded tip. Solenidium σ of genu III absent.

Male unknown.

Heteromorphic deutonymph (*n* = 3) (Figures 7–11). Body rounded (Figures 7 and 8), 1.2–1.3 times longer than wide, widest in sejugal region; idiosomal length 330–380, width 260–290. Gnathosoma (Figures 9A and 11E,F) short, subcapitulum 160 × 170, trapezoidal, with filiform setae *cm*, and setae *h* absent (their positions marked by somewhat refractile spots); palps 90, two-segmented, with filiform setae *sup* and palpal solenidia (ω); palp length slightly exceeds the length of the gnathosoma.

Dorsum (Figures 7 and 11A). Idiosoma smoothly punctate (there are two types of punctation—rare but large pits and numerous but very small dots between them); distinct

linear pattern present on anterior and lateral sides of prodorsal sclerite and hysterosomal shield. Apex of propodosoma anterior to anterior border of prodorsal shield, with apical internal vertical setae (*vi*) (bases separated). Anterior border of prodorsal shield rounded triangular, with setae *ve*, ocelli absent. External scapular setae *se* and internal scapular setae *si* situated on prodorsal shield; *si* distinctly posterior *se*. Supracoxal setae of legs I (*scx*) filiform. Sejugal furrow well developed. Prodorsal shield 100–116, hysterosomal shield 210–220, ratio hysterosomal shield/prodorsal shield length = 1.9–2.1. Hysterosoma with 11 pairs of simple filiform setae on hysterosomal shield (*c*₁, *c*₂, *c*_p, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃); setae *h*₃ distinctly longer than other setae. Opisthonotal gland openings (*gla*) situated laterally on hysterosomal shield, slightly anterior setae *c*₃, much closer to seta *c*_p than to *c*₃. Four pairs of fundamental cupules (*ia*, *im*, *ip* and *ih*) present.

Venter (Figures 8 and 11B–D,G). Coxal fields smooth. Anterior apodemes of coxal fields I fused forming sternum; coxal fields I closed, sternum fused with processes of anterior apodemes of coxal fields II (in one paratype, the connection was broken during preparation); coxal fields II closed, anterior and posterior apodemes of coxal fields II curved medially. Sternal and ventral shield contiguous. Anterior apodemes of coxal fields III connected to the anterior apodemes of coxal fields IV but not forming a common medial apodeme III (medial apodeme III divided into two parallel apodemes with setal pair *4b*); coxal fields III closed. Ventrum present, connected to the medial apodemes III, but well separated from genital opening. Setae *c*₃ filiform, situated on ventral surface between legs II and III, near region separating sternal and ventral shields. Coxal setae *1a*, *3a*, *4b* and genital setae *g* filiform; *4a* in form of rounded conoids. Genital region in posterior portion of coxisternal fields IV; progenital opening elongated, with two pairs of genital papillae within genital atrium; genital papillae two-segmented, with cone-shaped rounded apices. Genital setae laterad of genital opening. Attachment organ (Figure 11D,G) posterior to coxal fields IV. Anterior suckers (*ad*₃) round, median suckers (*ad*₁₊₂) distinctly larger, with paired vestigial alveoli (situated on common sclerite); pair of small refractile spots anterolaterad median suckers (*ps*₃); lateral conoidal setae of attachment organ (*ps*₂) situated slightly posterior to line joining centers of median suckers; anterior and posterior lateral and posterior median cuticular conoids well developed; anus situated between anterior suckers (*ad*₃).

Legs (Figure 9B–E, Figures 10 and 11H–M). Legs short; all segments free. Trochanters I–III each with long filiform seta, *pR* I–II, *sR* III. Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV long (*vF* I longer than *vF* II), filiform. Genua setation 2-2-1-0; setae *mG* I–II spiniform, finely serrated, *cG* I–II spiniform, *nG* III weakly spiniform. Tibial setation 2-2-1-1; setae *gT*, *hT* I–II and *kT* III–IV spiniform, finely serrated; setae *gT* and *hT* approximately the same length. Tarsal setation 10-9-8-8. All pretarsi consisting of empodial claws attached to short paired condylophores; claws I–II hooked, III–IV slightly curved and long. Tarsus I with setae *ra*, *la*, *f* foliate; seta *d* filiform, shorter than *e*; seta *e* wide, cylindrical with sucker-like apex, different in form from simply foliate seta *f*; setae *wa* spiniform; seta *aa* weakly spiniform; *p* and *q* small spiniform; *ba* I absent. Tarsus II similar to tarsus I except spiniform seta *ba* present; *aa* absent and *wa* finely serrated. Tarsus III with setae *w*, *r*, *s*, *e* and *f* smooth and foliate; seta *d* filiform, longer than leg; setae *p* and *q* small spiniform. Tarsus IV similar to tarsus III except seta *r* weakly foliate, *w* filiform, finely serrated and *f* smooth filiform. Solenidia ω_1 on tarsi I–II cylindrical, with slightly clavate apices; ω_3 on tarsus I longer than ω_1 , with rounded apex, situated slightly distal to ω_1 ; ω_1 and ω_3 separated by spiniform famulus (ϵ); solenidium ω_2 of tarsus I slightly expanding apically, situated somewhat more basal and posterior to $\omega_1 + \epsilon + \omega_3$ group. Solenidia ϕ of tibiae I–IV elongate, tapering; ϕ I longer than tarsus I with ambulacra; solenidium ϕ II shorter than tarsus II; solenidium ϕ III longer than tarsus III without ambulacra; solenidium ϕ IV short

(in one specimen, on one leg, it is attached at base of tibia). Solenidion σ of genu I elongate, cylindrical, nearly reaching tip of tibia I; solenidion σ of genu II much shorter, slightly expanding apically, not reaching midlength of tibia II; solenidion σ of genu III absent.

Etymology. The new species is named in honor of the Japanese acarologist Dr. Kazuyoshi Kurosa, who independently discovered it in Japan [82].

Type deposition. Holotype and all paratypes are deposited in the collection of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP).

Biology. Mites live in sporocarps of old puffballs *Lycoperdon* spp. (Agaricales, Lycoperdaceae), feeding on spores (as evidenced by gut contents). Heteromorphic deutonymphs are phoretic on beetles *Lycoperdina koltzei*, larvae of which are also associated with the same fungal species. Co-occurring mite species: *Viedebanttia egorovi* Klimov, 1998.

Distribution. Russia: Primorskiy Kray; Japan.

Obelacarus gen. nov.

Type species: *Obelacarus gulosus* sp. nov.

“AD469_puffball_mite” Klimov and OConnor, 2013: 413 [6]

urn:lsid:zoobank.org:act:AD96C317-7757-47DA-B0E9-A308F946A926

Diagnosis. Adult. Central trunk of supracoxal setae *scx* broadly flattened with numerous lateral processes and terminal long processes. Grandjean’s organ with one pointed trunk and numerous small spines. Prodorsal shield vestigial. Seta *ve* well developed, located on the same transverse line as *vi*. Posterior coxal apodeme II present, with sclerite located at end of apodeme. Tarsal setae *u* and *v* developed, spiniform. Solenidia φ I–II short, not reaching the apices of their respective tarsi without ambulacra. Solenidion σ'' I shorter than σ' . Solenidion σ III present. Inseminatory canal of spermatheca narrow. Paired efferent ducts cone-shaped, with long stem.

Heteromorphic deutonymph. Seta *ve* present. Ratio hysterosomal shield/prodorsal shield length = 4.7. Coxal field I free. Coxal setae *1a* and *3a* conoids. External conoidal setae *ps*₂ of attachment organ lateral to median sucker *ad*₁₊₂. Tibiae I–II similar in length or only slightly longer than corresponding genua. Seta *aa* I filiform, long (longer than ω_3). Setae *e* I–II cylindrical with sucker-like apex, different in form from simply foliate seta *f*. Setae *d* I–II longer than *e* I–II. Seta *ba* II longer than ω_1 II. Setae *p* and *q* I–IV foliate. Seta *f* IV shorter than leg IV. Solenidion σ III represented refractile spots.

Etymology. The generic name *Obelacarus* is derived from the Latinized form of Obelix, a corpulent fictional Gaulish character from French comics and films, in reference to the robust body shape of the mite.

Remarks. The differences between both genera of Lycoglyphidae fam. nov. are presented in the key below.

Obelacarus gulosus sp. nov.

urn:lsid:zoobank.org:act:09506039-C499-4B86-8427-D2468804FC82

“AD469_puffball_mite” Klimov and OConnor, 2013: 413 [6]

Figures 12–27

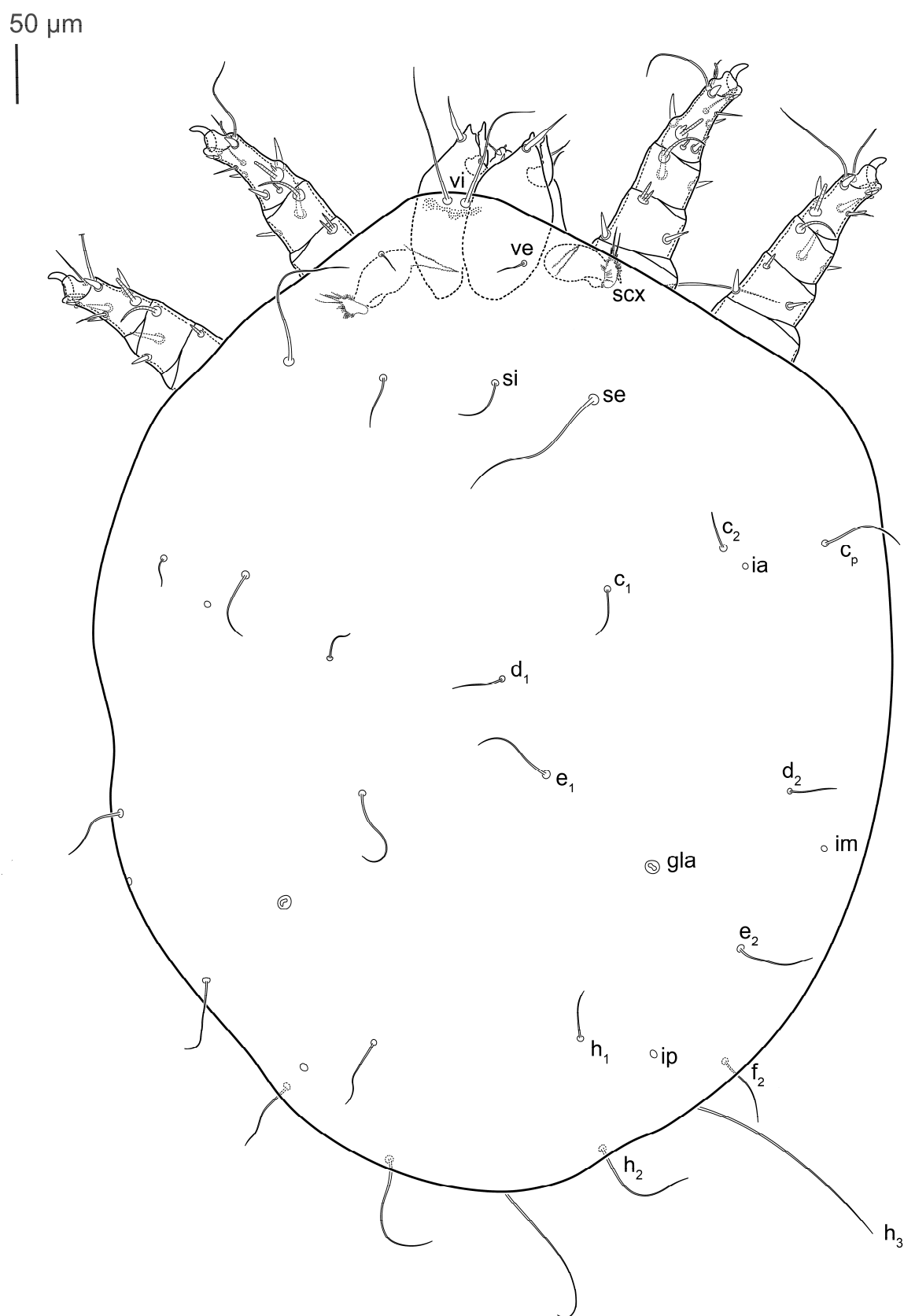


Figure 12. *Obelacarus gulosus* sp. nov. and gen. nov., female, holotype, dorsal view.

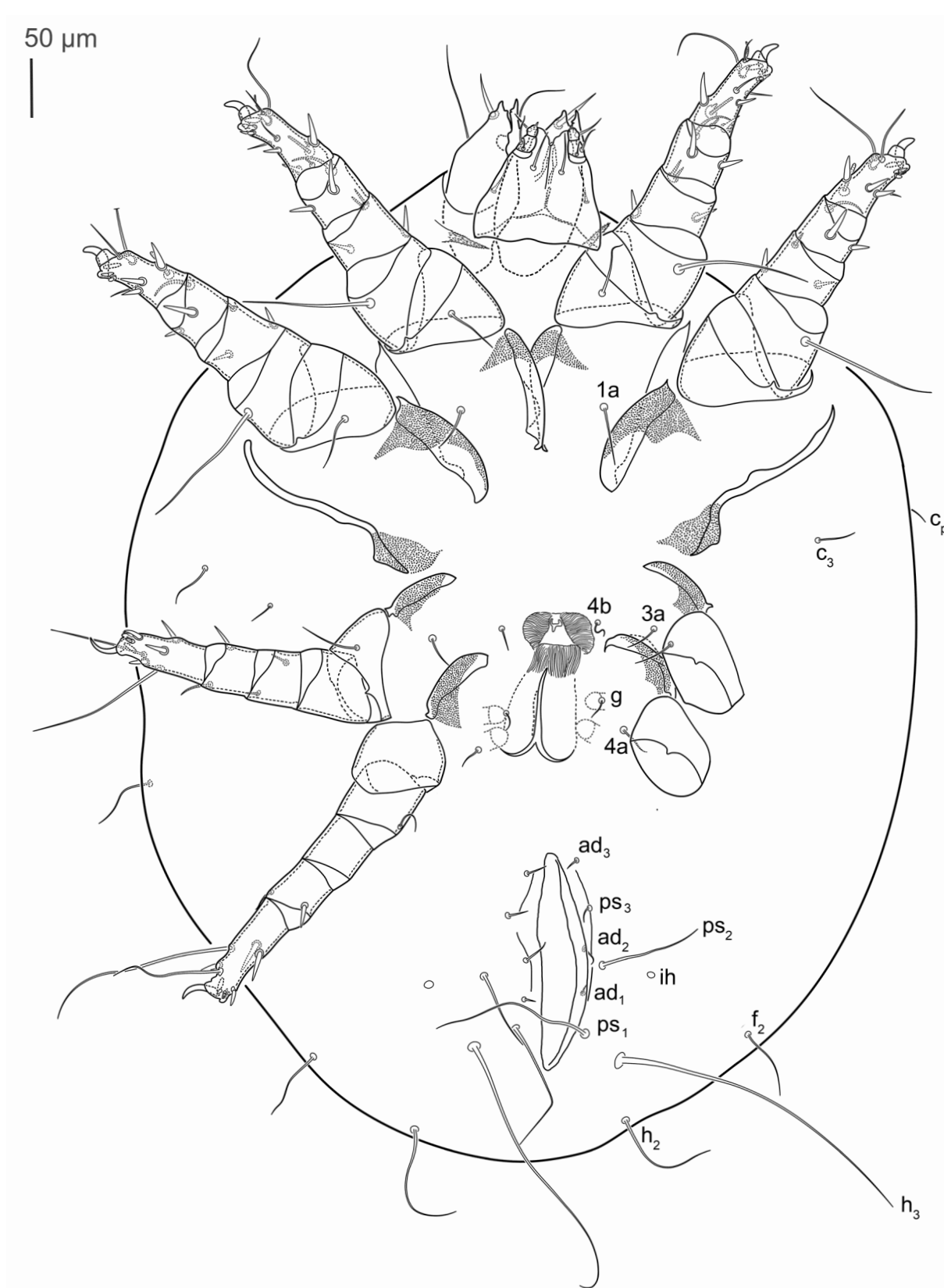


Figure 13. *Obelacarus gulosus* sp. nov. and gen. nov., female, holotype, ventral view.

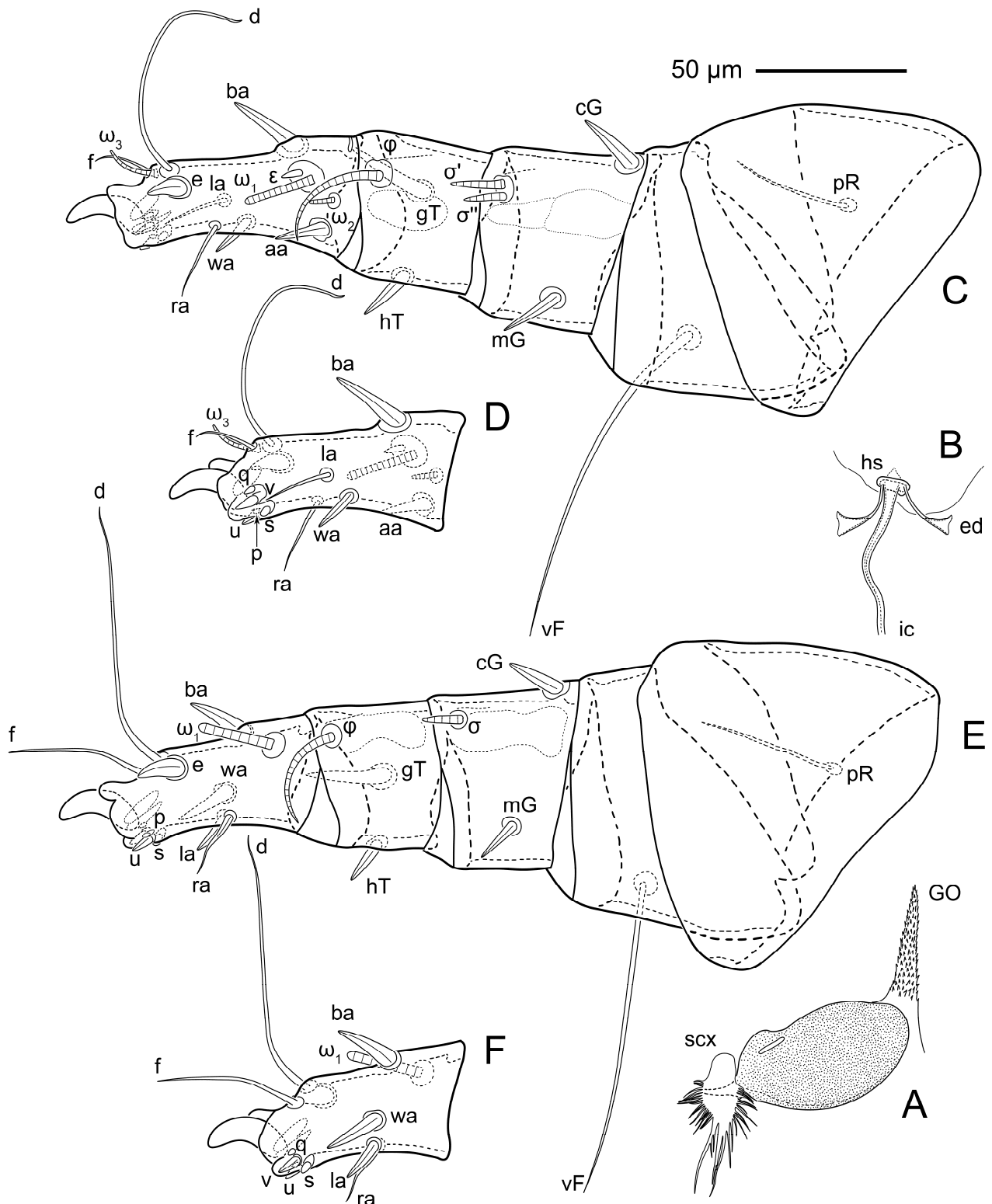


Figure 14. *Obelacarus gulosus* sp. nov. and gen. nov., female, holotype: (A)—supracoxal shield, supracoxal seta and Grandjean's organ; (B)—spermatheca; (C)—leg I, posterior view; (D)—tarsus I, anterior view; (E)—leg II, posterior view; (F)—tarsus II, anterior view.

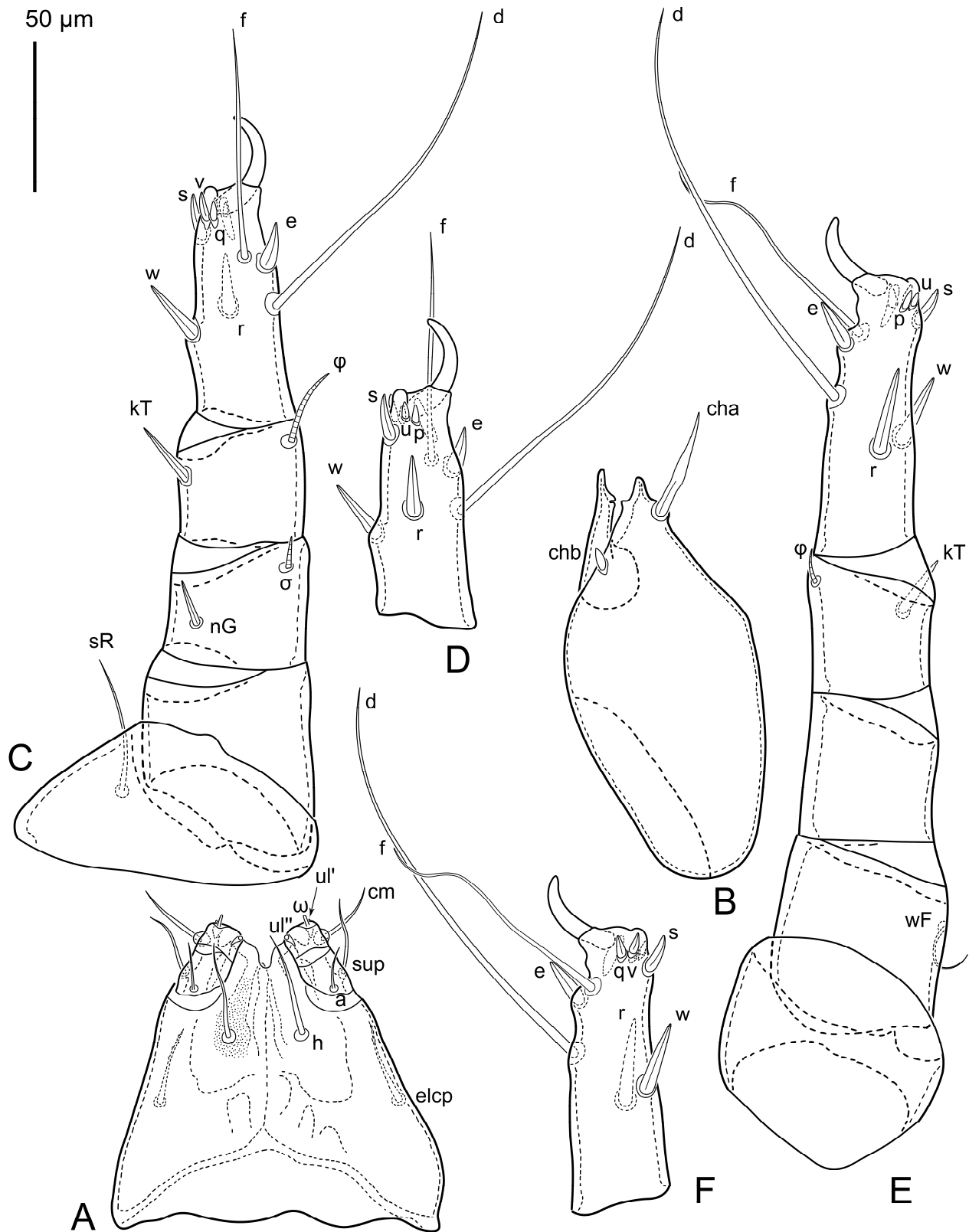


Figure 15. *Obelacarus gulosus* sp. nov. and gen. nov., female, holotype: (A)—subcapitulum; (B)—chelicera; (C)—leg III, posterior view; (D)—tarsus III, anterior view; (E)—leg IV, posterior view; (F)—tarsus IV, anterior view.

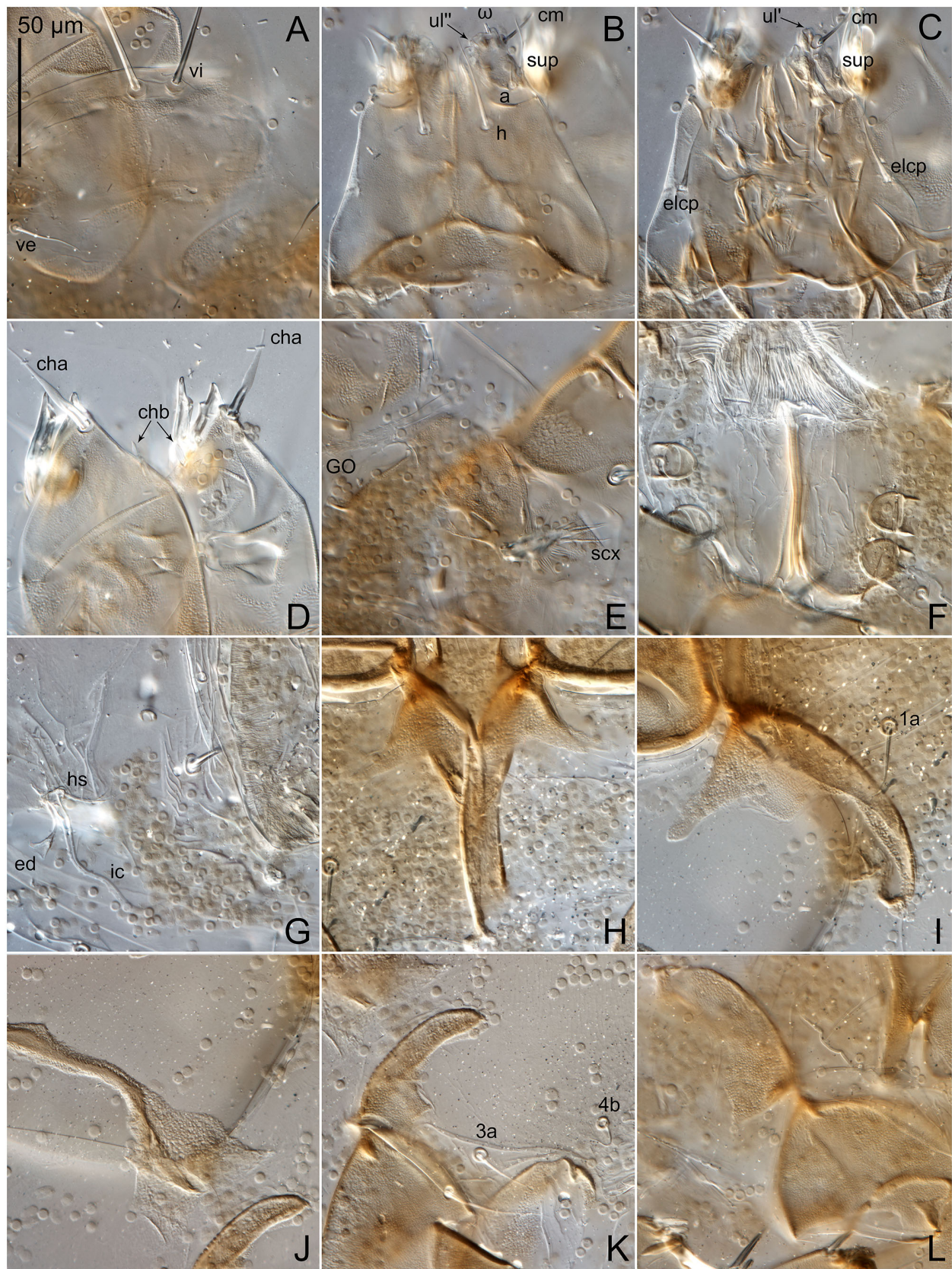


Figure 16. *Obelacarus gulosus* sp. nov. and gen. nov., female, holotype, DIC images: (A)—prodorsal shield; (B,C)—subcapitulum; (D)—chelicerae; (E)—supracoxal shield, supracoxal seta and Grandjean's organ; (F)—genital opening; (G)—spermatheca; (H)—apodemes I; (I)—apodeme II; (J)—sejugal apodeme; (K)—apodeme III; (L)—apodeme IV.

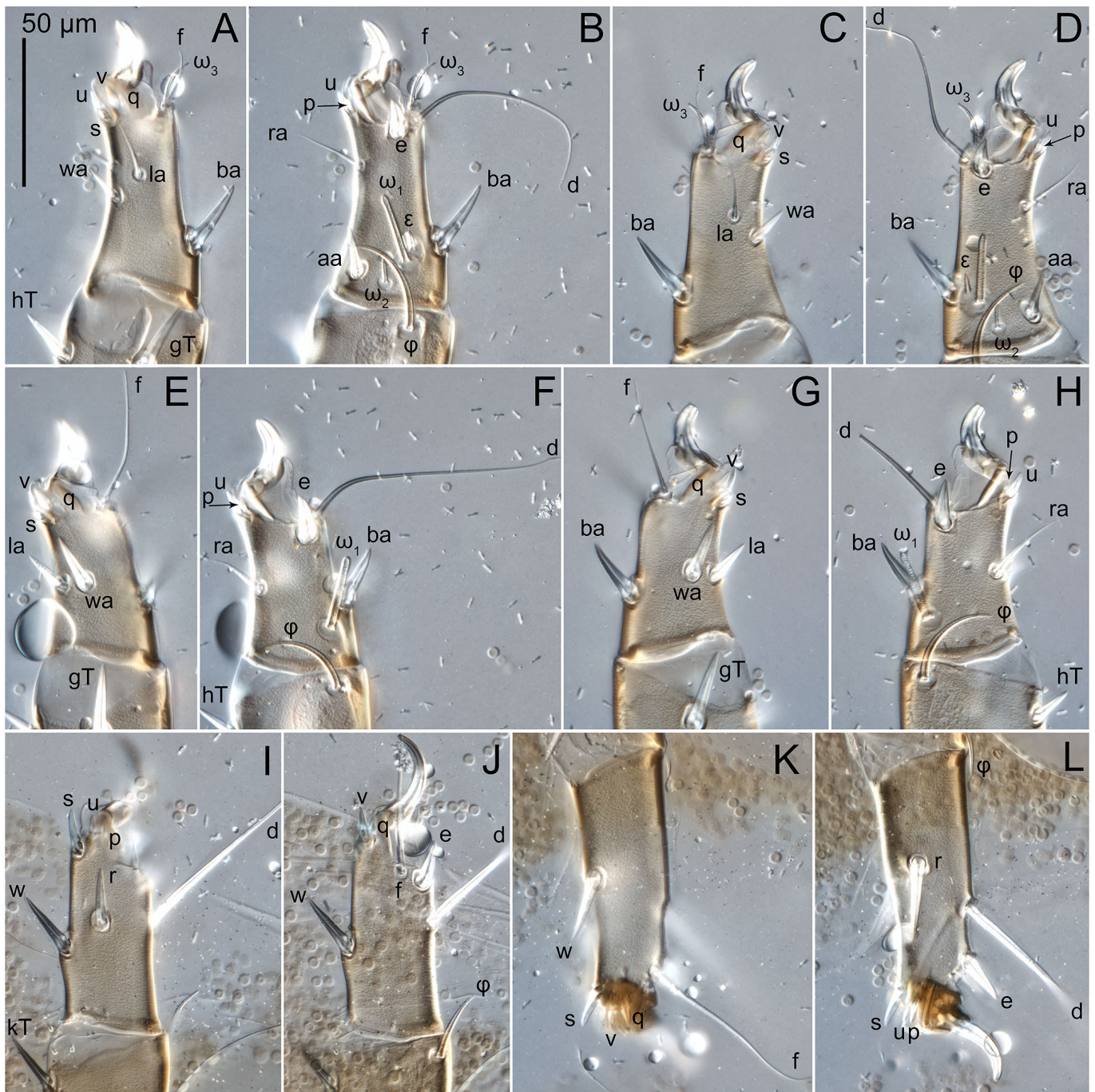


Figure 17. *Obelacarus gulosus* sp. nov. and gen. nov., female, holotype, DIC images: (A,C)—tarsi I, anterior view; (B,D)—tarsus I, posterior view; (E,G)—tarsi II, anterior view; (F,H)—tarsi II, posterior view; (I)—tarsus III, anterior view; (J)—tarsus III, posterior view; (K)—tarsus IV, anterior view; (L)—tarsus IV, posterior view.

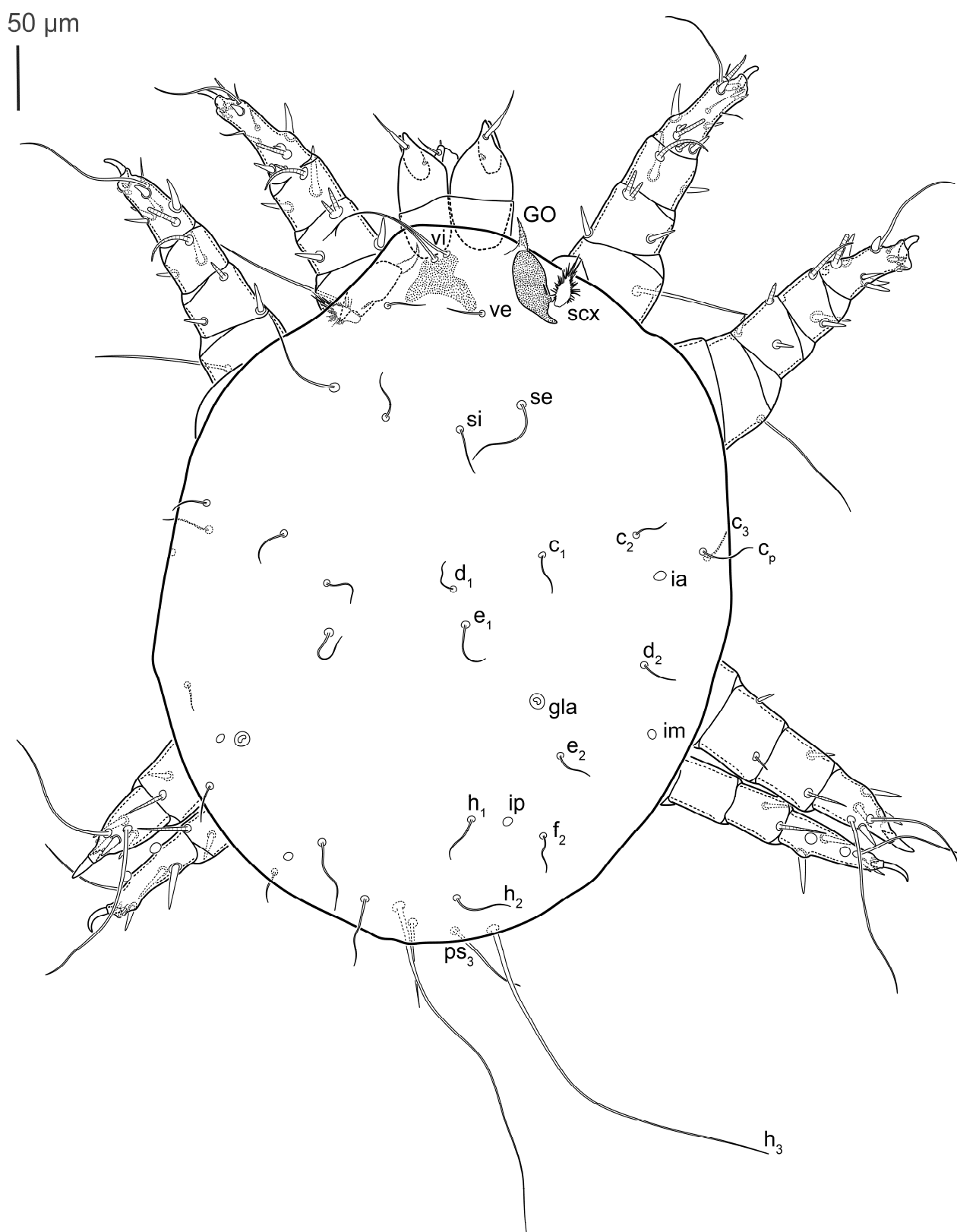


Figure 18. *Obelacarus gulosus* sp. nov. and gen. nov., male, dorsal view.



Figure 19. *Obelacarus gulosus* sp. nov. and gen. nov., male, ventral view.

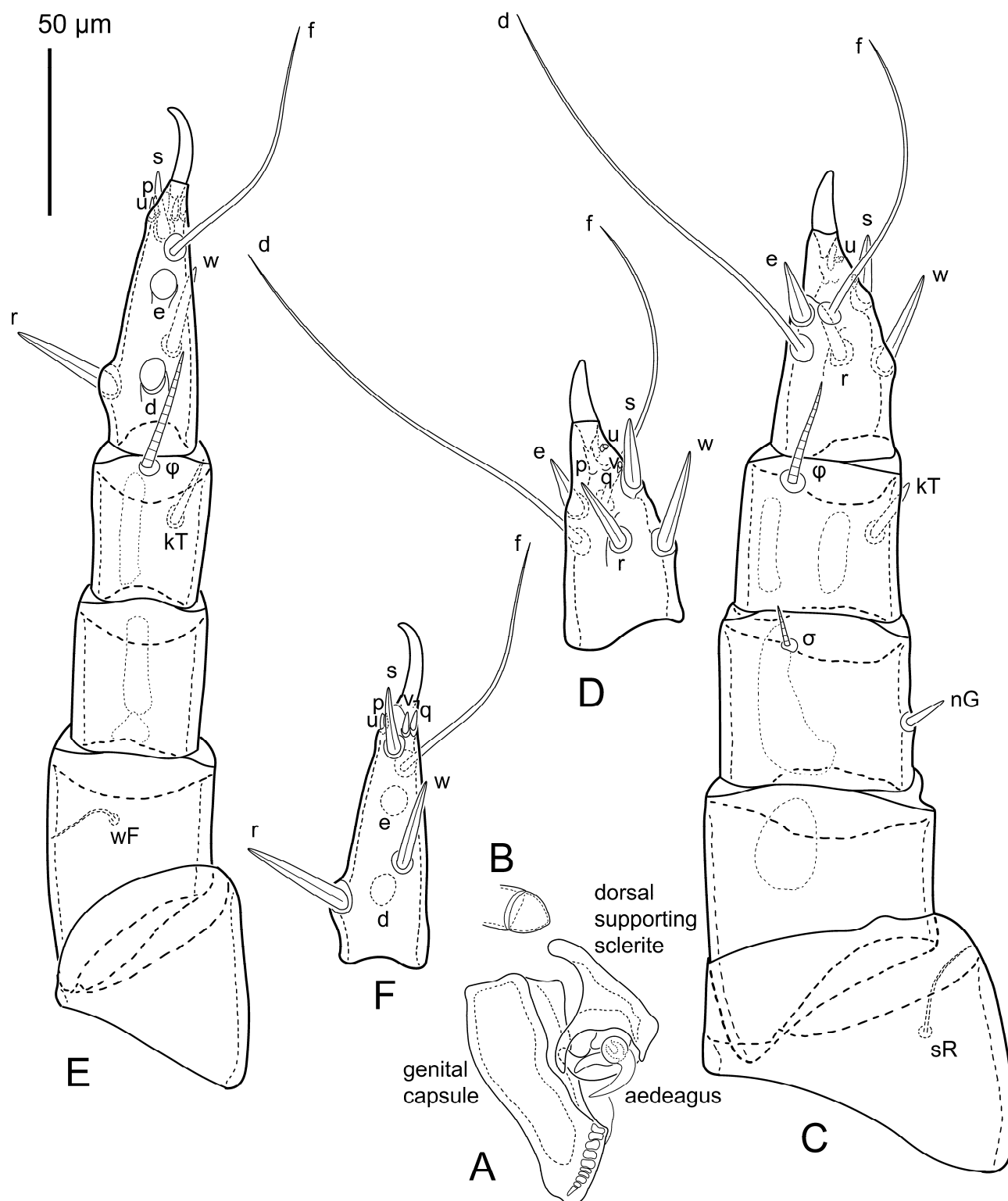


Figure 20. *Obelacarus gulosus* sp. nov. and gen. nov., male: (A)—genitalia; (B)—genital papilla; (C)—leg III, posterior view; (D)—tarsus III, anterior view; (E)—leg IV, posterior view; (F)—tarsus IV, anterior view.

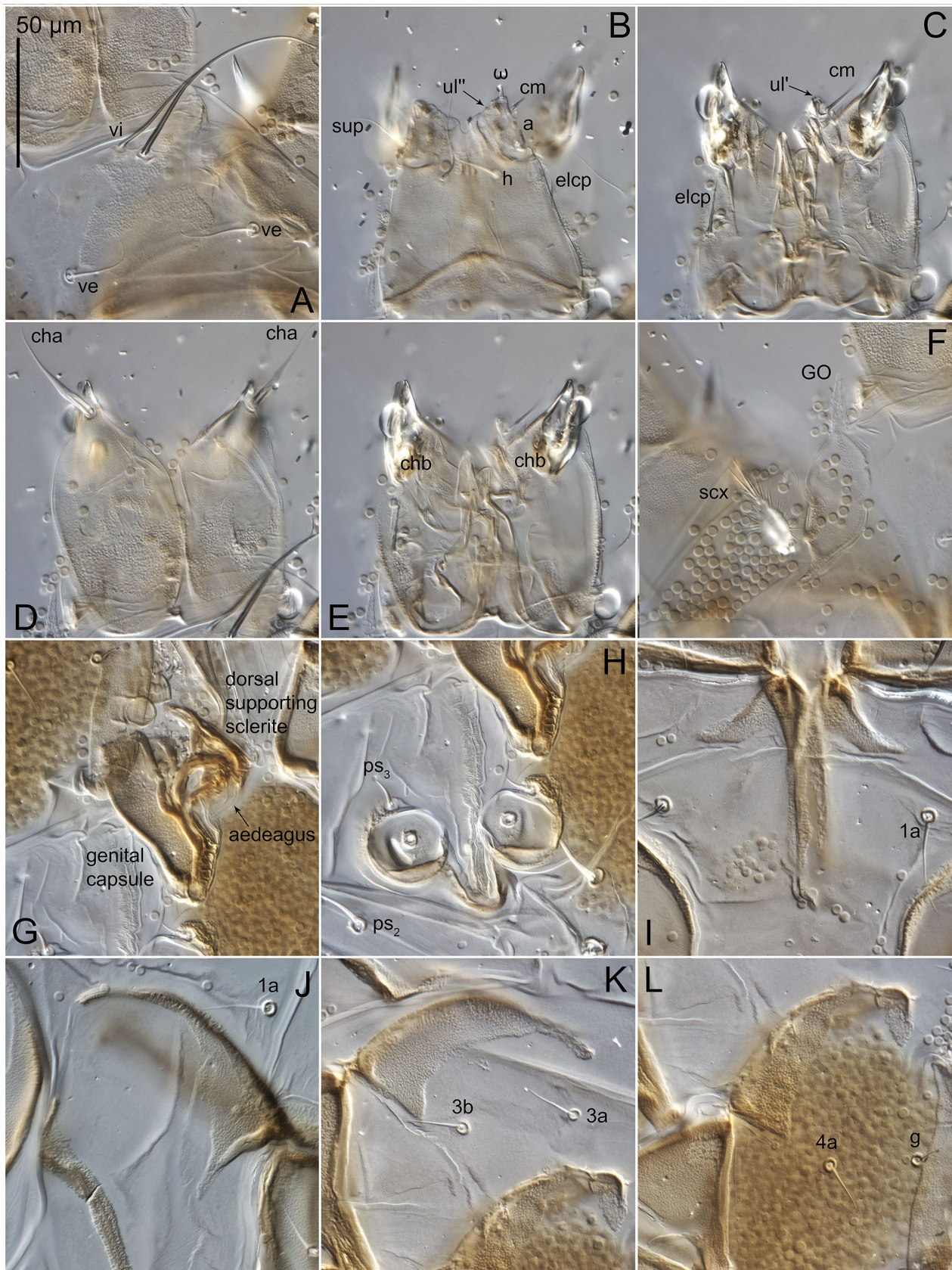


Figure 21. *Obelacarus gulosus* sp. nov. and gen. nov., male, DIC images: (A)—prodorsal shield; (B,C)—subcapitulum; (D,E)—chelicerae; (F)—supracoxal shield, supracoxal seta and Grandjean's organ; (G)—genitalia; (H)—anal region; (I)—apodemes I; (J)—apodemes II; (K)—apodeme III; (L)—apodeme IV.

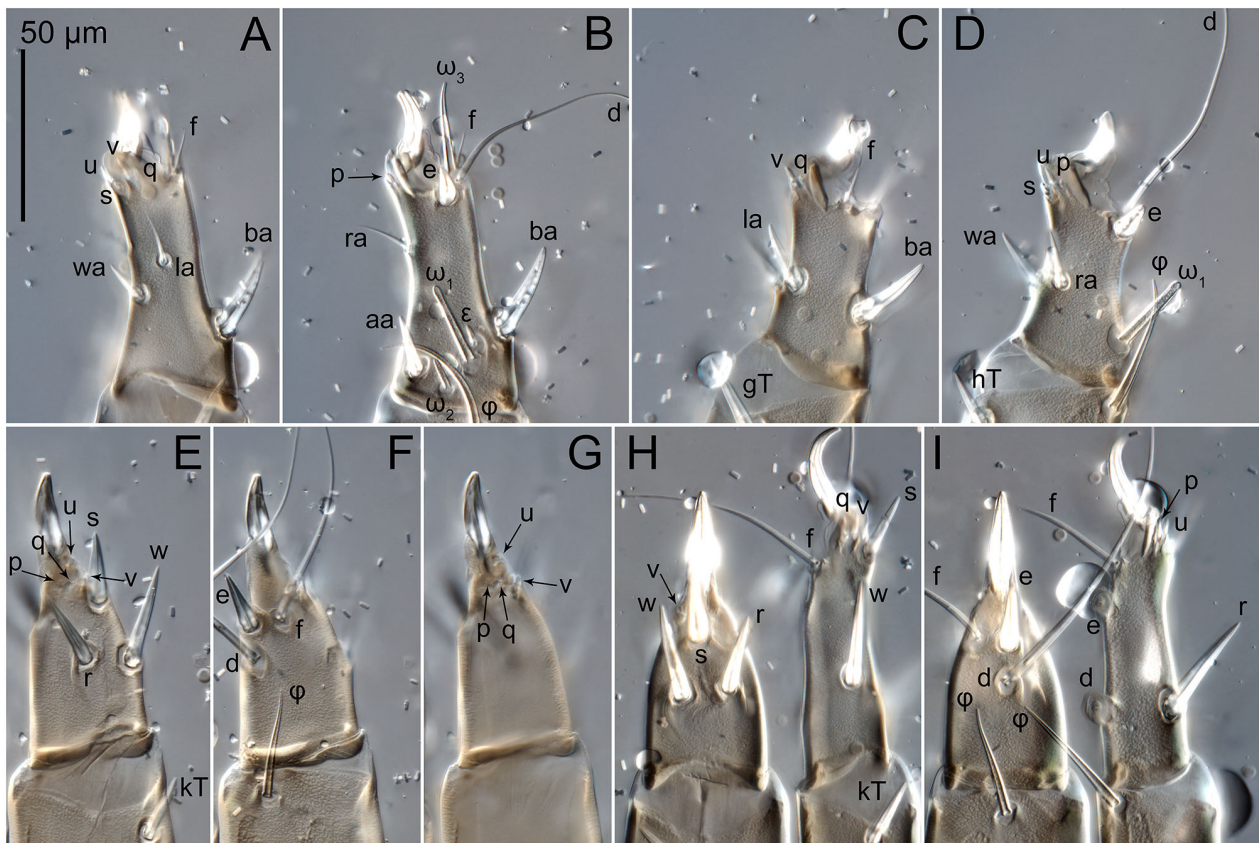


Figure 22. *Obelacarus gulosus* sp. nov. and gen. nov., male, DIC images: (A)—tarsus I, anterior view; (B)—tarsus I, posterior view; (C)—tarsus II, anterior view; (D)—tarsus II, posterior view: (E,G)—tarsus III, ventral view; (F)—tarsus III, dorsal view; (H)—tarsi III and IV, ventral view; (I)—tarsi III and IV, dorsal view.

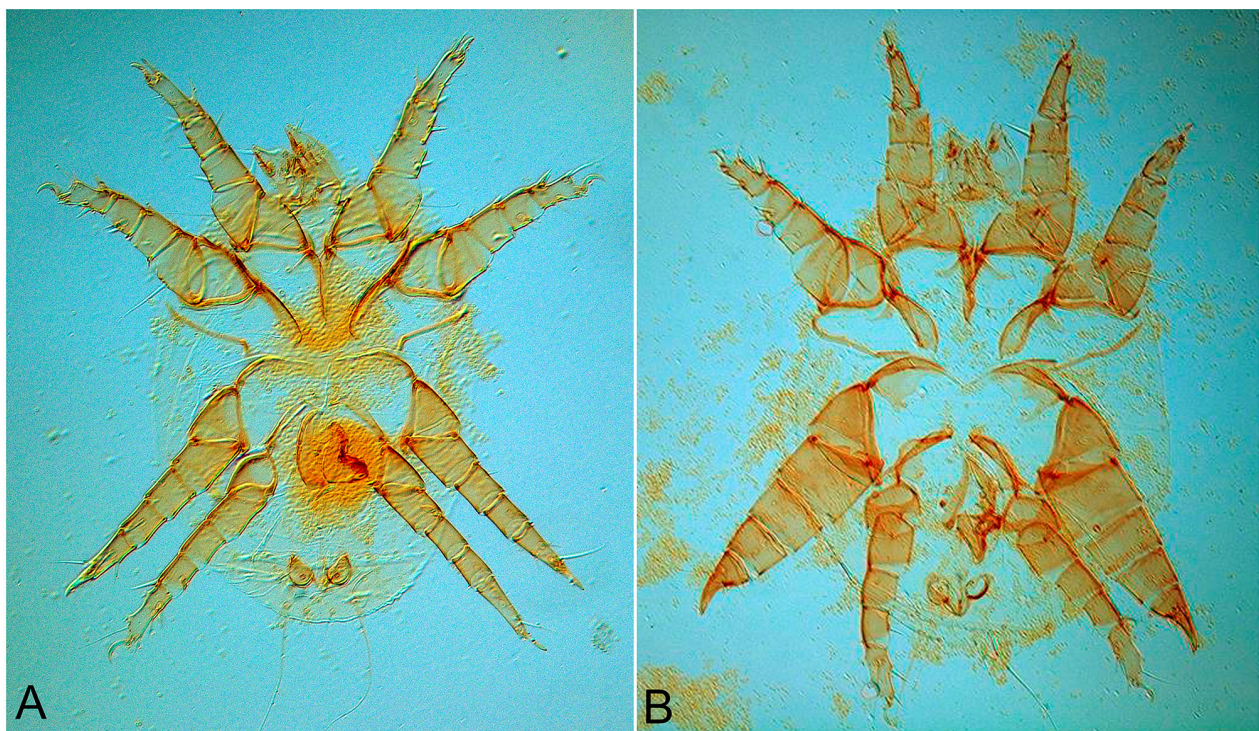


Figure 23. *Obelacarus gulosus* sp. nov. and gen. nov., male, DIC images: (A)—homeomorphic; (B)—heteromorphic.

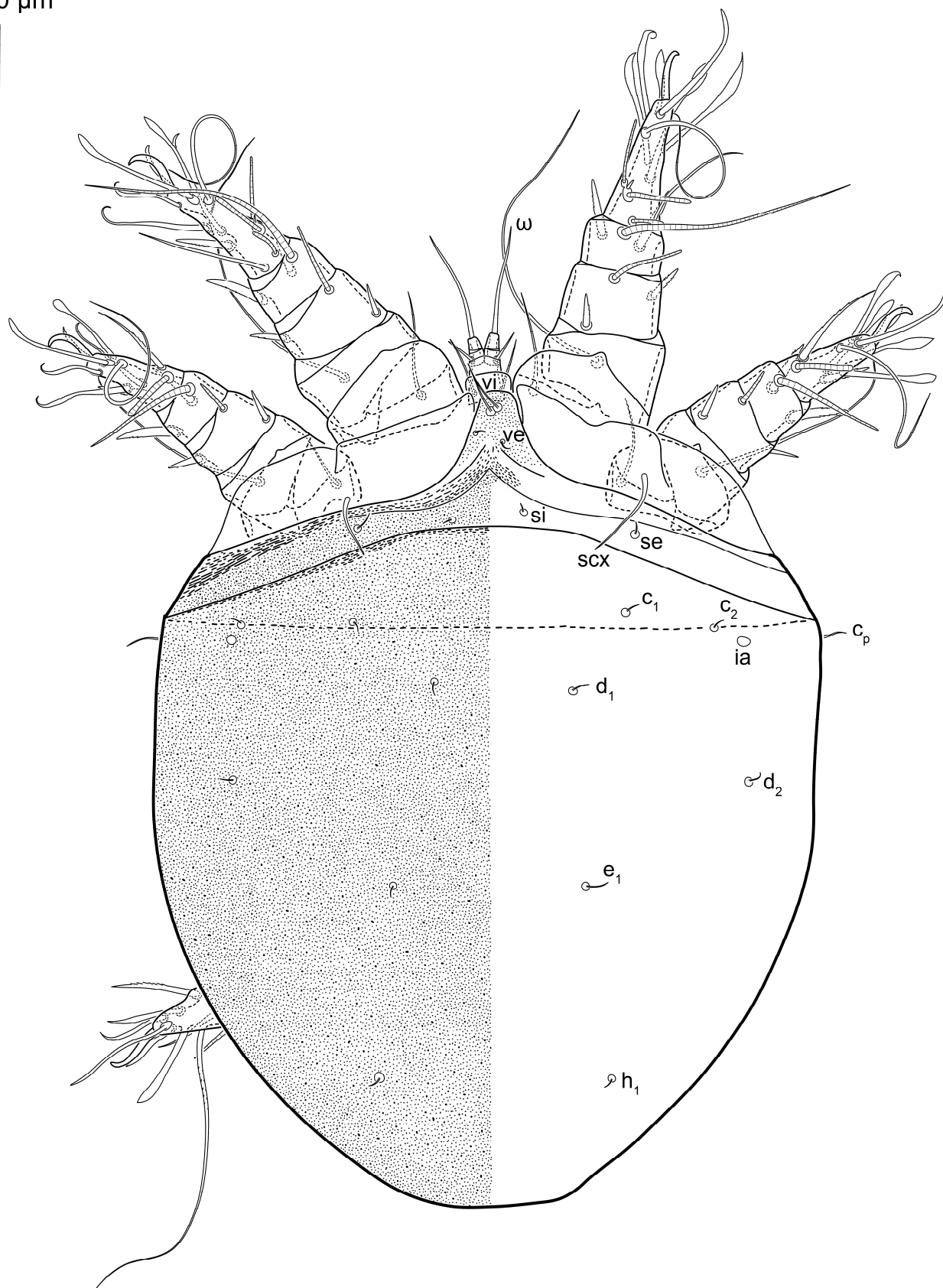
50 μ m

Figure 24. *Obelacarus gulosus* sp. nov. and gen. nov., phoretic deutonymph, dorsal view.

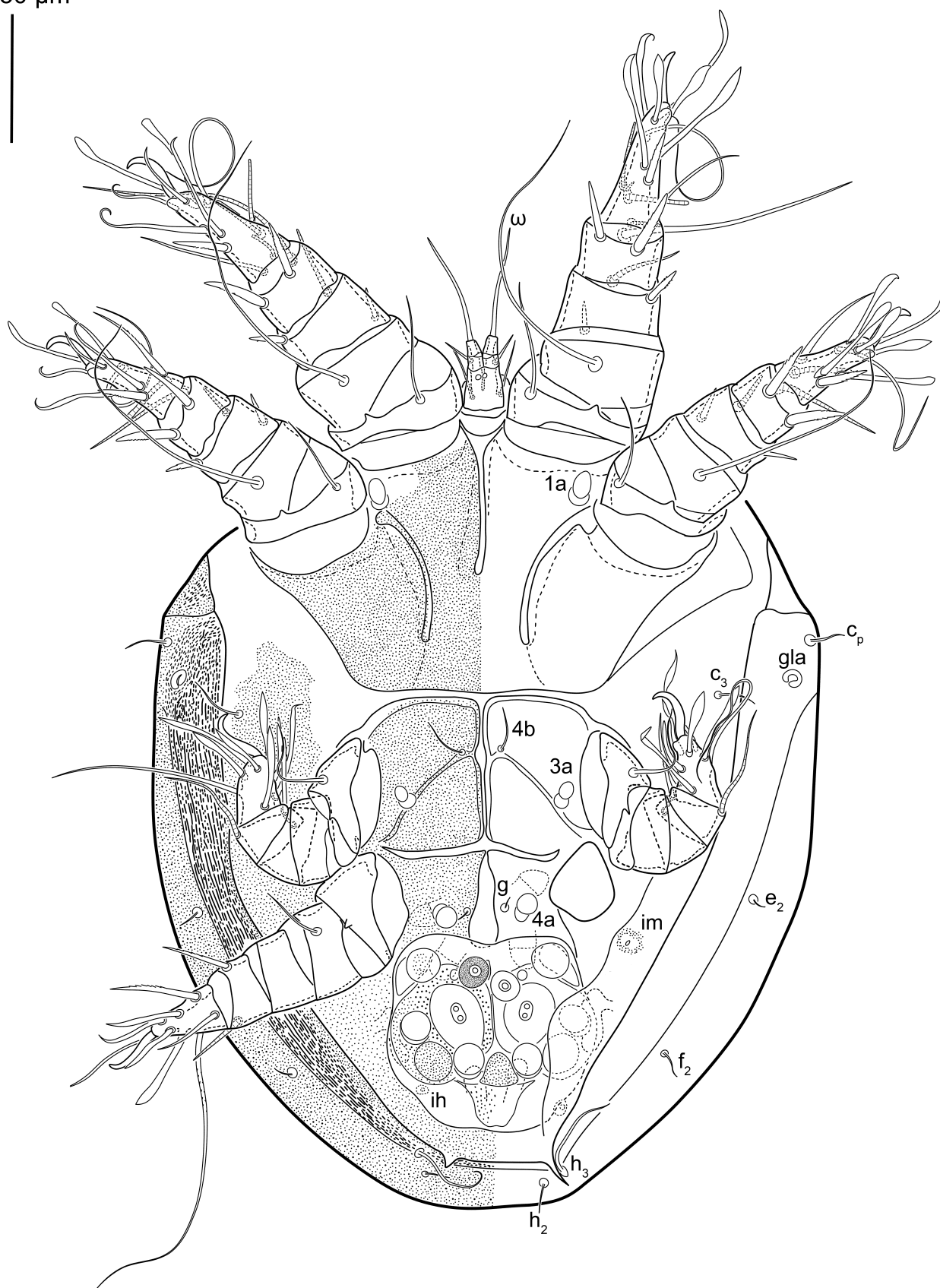
50 μ m

Figure 25. *Obelacarus gulosus* sp. nov. and gen. nov., phoretic deutonymph, ventral view.

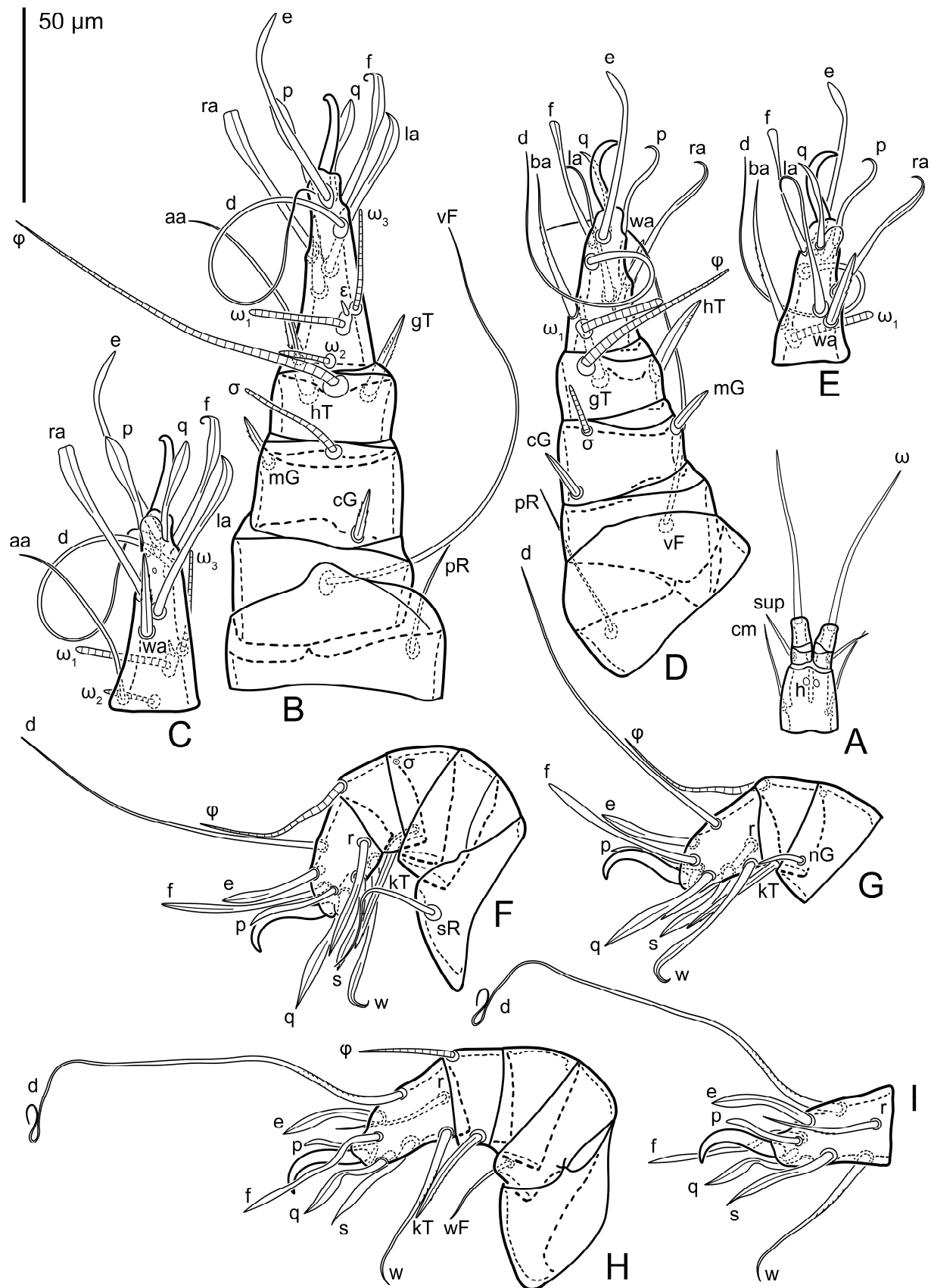


Figure 26. *Obelacarus gulosus* sp. nov. and gen. nov., phoretic deutonymph: (A)—gnathosoma, ventral view; (B)—leg I, dorsal view; (C)—tarsus I, ventral view; (D)—leg II, dorsal view; (E)—tarsus II, ventral view; (F)—leg III, ventral view; (G)—tarsus, tibia and genua III, dorsal view; (H)—leg IV, ventral view; (I)—tarsus IV, ventral view.

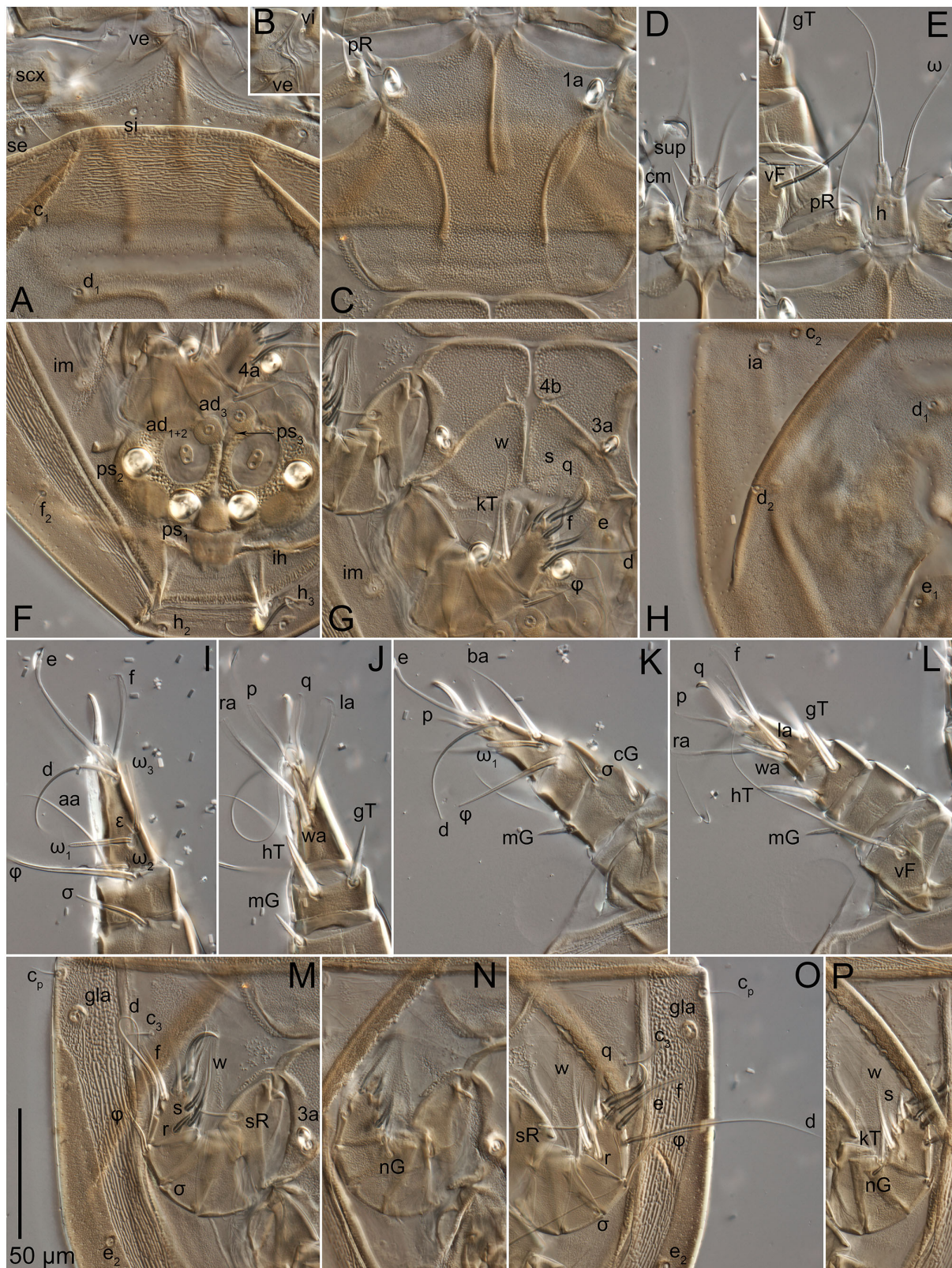


Figure 27. *Obelacarus gulosus* sp. nov. and gen. nov., phoretic deutonymph, DIC images: (A,B)—anterior part of propodosoma, dorsal view; (C)—anterior part of propodosoma, ventral view; (D)—gnathosoma, dorsal view; (E)—gnathosoma, ventral view; (F)—attachment shield; (G)—apodemes III and IV; (H)—part of hysterosomal shield; (I)—tarsus I, dorsal view; (J)—tarsus I, ventral view; (K)—leg II, dorsal view; (L)—leg II, ventral view; (M)—leg III, ventral view; (N)—leg III, dorsal view; (O)—leg IV, ventral view; (P)—leg IV, dorsal view.

Material. Holotype: female—USA: New York, Chautauqua County, Westfield, ex *Lycoperdon pyriforme* (Agaricales: Lycoperdaceae), 8 October 1981, BMOC #81-1008-15 (UMMZ). Paratypes: 1HDN—same data; 1 heteromorphic male—same data (UMMZ).

Additional materials. 26 females, 10 males, 12 deutonymphs, 5 protonymphs, 5 larvae + more unmounted—BMOC 81-1008-015—USA: New York, Chatauqua Co., Westfield (42°19'20" N, 079°34'40" W); 8 October 1981; B.M. OConnor; reared from tritonymphs in *Apioperdon pyriforme* (Schaeff.) Vizzini (= *Lycoperdon pyriforme*) (Agaricales: Lycoperdaceae); 3 females, 2 males, 7 deutonymphs—BMOC 81-0407-001—Tompkins Co., Ringwood Preserve, 7.6 km E Ithaca (42°26'58" N, 076°22'25" W); October 1980; J. Pakaluk; reared from deutonymphs under elytra of *Lycoperdina ferruginea* LeConte, 1824 (Coleoptera: Endomychidae); 6 females 7 males, 6 deutonymphs—BMOC 82-0729-001—Tompkins Co., Ithaca (42°26'26" N, 076°29'49" W); summer 1981; J. Pakaluk; ex *A. pyriforme*; 12 deutonymphs—BMOC 80-0506-009—Cortland Co., McLean Reserve (now Lime Hollow Nature Center), 42°34'07" N, 076°15'02" W; 6 May 1980; B.M. OConnor; ex *Fomitopsis betulina* (Bull.) B.K.Cui, M.L.Han & Y.C.Dai (2016); 25 deutonymphs—BMOC 81-0407-003—Tompkins Co., Ringwood Preserve, 7.6 km E Ithaca (42°26'58" N, 076°22'25" W); October 1980; J. Pakaluk; ex *A. pyriforme*; 3 deutonymphs—BMOC 86-0407-003—Tompkins Co., Ringwood Preserve, 7.6 km E Ithaca (42°26'58" N, 076°22'25" W); October 1980; J. Pakaluk; ex *L. ferruginea* larva in *A. pyriforme*; 10 deutonymphs—BMOC 81-1008-017—Chatauqua Co., Westfield (42°19'20" N, 079°34'40" W); 8 October 1981; B.M. OConnor; ex 2 *L. ferruginea* in rotting stump with mycelia of *A. pyriforme*; 4 tritonymphs, 7 deutonymphs, 4 larvae—BMOC 96-0809-036—USA: Michigan, Lake Co., Elk twp. 6.9 km S Irons, (44°05'39" N, 085°58'24" W); 9 August 1996; K. Okabe; ex *A. pyriforme*; 2 deutonymphs—BMOC 17-1026-001—Washtenaw Co., Ann Arbor (42°16'40" N, 83°44'08" W); 25 October 2017; T. McKnight; ex *L. ferruginea*; 13 deutonymphs—BMOC 81-1010-001—Washtenaw Co., Stinchfield Woods, 6.4 km SSE Pinckney (42°24'04" N, 083°55'50" W); 10 October 1981; B.M. OConnor; ex 3 *L. ferruginea* in *A. pyriforme*; 24 deutonymphs on 7 beetles; 3 females, 1 male, abundant protonymphs and larvae reared—BMOC 83-1001-001—Washtenaw Co., Hudson Mills Metropark, 5 km NW Dexter (42°22'43" N, 083°54'45" W); 1 October 1983; B.M. OConnor; reared ex 7 *L. ferruginea* on *Lycoperdon perlatum* Pers. (1796) (Agaricales: Lycoperdaceae); 38 deutonymphs—BMOC 00-1005-005, 7, 8, 9—Livingston Co., E.S. George Reserve, 5 km E Pinckney (42°26'55" N, 84°01'19" W); 5 October 2000; B.M. OConnor, P. Klimov, A. Dowling & M. Lekveishvili; ex 9 *L. ferruginea* on *L. perlatum*; 2 deutonymphs—BMOC 00-1005-010—Livingston Co., E.S. George Reserve, 5 km E Pinckney (42°26'55" N, 84°01'19" W); 5 October 2000; B.M. OConnor, P. Klimov, A. Dowling & M. Lekveishvili; ex 9 *L. ferruginea* on *A. pyriforme* (Agaricales: Lycoperdaceae); 10 deutonymphs—BMOC 81-1220-001, 2, 3—Washtenaw Co., Ann Arbor (42°16'40" N, 83°44'08" W); 21 October 1928; W. Clanton; ex 3 *L. ferruginea*; 14 deutonymphs—BMOC 81-1220-004, 5—Schoolcraft Co., Manistique (45°57'28" N, 86°14'57" W); 10 September 1923; S. Moore; ex 2 *L. ferruginea*; 8 deutonymphs—81-1220-006, 7—Mackinac Co., Naubinway (46°05'32" N, 085°26'51" W); 7 October 1920; S. Moore; ex 2 *L. ferruginea*; 1 deutonymph—BMOC 81-1220-008—Emmet Co., McGulpin Point (45°46'49" N, 084°47'34" W); 8 September 1921; S. Moore; ex *L. ferruginea*; 4 deutonymphs—BMOC 81-1220-009—Charlevoix Co., High Island (45°43'13" N, 084°47'34" W); 4 September 1923; S. Moore; ex *L. ferruginea*; 3 deutonymphs—BMOC 81-1220-010—Gogebic Co., Hughitt-Rawson Preserve, south shore Thousand Island Lake (46°13'13" N, 89°23'57" W); 10 August 1919; T.H. Hubbell; ex *L. ferruginea* in *Betula alleghaniensis* Britt. log.; 4 deutonymphs—BMOC 81-1220-012—Livingston Co., E.S. George Reserve, 5 km E Pinckney (42°26'55" N, 84°01'19" W); 14 May 1933; A. W. Andrews; ex *L. ferruginea*; 2 males and 2 females—BMOC 04-1209-003—Michigan: Livingston Co., E.S. George Reserve, 42°27'03.9" N 084°45'53" W; 9 December 2004; A. Dowling & P. Klimov; ex

Lycoperdon pyriforme; 3 deutonymphs—BMOC 81-1220-013—USA: Pennsylvania: Washington Co., Canonsburg, Mt. Blain (40°15'43" N, 80°11'06" W); 20 July 1920; G.A. Ackerlind; ex *L. ferruginea*; 17 deutonymphs—BMOC 81-1220-014—USA: Illinois, Cook Co., Willow Springs (41°44'30" N, 87°52'40" W); 11 July 1916; no collector; ex *L. ferruginea*; 2 females, 2 males, 11 tritonymphs, 15 deutonymphs (including 8 pharate tritonymphs)—BMOC 86-0928-006—CANADA: Ontario, Parry Sound Co., Sequin Twp., Portage Lake (45°13'12" N, 079°48'38" W); 28 September 1986; B.M. OConnor; reared from deutonymphs on *L. ferruginea* on *A. pyriforme*.

Description. Female (n = 1) (Figures 12–17). Idiosoma oval (Figures 12 and 13), saccular, 820 × 660, 1.2 times longer than wide. Idiosomal cuticle smooth.

Gnathosoma (Figure 15A,B and Figure 16B–D): subcapitulum (Figures 14A and 15B,C) wide, 96 × 112, evenly punctated; subcapitular setae (*h*) long, widened basally; supracoxal seta *elcp* present, weakly barbed; palps wide; lateral dorsal palp tibial setae (*sup*) and palp tibial setae (*a*) filiform; dorsal palp tarsal seta (*cm*) weakly lanceolate, base located on large rounded lateral protrusion of palp tarsus; terminal palp tarsal solenidion ω short; terminal eupathidium *ul''* small, dome-shaped; terminal eupathidium *ul'* small, rounded. Chelicera (Figures 15B and 16D) with two setae: *cha* large, lanceolate, distal on fixed digit, *chb* short, spiniform. Fixed finger of chelicera with one tooth, movable with three teeth (anterior double).

Prodorsal shield (Figure 16A) vestigial, represented by a short weakly sclerotized area with punctation behind bases of setae *vi*. Grandjean's organ (GO) with one pointed trunk and numerous small spines (Figures 14A and 16E). Supracoxal setae (*scx*) pinnate—central trunk broadly flattened with numerous (15–18) long pointed lateral processes and three terminal long processes (Figures 14A and 16E). Supracoxal shield oval, punctate, with small pointed projection near base of *scx*. Idiosomal setae (*vi*, *ve*, *si*, *se*, *c*₁, *c*₂, *c*_p, *c*₃, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃, *ps*₁, *ps*₂, *ps*₃) smooth, filiform, setae *h*₃, *se*, *vi* longer than other setae. Opisthosomal gland openings between setal bases *e*₁ and *e*₂. Four pairs of fundamental cupules (*ia*, *im*, *ip* and *ih*) present. Ventral idiosoma with four pairs of coxal setae (*1a*, *3a*, *4a* and *4b*) and one pair of genital setae (*g*). Coxal sclerites: I—short, triangular (Figure 16H); anterior II—extended along anterior apodeme II, expanded at base (Figure 16I); sclerite posterior coxal apodeme II shapeless, located at end posterior apodeme (Figure 16J); III and IV—extended along apodemes, expanded at base (Figure 16K,L). Genital region situated between coxal fields III and IV; genital valves form an inverted Y; epigynal apodeme absent (Figure 16F). Genital papillae (Figure 16F) wide, with rounded ends. Anal opening ventral, long; distance between ovipore and anal opening less than length of anal opening. Copulatory tube absent. Inseminatory canal of spermatheca narrow, slightly widened at junction with base of spermatheca (Figures 14B and 16G). Base of spermatheca flat, ring-shaped. Paired efferent ducts cone-shaped, with long stem (same length as funnel). Three pairs adanal (*ad*_{1–3}) setae.

All legs shorter than body; all segments free (Figure 14C–F, Figure 15C–F and Figure 17). Trochanters I–III each with long filiform seta, *pR* I–II, *sR* III; trochanter IV without setae. Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV long filiform. Genua setation 2-2-1-0; setae *mG* and *cG* I–II spiniform; seta *nG* III filiform. Tibial setation 2-2-1-1; setae *hT* I–II, *gT* I–II and *kT* III–IV spiniform, *hT* slightly shorter than *gT*. Tarsal setation 13-12-10-10; pretarsi I–II consist of hooked, III–IV slightly curved and long empodial claws attached to short paired condylophores. Tarsus I with setae *ra*, *la*, *f* and *d* filiform, *aa*, *ba*, *e*, *wa* larger spiniform, *s*, *v*, *u*, *p* and *q* short spiniform (*u* and *v* longer than *s*, *p* and *q*). Tarsus II has the same setae except that *la* spiniform, *ra* spiniform with filiform ends and absent *aa*. Tarsus III and IV with setae *f* and *d* filiform, *r*, *w*, *e* and *s* larger spiniform, *u*, *v*, *p* and *q* small spiniform. Solenidia ω_1 on tarsus I and II cylindrical, with clavate apex, not bent. Solenidion ω_2 on

tarsus I shorter than ω_1 , cylindrical, with rounded apex, situated distinctly posterior to ω_1 , at equal distance between ω_1 and *aa*. Solenidion ω_3 on tarsus I cylindrical, with rounded tip, shorter than ω_1 . Famulus (ϵ) of tarsus I spiniform. Solenidia ϕ of tibiae I–IV elongate, tapering, not reaching apices of their respective tarsi without ambulacra. Solenidia σ' and σ'' on genu I elongate, tapering, not reaching bases of ϕ I, σ' longer than σ'' . Solenidion σ on genu II 5 times longer than its width, tapering. Solenidion σ of genu III present, 6 times longer than its width, tapering.

Male (Figures 18–23) with apparent size-based allometric development of legs III. Individuals of body size intermediate between large and small forms (below) with development of legs III intermediate between largest and smallest forms.

Heteromorphic male ($n = 1$) (Figures 18–23). Idiosoma (Figures 18 and 19) oval, saccular, 580×450 , 1.2 times longer than wide. Idiosomal cuticle smooth.

Gnathosoma (Figure 21B–E): subcapitulum (Figure 21B,C) wide, 74×80 , other characteristics are same as in females.

Prodorsal shield (Figure 21A) vestigial, represented by a short weakly sclerotized area with punctation behind bases of setae *vi*. Grandjean's organ (GO), supracoxal setae (*scx*) and supracoxal shield as female (Figure 21F). Idiosomal setae (*vi*, *ve*, *si*, *se*, *c*₁, *c*₂, *c*_p, *c*₃, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃, *ps*₁ and *ps*₂) smooth, filiform, setae *h*₃, *se*, *vi* longer than other setae (*h*₃ approximately half length of body). Opisthosomal gland openings between setal bases *e*₁ and *e*₂. Four pairs of fundamental cupules (*ia*, *im*, *ip* and *ih*) present. Ventral idiosoma with four pairs of coxal setae (*1a*, *3a*, *4a* and *4b*) and one pair of genital setae (*g*). Coxal sclerites: I—short, triangular (Figure 21I); anterior II—extended along anterior apodeme II, expanded at base (Figure 21J); posterior apodeme II narrow, extending along entire apodeme (Figure 21J); III and IV—extended along apodemes, expanded at base, between anterior apodemes III area of weak sclerotization present (Figure 21K,L). Genital region situated between coxal fields IV. Genital papillae (Figures 20B and 21G) wide, with cone-shaped rounded apices. Aedeagus short, not protruding beyond anterior edge of genital capsule (Figures 20A and 21G). Anal opening ventral, long, located posterior to genital region. Paranal suckers rounded (Figure 21H).

Legs I–II as in female except solenidion ω_3 wider and longer than female's and *ra* II without filiform ends. Leg III (Figure 20C,D and Figure 22E–I) wider and more robust than other legs, its chaetotaxy like that of female except for strong reduction of setae *u*, *v*, *p* and *q* (*u* and *v*—small vestigial remnants, *p* and *q* represented only by cuticular traces). Leg III with segments wider than long. Tarsus III shortened, conical, with strong empodial claw fused with tarsus apically, condylophores absent. Tarsal setae *r* and *w* adjacent to spine-like seta *s*. Leg IV as in female except setae *d* and *e* represented by suckers and solenidion ϕ longer (Figure 20E,F and Figure 22H,I).

Small male. Similar to large male but smaller. Leg III of different form: leg segments longer than wide. Pretarsal empodial claw smaller, not fused with tarsal apex, and small condylophores visible. Tarsus IV distinctly longer with setae *r* and *w* well posterior of seta *s*, and setae *p*, *q*, *u* & *v* present.

Heteromorphic deutonymph ($n = 1$) (Figures 24–27). Body rounded (Figures 24 and 25), 1.3 times longer than wide, widest in sejugal region; idiosomal length 420 width 330. Gnathosoma (Figures 26A and 27D,E) short, subcapitulum 170×150 , trapezoidal, with filiform setae *cm*, setae *h* absent (their positions marked by somewhat refractile spots); palps 120, two-segmented, with filiform setae *sup* and palpal solenidia (ω), whose length significantly exceeds gnathosomal length.

Dorsum (Figures 24 and 27A,B,H). Idiosoma smoothly punctate (two types of punctation—relatively few large pits and numerous but very small dots between them); distinct linear pattern present on anterior and lateral sides of prodorsal sclerite and hystero-

somal shield. Anterior border of prodorsal shield trapezoidal elongated, with setal pairs *ve* and *vi*, ocelli absent. Externalscapular setae *se* and internal scapular setae *si* situated on prodorsal shield, *si* slightly anterior *se*. Supracoxal setae of legs I (*scx*) filiform. Sejugal furrow well developed. Prodorsal shield 70, hysterosomal shield 330, ratio hysterosomal shield/prodorsal shield length = 4.7. Hysterosoma with 11 pairs of simple filiform setae on hysterosomal shield (*c*₁, *c*₂, *c*_p, *d*₁, *d*₂, *e*₁, *e*₂, *f*₂, *h*₁, *h*₂, *h*₃), setae *h*₃ distinctly longer than other setae. Opisthonotal gland openings (*gla*) situated ventrally on hysterosomal shield, slightly anterior setae *c*₃, much closer to seta *c*_p than to *c*₃. Four pairs of fundamental cupules (*ia*, *im*, *ip* and *ih*) present.

Venter (Figures 25 and 27C,F,G). Coxal fields sclerotized, smoothly punctate. Anterior apodemes of coxal fields I fused forming sternum; sternum not reaching posterior border of sternal shield by distance not exceeding its length; coxal fields I and II open; anterior and posterior apodemes of coxal fields II curved medially. Sternal and ventral shield contiguous. Anterior apodemes of coxal fields III connected to anterior apodemes of coxal fields IV but not forming a common medial apodeme III (medial apodeme III divided into two parallel communicating apodemes with setal pairs 4*b*), coxal fields III closed. Ventrums present, divided into two parallel apodemes connected to two parallel medial apodemes III but separated from genital opening. Subhumeral setae (*c*₃) filiform, situated on ventral surface between legs II and III, near region separating sternal and ventral shields. Coxal setae 1*a*, 3*a* and 4*a* conoids, 4*b* and genital setae *g* filiform. Genital region in posterior portion of coxisternal fields IV; genital opening elongated, with two pairs of genital papillae within genital atrium; genital papillae two-segmented, with cone-shaped rounded apices. Genital setae laterad of genital opening. Attachment organ (Figure 27F) posterior to coxal fields IV. Anterior suckers (*ad*₃) round, median suckers (*ad*₁₊₂) distinctly larger, with paired vestigial alveoli (situated on common sclerite); pair of small refractile spots anterolaterad median suckers (*ps*₃); lateral conoidal setae of attachment organ (*ps*₂) situated lateral to line joining centers of median suckers; posterior conoidal setae (*ps*₁) directly posterior to median suckers; anterior and posterior lateral and posterior median cuticular suckers well developed; large trapezoidal cuticular sclerite (larger than diameter of cuticular conoids) situated behind posterior median cuticular suckers; anus situated between anterior suckers (*ad*₃).

Legs (Figure 26B–I and Figure 27I–P). Legs short; all segments free. Trochanters I–III each with long filiform seta, *pR* I–II, *sR* III. Femoral setation 1-1-0-1; setae *vF* I–II and *wF* IV long (*vF* I longer than *vF* II), filiform. Genua setation 2-2-1-0; setae *mG* I–II spiniform, finely serrated, *cG* I–II spiniform, *nG* III weakly spiniform. Tibial setation 2-2-1-1; setae *gT*, *hT* I–II and *kT* III–IV spiniform, finely serrated; setae *gT* and *hT* approximately the same length. Tarsal setation 10-9-8-8. All pretarsi consisting of long hooked and thin empodial claws attached to short paired condylophores. Tarsus I with setae *ra*, *la*, *f*, *p* and *q* foliate; seta *d* filiform, long; seta *e* long, cylindrical with sucker-like apex, different in form from simply foliate seta *f*; setae *wa* spiniform, finely serrated; seta *aa* long, filiform; *ba* I absent. Tarsus II similar to tarsus I except long and finely serrated seta *ba* present and *aa* absent. Tarsus III with setae *w*, *r*, *s*, *e*, *f*, *p* and *q* smooth and foliate; seta *d* filiform, longer than leg. Tarsus IV similar to tarsus III except seta *r* and *w* finely serrated. Solenidia ω_1 on tarsi I–II cylindrical, with slightly clavate apices; ω_3 on tarsus I equal in length ω_1 , with rounded apex, situated slightly distal to ω_1 ; ω_1 and ω_3 separated by spiniform famulus (ϵ); solenidium ω_2 of tarsus I slightly expanding apically, situated somewhat more basal and posterior to $\omega_1 + \epsilon + \omega_3$ group. Solenidia ϕ of tibiae I–IV elongate, tapering; ϕ I longer than tarsus I with ambulacra; solenidium ϕ II shorter than tarsus II without ambulacra; solenidium ϕ III longer than tarsus III without ambulacra; solenidium ϕ IV short. Solenidium σ of genu I elongate, cylindrical, reaching apex of tibia I; solenidium σ of genu II much

shorter, slightly expanding apically, not reaching midlength of tibia II; solenidion σ of genu III represented by refractile spots.

Etymology. The species name is derived from the Latin *gulosus*—gluttonous, greedy for food. Gender masculine.

Type deposition. Holotype and paratypes are deposited in UMMZ. Additional paratypes and non-paratype specimens deposited in CNC, OSAL, USNMHN, and ZISP.

Biology. Feeding stages of this species live in the sporocarps of puffballs, *Apioperdon* (= *Lycoperdon*) *pyriforme* (Basidiomycetes, Agaricales, and *Lycoperdaceae*), feeding on spores. Adult body form globular, appearing to “swim” through spores. When removed from sporocarps, adult mites were unable to walk on a flat surface. Phoretic deutonymphs occur on *Lycoperdina ferruginea* LeConte, 1824 (Coleoptera: Endomychidae), the larvae of which also feed in fungal sporocarps. Adult beetles carrying mites were found on *A. pyriforme* and *Lycoperdon perlatum* Pers. (1796); however, no post-deutonymphal stages of *O. gulosus* were found in sporocarps of *L. perlatum*. Similarly, one collection of *O. gulosus* was obtained from *L. ferruginea* on *Fomitopsis betulina* (Bull.) B.K.Cui, M.L.Han & Y.C.Dai (2016), but, again, no post-deutonymphal stages were found in the sporocarp. Based on our collections this species may overwinter as deutonymphs on host beetles or in fungal mycelia in the woody substrate.

Distribution. CANADA: Ontario; USA: Illinois, Michigan, New York, Pennsylvania.

Remarks. Males of *Obelacarus* exhibit polymorphism in body size and development of legs III. Although not directly tested, this polymorphism may reflect allometric enlargement of leg III related to body size. Males of *Obelacarus*, like some Acaridae, have modified legs III, the armament of which has a number of significant differences from Acaridae (for other families of Acaroidea male polymorphism is unknown). In Acaridae, two types of polymorphism in males are known, continuous and discrete. In *Schwiebea*, *Thyreophagus* and *Rhizoglyphus*, polymorphism is more or less continuous, while in *Sancassania* it is discrete, with distinct homeomorphic and heteromorphic forms. In this genus, two morphological features may vary (enlargement of legs III and dorsal setal length). These can vary independently, yielding four distinct morphs [17,69,83–85]. In large males of *Obelacarus* legs III have thickened empodial claws (vs. greatly thickened in *Schwiebea*, *Thyreophagus* and *Rhizoglyphus* or absent or fused with tarsus in *Sancassania*). Condylaphores are present in small males but absent or not visible in large males (vs. condylaphores absent in other genera). Unlike *Sancassania* and *Rhizoglyphus*, large males of the new genus have setae *e*, *r* and *w* spiniform (vs. filiform) and rudimentary *p* and *q* (vs. absent except some *Sancassania* with spiniform *v* and *q*). In the form of the tarsal setae, the new genus resembles *Schwiebea*, which also has spiniform *e* and *w* (*w* in same species) and spiniform or rudimentary *p* and *q*. But in *Obelacarus*, setae *r* are spiniform (vs. filiform in *Schwiebea* and *Thyreophagus*) and rudimentary *p*, *q* (vs. spiniform in *Schwiebea* and *Thyreophagus*).

Heteromorphic deutonymphs of *Obelacarus* are very similar to *Sancassania* but differ in the following character states: seta *aa* on tarsus I situated at the level of solenidion ω_2 (more apical in *Sancassania* except *S. geotruporum* (Zachvatkin, 1941)); insertion alveoli of solenidia ω_1 and ω_3 are merged (separated in *Sancassania*), seta *ba* II is close to ω_1 , spiniform (*ba* II and ω_1 well –separated; *ba* II filiform in *Sancassania*).

Viedebanttia Oudemans, 1929

Viedebanttia Oudemans, 1929: 485 [86]; Zachvatkin, 1941: 218 [87]; Eyndhoven, 1944: 41 [88]; Baker and Wharton, 1952: 332 [89]; Zachvatkin, 1953: 74 [44]; Fain and Schwan, 1984: 93 [90]; Fain, 1985: 276 [91]; OConnor and Pfaffenberger, 1987: 1189 [92]; Fan and Beaucournu, 1993: 79 [93]; OConnor, 1994: 144 [41]; Klimov, 1998a: 24 [94]; Klimov, 1998b: 251 [95]; Klimov, 2000: 106 [96]; OConnor, 2001: 78 [97]; Okabe and OConnor, 2001: 495 [98]; Klimov et al., 2003: 470 [69]; Szilman et al., 2006: 377 [99]; Klimov and Tolstikov, 2011:

255 [100]; Haitlinger, 2008: 117 [101]; Swafford and Bond, 2009: 448 [102]; Siepel et al., 2016: 87 [103]; Fujii et al., 2021: 2 [104]; Haitlinger, 2025: 72 [105].

Robinisca (non Zachvatkin, 1941): Zachvatkin, 1941: 215 (part.) [87]; Volgin, 1951: 36 [106]; Sevastianov and Marroch, 1993: 149 [107]; Bugrov, 1997: 152 (part.) [108].

Acotyledon (non Oudemans, 1903): Türk and Türk, 1957: 93 (HDN but not adults; part.) [70]; Černý and Samšínák, 1971: 508 (part.) [109]; Haitlinger, 1991: 81 [110] (part.).

Caloglyphus (non Berlese, 1923): Mahunka, 1979: 326 (part.) [111].

Viedebantia Eyndhoven, 1944: 54 [88] (lapsus, corrected in Errata); Buitendijk, 1945: 353 [112] (lapsus); Radford, 1950: 151 (lapsus); Haitlinger, 2008: 116 [101] (lapsus); Haitlinger and Łupicki, 2012: 39 [113] (lapsus); Haitlinger, 2025: 93 [105] (lapsus).

Type species: *Viedebantia schmitzi* Oudemans, 1929, by monotypy.

Gender: feminine.

Figure 28

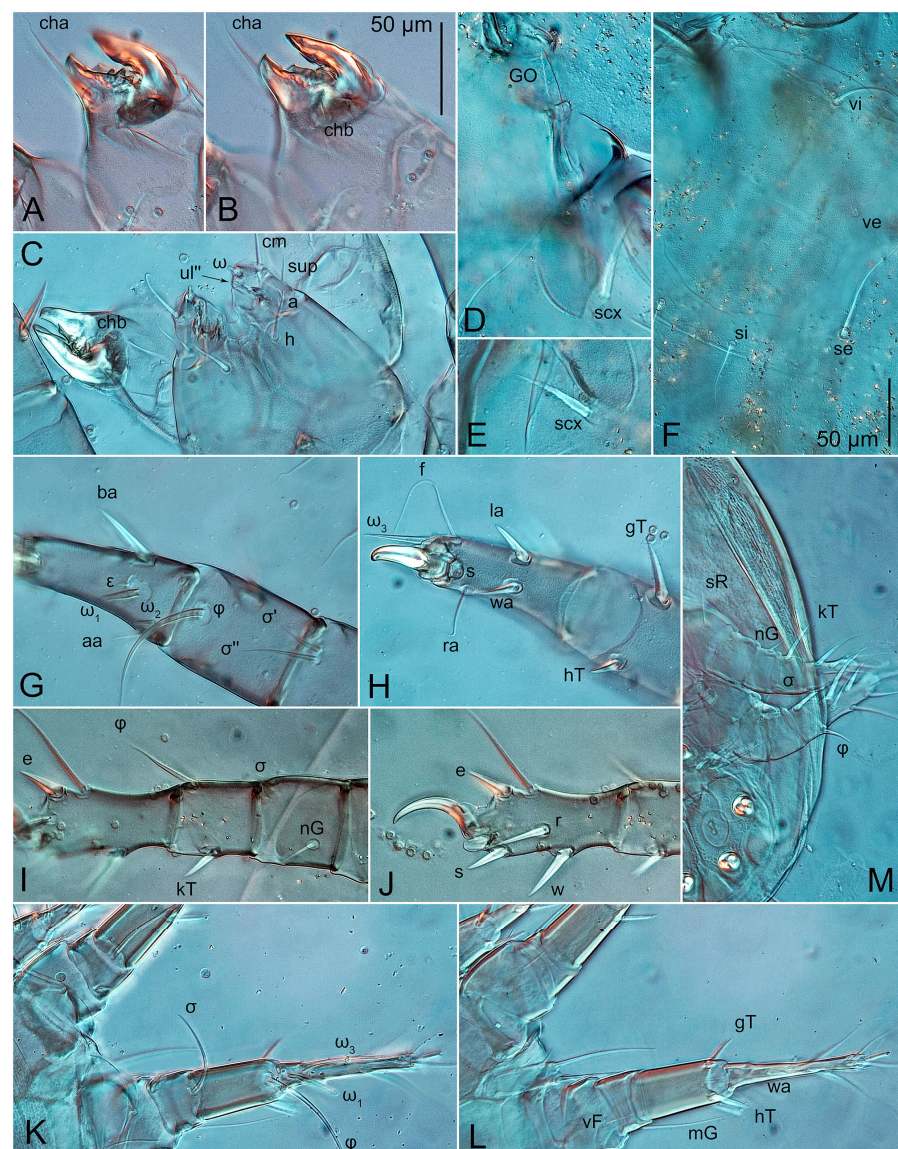


Figure 28. *Viedebantia schmitzi* Oudemans, 1929, DIC images: (A,B)—female chelicera; (C)—male gnathosoma, ventral view; (D)—female Grandjean's organ; (E)—female supracoxal seta; (F)—female prodorsal shield; (G)—female tarsus and tibia I, dorsal view; (H)—female tarsus and tibia I, ventral view; (I)—male leg III, anterior view; (J)—male leg III, posterior view; (K,L)—leg I of deutonymph; (M) – legs III-IV of deutonymph.

Diagnosis. Adult. Central trunk of supracoxal setae lanceolate with numerous lateral processes. Grandjean's organ with additional tongue-shaped process and numerous small spines. Prodorsal shield well developed, not divided. Seta *ve* vestigial. Sclerite of posterior medial apodemes II irregular, situated at end apodemes. Tarsal setae *u* and *v* present, spiniform. Solenidia ϕ I–II reach apices of their respective tarsi without ambulacra. Solenidion σ'' I longer than σ' . Solenidion σ III present. Female inseminatory canal of spermatheca narrow, conically expanded at entrance of spermatheca. Paired efferent ducts (sclerites) elongated, with very short stems.

Heteromorphic deutonymph. Seta *ve* absent. Ratio hysterosomal shield/prodorsal shield length = 6.0–7.0. Coxal field I free. Coxal setae *1a* and *3a* conoids. External conoidal setae *ps*₂ of attachment organ lateral to median sucker *ad*₁₊₂. Tibiae I–II much longer than corresponding genua. Seta *aa* I present. Setae *e* I–II with relatively small foliate end. Setae *d* I–II shorter than *e* I–II. Seta *ba* II longer than ω_1 II. Setae *p* and *q* I–IV filiform. Seta *f* IV shorter than leg IV. Solenidion σ III present.

Species included: *Viedebanttia confiferae* (Sevastianov & Marroch, 1993), *V. diamanus* Fain & Schwan, 1984, *V. egorovi* Klimov, 1998, *V. fuscipes* (Vitzthum, 1924), *V. longipes* (Volgin, 1951), *V. macrocnemis* (Zachvatkin, 1941), *V. schmitzi* Oudemans, 1929, *V. vitzthumi* (Mahunka, 1979).

3.4. Key to Families of Non-Psoroptidan Astigmatid Mites (Adults)

(Modified from OConnor [5] based on an older classification; a revised classification will be published separately. See Figure 1 for guidance.)

1 Chelicerae laterally compressed, often attenuate, usually with numerous finely divided teeth, non-chelate; palp with a terminal solenidion and usually at least one elongate, eupathidial seta, normal setae strongly reduced, palp usually reflexed outward; female genital valves fused to body posteriorly, open anteriorly forming a transverse oviporus; genital papillae of both sexes often in the form of large rings on ventral body surface.2

– Chelicerae usually chelate, with few teeth, rarely chelicerae vestigial or fixed digit absent; palp reflexed inward, usually bearing 3 filiform setae and terminal solenidion; female oviporus longitudinal with genital valves fused to body anteriorly, free posteriorly; genital papillae always associated with genital opening and never in the form of large rings.3

2 Genital papillae small, arising from a common furrow on either side of genital opening or apparently absent in males; body strongly sclerotized, dorsoventrally flattened and with legs laterally positioned; very small species. Two genera in bat guano; Afrotropical, Neotropical. **Guanolichidae** Fain, 1968

– Genital papillae ring-like, usually large, not arising from a common furrow and not directly associated with the genital opening; body relatively larger and not dorsoventrally flattened. Many genera in a wide variety of wet habitats; cosmopolitan. **Histiostomatidae** Berlese, 1897 (=Anoetidae Oudemans, 1904)

3 Female with a sub-globular terminal hysterosomal pad-like organ bearing five pairs of setae and copulatory opening; solenidion ω_1 on tip of tarsus I. One genus, *Glaesacarus*; fossil (Baltic amber). **Glaesacaridae** Sidorchuk and Klimov, 2011

– Female without a sub-globular terminal hysterosomal pad-like organ bearing five pairs of setae and copulatory opening; solenidion ω_1 on base of tarsus I.4

4 Pretarsal ambulacrum usually greatly expanded; legs laterally positioned; commensals or parasites of adult insects or myriapods, or nidicoles in social insect nests.5

- Pretarsal ambulacrum not greatly expanded; legs ventrally positioned or rarely dorsal or lateral; not associated with adult insects in all instars (*Linobia coccinellae* (Scopoli, 1763), a hemisarcotid parasite of chrysomelid beetles is exceptional; this genus has reduced ambulacra and lacks the fixed cheliceral digit).10
- 5 Dorsum almost entirely covered by 1–2 large sclerites.6
 - Dorsum with only a rectangular propodosomal sclerite; supracoxal sclerites and rarely a small, median, opisthosomal sclerite.7
- 6 Body rounded, dorsum bearing a large domed sclerite with deep punctations; legs tapering; tarsi with proral setae foliate, partially fused to pretarsal ambulacrum. One genus in ant nests, Holarctic.**Lemanniellidae** Wurst 2001
 - Body flattened, dorsum with 1–2 large sclerites, smooth or with linear or transverse grooves, never with deep punctations; legs cylindrical; tarsi with proral setae simple or absent. External commensals or parasites of Coleoptera; Afrotropical, Oriental, Australian, Nearctic, Neotropical.**Heterocoptidae** Fain, 1967
- 7 Supracoxal seta of leg I displaced laterally away from supracoxal gland opening; tibiae I–II with 0–1 ventral seta (rarely 2), femur IV usually without seta. Associates of many beetle families; cosmopolitan except Nearctic.**Canestriniidae** Berlese, 1884
 - Supracoxal seta of leg I closely associated with supracoxal gland opening; tibiae I–II usually with 2 ventral setae; femur IV usually with 1 ventral seta.8
- 8 Body cuticle smooth, striate or scaly; solenidion ω_2 of tarsus I apical or absent; male without para-anal suckers.9
 - Body cuticle mammillate, at least in female; solenidion ω_2 of tarsus I basal in position; male with para-anal suckers and sucker-like setae on tarsus IV. Associates of Diplopoda; Afrotropical.**Chetochelacaridae** Fain, 1987
- 9 Body small, most dorsal hysterosomal setae with a shaft and numerous lateral rounded lobes; male with 1 sucker-like seta on tarsus IV. One species in ant nests, Palaearctic.**Myrmolichidae** Türk and Türk, 1957 stat. nov.
 - Body larger, dorsal hysterosomal setae simple or otherwise modified; male without sucker-like setae on tarsus IV. Associates of Blattaria, Dermaptera and possibly Diplopoda; Afrotropical, Neotropical, Nearctic.**Rosensteiniidae** Cooreman, 1954 (part) (=Lophonotacaridae Fain, 1987 syn. nov., =Troglotacaridae Fain, 1977 syn. nov.)
- 10 Prodorsum with setae *ve* absent; pretarsi with long thin condylophores or condylophores fused or absent; empodial claws present or absent; dorsal setae may be elongate but never heavily barbed; males without para-anal suckers or sucker-like setae on tarsus IV.25
 - Prodorsum with setae *ve* present, or, if absent, then pretarsi with short strong condylophores, or some dorsal setae long and heavily barbed, or empodial claws absent and opisthosoma bilobed posteriorly; males with or without para-anal suckers and sucker-like setae on tarsus IV.11
- 11 Anus positioned directly behind genital opening, displaced from posterior edge of body by a distance greater than length of anus; without ventral ridges on subcapitulum; male with para-anal suckers vestigial or absent.12
 - Anus positioned near posterior margin of body, or, if more anterior, then subcapitulum with a distinct pattern of ventral ridges (some Glycyphagidae); male with or without para-anal suckers.13
- 12 Dorsal setae relatively short heavily barbed; leg segments with strong ridges; female with copulatory opening surrounded by a large round sclerite; male with a pair of modified sucker-like setae on tarsus IV; male with 4 pairs of setae in anal

region (3 *p*, 1 *ad*). One genus, *Scatoglyphus* Berlese, 1913, in bird nests; Holarctic **Scatoglyphidae** Zachvatkin & Volgin, 1956

– Dorsal setae very long and barbed (*Euglycyphagus* Fain & Philips, 1977) or short and nude (*Lomelacarus* Fain, 1978); female copulatory opening not surrounded by a large sclerite; male without sucker-like setae on tarsus IV and with only 3 pairs of setae in anal region (3 *ps*). Two genera in bird nests and house dust; Holarctic, Afrotropical. **Euglycyphagidae** Fain & Philips, 1977

13 Female and sometimes male with empodial claws bifurcate; male with legs III enlarged, terminating in a large straight empodial claw and an enlarged straight spiniform seta similar in length and form to empodial claw; male with para-anal suckers and sucker-like setae on tarsus IV. One genus *Lardoglyphus* in vertebrate nests, carrion, and stored products; cosmopolitan. **Lardoglyphidae** Oudemans, 1927

– Both sexes with empodial claws simple or absent; male with legs III similar to legs IV, or, if legs III enlarged, then empodial claw shorter and curved and without an enlarged seta similar in form to empodial claw. 14

14 Ventral subcapitulum with a prominent pattern of external transverse and oblique ridges (not to be confused with internal pharyngeal sclerotization—ridges reduced in heavily sclerotized *Fusacarus* Michael, 1903); empodial claws small or absent; condylophores very thin or absent; female usually with an epigynal apodeme and often with an external copulatory tube; male without para-anal suckers or modified setae on tarsus IV. In nests of vertebrates, stored products, house dust, or occasionally in soil, litter, or plant foliage; cosmopolitan. **Glycyphagidae** Berlese, 1897

– Ventral subcapitulum without external ridges; other characters variable. 15

15 Body cuticle at least partially striated, often in dorsal propodosomal region or postero-ventrally, or with a pattern of striations broken into scale-like structures; if striations or scales absent, then with all dorsal setae elongate and heavily barbed except c_1 , which is long and nude; solenidion ω_2 of tarsus I more distal than ω_1 ; tarsus IV of both sexes with tectal setae absent. 16

– Body cuticle without striations; small rounded protuberances or small triangular microtrichae may be present; solenidion ω_2 variable in position, usually more basal than ω_1 ; tectal setae present on all tarsi or one member of pair may be absent on all tarsi. 17

16 Opisthosoma with a row of small closely spaced microtrichae extending between the bases of most lateral body setae; most dorsal setae elongate and heavily barbed; pretarsal ambulacra short, relatively simple; empodial claws reduced or absent. In bat roosts, vertebrate nests, stored products, house dust; cosmopolitan. **Aeroglyphidae** Zakhvatkin, 1941

– Opisthosoma without microtrichae running between the bases of lateral body setae; body often ornamented with scale-like protuberances; dorsal setae often highly modified, rarely elongate and heavily barbed; gnathosoma usually with a pair of enlarged rutellar processes; pretarsal ambulacrum usually large, divided into three distinct regions (reduced in *Troglotacarus* Fain, 1977); empodial claws well developed. In bat roosts or in fur of bats; cosmopolitan. **Rosensteiniidae** Cooreman, 1954 (part)

17 Discrete coxal apodemes III and sometimes IV absent; discrete propodosomal sclerite absent. 18

– Discrete coxal apodemes III and IV present, projecting obliquely from bases of trochanters; propodosomal sclerite usually present. 19

- 18 Body cuticle covered by small microtrichae; male without para-anal suckers or modified sucker-like setae on tarsus IV (a basal sucker may be present in tibio-tarsal articulation. In nests of mammals, stored products, and house dust; Australian, Nearctic, Neotropical; 1 genus (*Blomia* Oudemans, 1928) introduced cosmopolitan **Echimyopodidae** Fain, 1967
- Body without microtrichae; male with para-anal suckers and often with sucker-like setae on tarsus IV. In nests of mammals, stored products, and house dust; Afrotropical, Oriental, Australian, Nearctic, 1 species, *Chortoglyphus arcuatus* (Troupeau, 1879), introduced cosmopolitan. **Chortoglyphidae** Berlese, 1897
- 19 Tarsi with setae *f* and *e* asymmetrical, *e* usually spiniform, rarely filiform; ungual setae usually larger and stouter than proral setae. 23
- Tarsi with both setae *f* and *e* filiform, similar in length; proral setae spiniform or enlarged and claw-like; ungual setae spiniform, reduced or absent, never distinctly larger than proral setae. 20
- 20 Chelicera with two setae (*cha* and *chb*). One genus *Bulacarus* Fan and Zhao, 2024 **Bulacaridae** Fan and Zhao, 2024
- Chelicera with only seta *cha*. 21
- 21 Propodosoma with setae *ve* absent; empodial claws absent, tibiae I–II with two ventral setae; body cuticle usually smooth or with scale-like ornamentation; opisthosoma usually bilobed posteriorly; if rounded, then chelicerae vestigial or greatly enlarged (*Hy-podectes* de Filippi, 1862). In nests of birds or rarely mammals; cosmopolitan but few genera described as adults. **Hypoderatidae** Murray, 1877
- Propodosoma with setae *ve* present; empodial claws present, or, if absent, then tibiae I–II with only 1 ventral seta; body cuticle often with rounded protuberances; opisthosoma not bilobed posteriorly. 22
- 22 Body outline round, length similar to width; some dorsal setae often heavily pectinate or plumose, occasionally all short and simple (*Platyglyphus* Kurosa, 1976); tarsi with proral and ungual setae similar in form. In nests of social bees; Holarctic, Neotropical, Oriental. **Gaudiellidae** Atyeo, Baker & Delfinado, 1974
- Body distinctly longer than wide; dorsal setae filiform, unbarbed; tarsi with proral setae enlarged and claw-like; ungual setae reduced or absent. In vertebrate or insect nests, stored products, house dust, rarely in soil; cosmopolitan. **Suidasiidae** Hughes, 1948 (=Sapracaridae Fain, 1988 syn. nov.)
- 23 Chelicera with two setae (*cha* and *chb*), seta *cha* large, lanceolate, situated distally on fixed digit. **Lycoglyphidae** fam. nov.
- Chelicera with only one small and simple seta *cha*, basally on fixed digit. 24
- 24 Prodorsal sclerotization in the form of two thin elongate parallel sclerites; dorsal setae elongate and heavily barbed; cuticle ornamented with small triangular microtrichae; male with leg III much larger than leg IV but otherwise unmodified. One genus, *Glycacarus* Griffiths, 1977, in bird nests; subantarctic islands. **Glycacaridae** Griffiths, 1977
- Prodorsal sclerotization in the form of a rectangular shield that may be incised posteriorly, or prodorsal sclerotization absent; dorsal setae variable but not usually both elongate and heavily barbed; cuticle smooth or rarely with small rounded protuberances; male with leg III similar to leg IV, or leg III enlarged and bearing a large empodial claw and reduced tarsal setation. In a wide variety of habitats; cosmopolitan. **Acaridae** Latreille, 1802

25 Tarsi I–II very short, bearing a greatly enlarged, apical, claw-like seta; pretarsi I–II elongate, bearing a very small empodial claw; pretarsi III–IV shorter, empodial claws very large; supracoxal setae greatly elongate and heavily barbed; with a pair of lyriform organs posterior to the prodorsal sclerite. Marine, intertidal to subtidal, cosmopolitan in coastal areas. **Hyadesiidae** Halbert, 1915

– Tarsi I–II more elongate, without a greatly enlarged apical seta; pretarsi variable in form but similar on all legs; supracoxal setae short; without lyriform organs on prodorsum although ocelli may be present. 26

26 Supracoxal gland opening on, or adjacent to, a large sclerotized region directly above legs I. 27

– Supracoxal gland opening not associated with a large sclerotized region. 28

27 Supracoxal gland opening on an elongate, oval, sclerotized region, restricted to dorsal area above legs I; female pretarsus with paired elongate condylophores; male with condylophores fused along their length and emerging ventrobasally as a hook-like structure in the base of the pretarsus. In bee nests; cosmopolitan **Chaetodactylidae** Zachvatkin, 1941

– Supracoxal gland opening hidden by a large strap-like sclerotized region (axillary organ) that usually extends ventrally between legs I and II and may extend posteriorly over ventral surface; condylophores normally developed or absent in both sexes. In sap fluxes, phytotelmata, or fully aquatic habitats; Holarctic, Neotropical, Oriental, subantarctic islands. **Algophagidae** Fain, 1974

28 Prodorsal sclerite absent; setae *vi* situated about half-way between anterior edge of propodosoma and setae *si*; with a pair of large ocelli in propodosomal region; coxal apodemes I fused medially with coxal apodemes II closing coxal fields I in both sexes; condylophores elongate and separate in female, asymmetrical in male; male with genital setae (*g*) and coxal setae *4b* present. One genus, *Carpoglyphus* Robin, 1869, in stored products, vertebrate nests, bee nests, flowers; cosmopolitan. **Carpoglyphidae** Oudemans, 1923

– Prodorsal sclerite well developed; setae *vi* at anterior edge of propodosoma or absent; ocelli present or absent; apodemes I not fused medially with apodemes II, coxal fields I open; condylophores fused to each other or absent; male with genital setae vestigial or absent, setae *4b* filiform, or absent but with alveoli modified into a sucker. 29

29 Empodial claws present; condylophores usually fused into a V-shaped sclerite or a more elongate sclerite in base of ambulacral stalk; tibiae I–II with 1–2 ventral setae; male with all traces of genital setae and coxal setae *4b* absent; male usually with pretarsal ambulacra I–II arising from ventral apex of tarsus, often modified as a sucker. In a wide variety of habitats; cosmopolitan. **Winterschmidtidae** Oudemans, 1923 (=Saproglyphidae Oudemans, 1927)

– Empodial claws absent, condylophores apparently absent; tibiae I–II with 0–1 ventral setae. 30

30 Both sexes with genital opening between or posterior to coxal fields IV, female oviporus often confluent with anal opening; male with alveoli of setae *4b* fused medially forming a sucker anterior to aedeagus. In a variety of habitats; cosmopolitan. **Hemisarcoptidae** Oudemans, 1904

– Both sexes with genital opening between coxal fields III–IV; male with setae *4b* filiform, alveoli not fused to form a sucker. In nests of stingless bees (Apidae:

Meliponini), Neotropical, Oriental. **Meliponocoptidae**
Fain, 1983

3.5. Key to Families of Non-Psoroptidian Astigmata (Phoretic Deutonymphs)

(modified from OConnor [5])

1 Palp with 3 segments; chelicera present or rudimentary remnant of chelicera present; seta *aa* II present.2

– Palp with 1–2 segments or absent; chelicera absent; seta *aa* II absent.3

2 Genital valves with four or five pairs of minute setae; rudimentary remnant of chelicera present; tarsus II with 2 solenidia (ω_1 and ω_3). Associated with termites and tenebrionid beetle; New Guinea and New Zealand. **Schizoglyphidae**
Mahunka, 1978

– Genital valves with one pair of setae; chelicera present; tarsus II with 1 solenidia (ω_1). Fossil (Cretaceous Amber), 1 genus with 1 species. **Levantoglyphidae** Klimov, Vorontsov, Azar, Sidorchuk, Braig, Khaustov and Tolstikov, 2021*

3 Legs III–IV with femur–genu–tibia–tarsus partially or completely fused; legs III–IV flexed at trochanter–femur articulation and directed anteriorly in repose; rostral and lamellar pairs of setae absent; setae *4b* absent. Cosmopolitan on a variety of hosts. **Histiostomatidae** Berlese, 1897 (= Anoeidae Oudemans, 1904)

– Legs III–IV usually without this degree of fusion of segments; legs III–IV posteriorly or laterally directed in repose, or, if anteriorly directed, then attachment organ vestigial or absent and living in hair follicles of mammals; at least rostral setae usually present; setae *4b* usually present.4

4 Attachment organ with anterior and median suckers vestigial or absent; setae *ps*₁ and *ps*₂ in the form of ribbed claspers, small vestigial conoids, or absent.5

– Attachment organ with anterior and median suckers (*ad*₃ and *ad*₁₊₂) well developed and setae *ps*₁ and *ps*₂ in the form of conoids; if attachment organ is reduced, at least one pair of suckers remains.9

5 Coxal setae *3a* and *4a* present, *1a* present or absent; attachment organ vestigial or absent.6

– Coxal setae *1a*, *3a*, and *4a* absent (occasionally a vestigial *1a* present); attachment organ with *ps*₁ and *ps*₂ as claspers or vestigial.8

6 Genital region terminal or sub-terminal, with genital papillae projecting posteriorly; ventral setae of tibiae III–IV in the form of strongly toothed combs; dorsal opisthosomal setae spiniform, often bifurcate apically. Endofollicular parasites of Rodentia, Eulipotyphla and Primates; Nearctic, Afrotropical, Australasian. **Chortoglyphidae**
Berlese, 1897

– Genital region ventral with papillae in normal position; genital region often surrounded by a sclerotized ring; tibial setae of legs III–IV unmodified; dorsal setae variously formed.7

7 Coxal fields II closed; setae *vi* situated on a strong hooked anterior protuberance; setae *ps*₁ and *ps*₂ present as very small conoids; body elongate. One genus, *Pedetopus*, with 1 species in hair follicles of Pedetes; Afrotropical. **Pedetopodidae** Fain, 1969

– Coxal fields II open (closed in one undescribed species); setae *vi* near anterior apex of propodosoma; setae *ps*₁ and *ps*₂ absent; body elongate or rounded. In hair follicles and subcutaneous tissues of various marsupial orders, Rodentia, and Xenarthra; Neotropical, Nearctic, Australian. **Echimyopodidae**
Fain, 1967

8 Attachment organ with setae ps_1 and ps_2 in the form of ribbed claspers, or, if absent, then vestiges of their alveoli present as small sclerotized rings (*Baloghella*), or attachment organ reduced and tibiae III–IV with large ventral, comb-like setae; posterior coxal apodemes with distinct edges. On hairs or in hair follicles of Didelphimorphia, Paucituberculata, Xenarthra, Eulipotyphla, Afrosoricida and Rodentia, 1 species in ears of Carnivora; or sedentary or wind dispersed; cosmopolitan. **Glycyphagidae** Berlese, 1897

– All traces of attachment organ completely absent; legs well developed; tibiae III–IV without comb-like setae; posterior coxal apodemes often with indistinct edges. In subcutaneous tissues of birds and rodents; cosmopolitan. **Hypoderatidae** Murray, 1877

9 Legs I–II without pretarsi; coxal apodemes II–IV end freely. 10

– Pretarsal ambulacrum and/or empodial claw present on legs I–II; coxal apodemes II–IV end freely or fuse with other apodematal elements. 11

10 Dorsal sclerites smooth; propodosomal sclerite very short, setae se and si apparently absent; genua I–II without dorsal solenidion. One genus, *Lemanniella*, associated with ants; Holarctic. **Lemanniellidae** Wurst, 2001

– Dorsal sclerites smooth or with rounded protuberances; propodosomal sclerite normally developed, bearing interlamellar and exobothridial setae; genu I–II each with dorsal solenidion. **Suidasiidae** Hughes, 1948 (in part, genus *Sapracarus*)

11 Leg IV with empodial claw absent; leg IV often shorter than leg III, with some fusion of segments and usually with one or more long apical setae. 12

– Leg IV with empodial claw present, or, if absent, then empodial claw III also absent, but claws I–II present; leg IV generally similar in form to leg III. 16

12 Empodial claws I–III borne on membranous ambulacra (small in the Chaetodactylidae where claws are very large and hooked). 13

– Empodial claws I–III arising directly from tarsal apices, or some or all claws absent. Phoretic on Coleoptera and Hymenoptera; cosmopolitan. **Suidasiidae** Hughes, 1948 (part)

13 Pretarsal ambulacra with a pair of very thin symmetrical condylophores extending from tarsal apices to empodial claws; dorsal hysterosomal sclerite usually reticulate anteriorly, smooth or striate posteriorly. One genus, *Lardoglyphus* phoretic on *Dermestes* beetles; cosmopolitan. **Lardoglyphidae** Oudemans, 1927

– Condylophores either restricted to tarsal apices, or, if extending through ambulacral stalk, then very strong and asymmetrical. 14

14 Empodial claws greatly enlarged and hook-like, ocelli absent; body relatively circular in outline and with 2 dorsal sclerites, or ellipsoid and with 1 dorsal sclerite. Phoretic on bees: Apidae (s. lat.) and Megachilidae; cosmopolitan. **Chaetodactylidae** Zachvatkin, 1941

– Empodial claws usually small and simple; if enlarged and hook-like, then body fusiform and with 2 dorsal sclerites; ocelli often present. 15

15 Tarsus I with solenidia widely separated, solenidion ω_3 apical; coxal apodemes III usually free apically, rarely weakly fused to median ventral apodeme; ocelli present on apex of propodosoma, pigment spots underlying ocelli fused medially; coxal setae $4a$ well developed; tibiae I–II with 0–1 ventral seta. On a wide variety of insects; cosmopolitan. **Hemisarcopidae** Oudemans, 1904

– Tarsus I with solenidia closely associated, usually in the basal half of the tarsus; coxal apodemes III either fused together, to apodemes of coxal fields IV or to median apodeme, rarely free; ocelli present on apex of propodosoma with separate pigment spots, rarely widely separated, or occasionally absent; tibiae I–II with 1–2 ventral setae. On a variety of insect groups; cosmopolitan **Winterschmidtidae** Oudemans, 1923

16 Pretarsi with membranous ambulacra 17

– Pretarsi without membranous ambulacra, empodia arising from tarsal apices. 18

17 Coxal fields III closed but not fused to each other medially; posterior median ventral apodeme absent; ocelli present, widely separated on propodosoma. One genus, *Carpoglyphus*, phoretic on Lepidoptera and Coleoptera; cosmopolitan. **Carpoglyphidae** Oudemans, 1923

– Coxal fields III open or closed, but coxal apodemes III always fused medially; posterior median ventral apodeme present; ocelli, when present, at anterior apex of propodosoma. Phoretic on Diptera, Coleoptera, Lepidoptera; Holarctic, Neotropical, Oriental. **Algophagidae** Fain, 1974

18 Coxal apodemes III–IV ending freely; all coxal fields completely open; propodosomal ocelli absent. Associates of social bees; Holarctic, Neotropical, Oriental. **Gaudiellidae** Atyeo, Baker & Del-finado, 1974

– Coxal apodemes III–IV usually fused medially; if unfused (some Acaridae), then posterior apodemes II contiguous or fused with apodemes III, or propodosomal ocelli present. 19

19 Body very large, broadly tear-drop shaped, coxal fields III narrowing medially, connected by a short apodeme. One genus, *Megacaneistrinia*, on *Tefflus* spp. (Coleoptera: Carabidae), Afrotropical. **Canestriniidae** Berlese, 1884

– Body not greatly widened posteriorly; coxal fields variable but coxal fields III usually quadrate or longer than wide. 20

20 Setae *vi* situated on a ventral tubercle between gnathosoma and overhang-ing propodosoma. One genus, *Euglycyphagus*, on trogid beetles; Holarctic. **Euglycyphagidae** Fain & Philips, 1977

– Setae *vi* otherwise; if propodosoma overhangs gnathosoma anteriorly, then rostral setae inserted on its ventral surface. **Acaridae** Latreille, 1802 and **Lycoglyphidae** fam. nov.

*Published in an electronic-only journal; according to ICZN, here we provide ZooBank accession numbers (description by indication, with the same original au-thors): Levantoglyphidae Klimov, Vorontsov, Azar, Sidorchuk, Braig, Khaustov and Tol-stikov, 2021 (urn:lsid:zoobank.org:act:5866BE62-1C06-4B01-870A-383CEA30E6EC); *Levan-toglyphus* Klimov, Vorontsov, Azar, Sidorchuk, Braig, Khaustov and Tolstikov, 2021 urn:lsid:zoobank.org:act:0B899DC5-C0C4-451A-8748-C533C9F4624B.

3.6. Key to Genera of Acaroidea (Adults)

1 Anus positioned directly behind genital opening, displaced from posterior edge of body by distance greater than length of anus; male with para-anal suckers vestigial or absent. In bird nests; Holarctic. **Scatoglyphus** Berlese, 1913 (Scatoglyphidae)

– Anus positioned near posterior margin of body; male with or without para-anal suckers. 2

- 2 Female and sometimes male with empodial claws bifurcate; male with legs III enlarged, terminating in a large straight empodial claw and an enlarged straight spine-like seta similar in length and form to empodial claw; male with para-anal suckers and sucker-like setae on tarsus IV. In vertebrate nests, carrion, and stored products; cosmopolitan. *Lardoglyphus* Oudemans, 1927 (= *Hoshikadania* Sasa and Asanuma, 1951, = *Sinolardoglyphus* Jiang, 1991 syn. nov.) (Lardoglyphidae)
- Both sexes with empodial claws simple or absent; male with legs III similar to legs IV, or, if legs III enlarged, then empodial claw shorter and curved and without an enlarged seta similar in form to empodial claw.3
- 3 Tarsi with both setae *f* and *e* filiform, similar in length; proral setae spiniform or enlarged and claw-like; ungual setae spiniform, reduced or absent, never distinctly larger than proral setae.4
- Tarsi with setae *f* and *e* asymmetrical, *e* usually spiniform, rarely filiform; ungual setae usually larger and stouter than proral setae.13
- 4 Chelicera with two setae *cha* and *chb*. One species, *B. curvisetus*
 *Bulacarus* Fan and Zhao, 2024 (Bulacaridae)
- Chelicera with only setae *cha*.5
- 5 Body outline round, length similar to width; some dorsal setae often heavily pectinate or plumose, occasionally all short and simple; tarsi with proral and ungual setae similar in form (Gaudiellidae).6
- Body distinctly longer than wide; dorsal setae filiform, unbarbed; tarsi with proral setae enlarged and claw-like; ungual setae reduced or absent (Suidasiidae).9
- 6 Dorsal body surface smooth, without mammilations.7
- Dorsal body surface with rounded mammilations.8
- 7 Pretarsi with empodial claws well developed; all dorsal setae short and filiform. One species from a “bee nest”; Oriental. *Platyglyphus* Kurosa, 1976
- Pretarsi without empodial claws; some dorsal setae stout and strongly barbed. Associated with meliponine bees; Neotropical. *Gaudiella* Atyeo, Baker and Delfinado, 1974 (= *Trigonacoptes* Fain and Rosa, 1983)
- 8 Opisthosoma shortened, distance between genital region and anus less than length of anus; adult without prodorsal sclerotization; palps normally formed. Associated with meliponine bees; Neotropical. *Partamonacoptes* Fain and Rosa, 1983
- Opisthosoma normally developed, distance between genital region and anus greater than length of anus; adult with well-developed prodorsal sclerite; palps attenuated distally, palpal solenidion as long as basal palpal segment. Associated with *Bombus*, Holarctic. *Cerophagus* Oudemans, 1902
- 9 Pretarsi with empodial claws and condylophores reduced or absent; tibiae I–II with 1 ventral barbed seta. In soil, vertebrate nests, stored products; widespread.
 *Sapracarus* Fain and Philips, 1978
- Pretarsi with well-developed empodial claws and condylophores; tibiae I–II with 2 ventral setae.10
- 10 External scapular setae at least twice as long as internal scapular setae; solenidion ω_2 of tarsus I distinctly distal to solenidion ω_111
- External scapular setae only slightly longer than internal scapulars; solenidion ω_2 of tarsus I at same level or only slightly more distal than ω_1 . Two species in stored products; India, Africa, Europa. *Neosuidasia* Ranganath and ChannaBasavanna, 1983
- 11 Female with oviporus about as wide posteriorly as long; male with para-anal suckers completely absent. In nests of Hymenoptera. *Tortonia* Oudemans, 1911

(=*Donnadieuia* Zachvatkin, 1941, *Neottiglyphus* Volgin, 1974 syn. nov.; =*Ebertia* Oudemans, 1924 syn. nov.)

– Female oviporus at least twice as long as posterior width; male with para-anal suckers present, well developed or vestigial.12

12 Supracoxal seta *scx* simply barbed; may be apically bifurcate but not divided in a Y-shape. In stored products, vertebrate nests, bat guano, often associated with dead insects; probably cosmopolitan. . . .*Suidasia* Oudemans, 1905 (= *Sinosuidasia* Jiang, 1996 syn. nov.)

– Supracoxal seta *scx* barbed and divided into a Y-shape. One species from desert sands, Namibia.*Namibacarus* Fain, Coineau and André, 1993

13 Prodorsal sclerotization in the form of two thin elongate parallel sclerites; dorsal setae elongate and heavily barbed; cuticle ornamented with small triangular microtrichae; male with leg III much larger than leg IV but otherwise unmodified. In bird nests; sub-antarctic islands.*Glycacarus* Griffiths, 1977 (Glycacaridae)

– Prodorsal sclerotization in the form of a rectangular shield that may be incised posteriorly, or prodorsal sclerotization absent; dorsal setae variable but not usually both elongate and heavily barbed; cuticle smooth or rarely with small rounded protuberances; male with leg III similar to leg IV, or leg III enlarged and bearing a large empodial claw and reduced tarsal setation.14

14 Chelicera with two setae (*cha* and *chb*), seta *cha* large, lanceolate, situated distally on fixed digit (Lycoglyphidae fam. nov.).15

– Chelicera with one unmodified seta *cha*, situated on proximally to digit (Acaridae). . . .17

15 Prodorsal shield well developed. Setae *ve* vestigial or very short, distinctly shorter than other short dorsal setae. Grandjean's organ with a main trunk and an auxiliary tongue-shaped process.*Viedebanttia* Oudemans, 1929

– Prodorsal shield small or vestigial. Setae *ve* well developed, subequal with other short dorsal setae. Grandjean's organ with a main trunk, auxiliary process absent.16

16 Central trunk of supracoxal setae lanceolate with numerous lateral processes. Sclerite of posterior coxal apodeme II present, but apodeme absent. Tarsal setae *u* and *v* vestigial. Solenidia ϕ I–II reach the apices of their respective tarsi without ambulacra, solenidion σ'' I longer than σ' , solenidion σ III absent.*Lycoglyphus* gen. nov.

– Central trunk of supracoxal setae broadly flattened with numerous lateral processes and terminal long processes. Sclerite of posterior apodeme II located at end apodemes. Tarsal setae *u* and *v* developed, spiniform. Solenidia ϕ I–II not reaching the apices of their respective tarsi without ambulacra, solenidion σ'' I shorter than σ' , solenidion σ III present.*Obelacarus* gen. nov.

17 External vertical setae *ve* located on the same transverse line as internal vertical setae *vi* or displaced posteriorly at most one-third the distance to scapular setae *se* and *si*; hysterosoma with 12 pairs of setae, some of which are often elongate and finely barbed.18

– External vertical setae *ve* located approximately midway between internal vertical setae *vi* and scapular setae *se* and *si* or external vertical setae *ve* absent; hysterosoma sometimes with fewer than 12 pairs of setae; setae rarely elongate and barbed.35

18 Tarsus I with solenidion ω_2 about midway between base and apex; proral (*p*, *q*) and ungual (*u*, *v*) setae at lateroventral apex of tarsi thin; dorsal hysterosomal setae *e*₂ and *f*₂ very closely associated; cheliceral digits thin with only small apical teeth.19

- Tarsus I with solenidion ω_2 near base of segment near ω_1 or ω_2 absent; proral and unguinal setae thin or stout spines; dorsal hysterosomal setae e_2 and f_2 not closely associated (except *Paulacarellus*); cheliceral digits robust, usually with teeth along length of digits.....20
- 19 Palps elongate, longer than length of subcapitulum. One species, *D. maculatus* from salted hides; Argentina.*Diphtheroglyphus* Nesbitt, 1950
- Palps normally developed, shorter than length of subcapitulum. In beach wrack; Holarctic.*Pontoppidania* Oudemans, 1923
- 20 Genu I with solenidion σ'' at least three times longer than σ' ; ventral apex of tarsus with proral (p , q) and unguinal (u , v) setae thin, not short, stout spines; male with leg I enlarged and bearing a ventral apophysis on femur; in stored products and vertebrate nests. . .*Acarus* Linnaeus, 1758 (= *Tyroglyphus* Latreille, 1796, = *Aleurobius* Canestrini, 1888)
- Genu I with solenidion σ'' no more than three times longer than σ' ; ventral apex of tarsi with proral and unguinal setae usually in the form of short and stout spines, occasionally one or both pairs strongly reduced or absent; male without modifications of leg I. 21
- 21 External vertical setae ve barbed, more than half the length of internal vertical setae vi , and usually positioned at or near anterior lateral corners of prodorsal shield. 22
- External vertical setae ve generally smooth, less than 1/4 the length of internal vertical setae vi and positioned along edge of prodorsal shield somewhat posterior to anterior lateral corners. 29
- 22 Internal scapular setae si similar in length or shorter than external scapular setae se 23
- Internal scapular setae si distinctly longer than external scapular setae se 26
- 23 At least some anterior hysterosomal setae rounded at tips. In nests of ants and honey bees.*Forcellinia* Oudemans, 1924 (= *Hungaroglyphus* Mahunka, 1962 syn. nov., = *Paraforcellinia* Kadzhaya, 1974 syn. nov.)
- All dorsal setae thin and tapering to fine points. 24
- 24 Scapular setae se and si very long, extending beyond tip of palp; all dorsal hysterosomal setae except c_1 longer than length of hysterosoma; setae c_1 very short and smooth. One species, *V. talyshiana*, in forest litter and moss; Caucasus.*Volginia* Kadzhaya, 1969
- Scapular setae se and si short, not extending to anterior edge of propodosoma; most dorsal idiosomal setae shorter than distance to next posterior seta; setae c_1 barbed. 25
- 25 Tarsi with unguinal setae in the form of simple spines generally similar to proral setae. Two species in stored products, mainly tropical.*Madaglyphus* Fain, 1971 (= *Comerinia* Ferguson, 1985)
- Tarsi with unguinal setae stout and claw-like, distinctly larger and thicker than proral setae. Three species in stored products; widespread.*Aleuroglyphus* Zachvatkin, 1940
- 26 All hysterosomal setae except c_1 elongate, longer than the distance to the next posterior seta. 27
- Hysterosomal setae c_1 and at least one other pair of setae (typically d_1 or d_2) shorter than the distance to the next posterior seta. 28
- 27 Hysterosomal setae c_1 unbarbed, positioned often very close to seta d_1 ; tarsi tanned, with a distinct dorsal ridge; some paraproctal setae of female shorter than distance between them. In nests of *Bombus* bees (Apidae).*Kuzinia* Zachvatkin, 1941
- Setae c_1 barbed, positioned more anteriorly; tarsi without dorsal ridge; all paraproctal setae of female longer than the distance between them. One species, *T. casei*, in a variety of habitats often involving sugar-based substrates.*Tyrolichus* Oudemans, 1924

- 28 Tarsi I–II short, approximately twice as long as basal width; tarsi with proral setae (p , q) very reduced; Grandjean's organ flattened and fimbriate. Three species in stored products. *Tyroborus* Oudemans, 1924
- Tarsi I–II more than twice as long as basal width; proral setae thinner than unguinal setae but similar in length; Grandjean's organ finger-like. In a variety of field and storage habitats. *Tyrophagus* Oudemans, 1924
- 29 Supracoxal seta scx of leg I long, thick and strongly barbed. In nests of small sphecoid wasps (*Psenulus*, *Stigmus*). *Sphecacarus* Klimov, 2011
- Supracoxal seta scx of leg I thin, smooth or very weakly barbed. 30
- 30 Male with bilobed posterior hysterosomal projection bearing flattened fan-like setae h_3 and p_1 , female unknown. In beach wrack, Far Eastern Russia, NW North America; subantarctic islands. *Paulacarellus* Fain, 1976
- Male without posterior terminal modifications as above. 31
- 31 External scapular setae se positioned distinctly anterior to level of internal scapular setae si . In nests of *Megachile* (*Chalicodoma* and related subgenera) bees (Megachilidae), occasionally in honey-bee hives. One species, *C. indicus*, in stored products. *Cerophagopsis* Zachvatkin, 1941 and *Megachilopus* Fain, 1974
- External and internal scapular setae positioned on the same transverse line. 32
- 32 Posterior edge of prodorsal sclerite incised; tarsi with unguinal setae (u , v) thin or absent. In nests of *Anthophora* and *Diadasia* bees (Apidae). 33
- Posterior edge of prodorsal sclerite entire; tarsi with unguinal setae well developed. 34
- 33 Pretarsi with empodial claws present; tarsi relatively short, at most three times longer than wide; tarsi with ventro-terminal seta s shorter than apical width of tarsus; coxal seta $3a$ absent. Primarily associated with *Anthophora* bees (Apidae), occasionally with *Diadasia*; Holarctic. *Medeus* Volgin, 1974
- Pretarsi lacking empodial claws; tarsi at least six times longer than wide; tarsi with ventro-terminal seta s strongly enlarged, hooked, longer than apical width of tarsus; coxal seta $3a$ present; primarily associated with *Diadasia* bees, occasionally with *Anthophora*; New World. *Diadasiopus* OConnor, 1997
- 34 Female paraproctal region with ps_{1-3} and ad_{1-3} setal pairs, spermatheca large; male with aedeagus long, longer than diameter of para-anal suckers. In stored products, vertebrate nests. *Mycetoglyphus* Oudemans, 1932
- Female paraproctal region with only ps_{1-3} setal pairs, ad_{1-3} setae absent; spermatheca small, some species thelytokus; known males with aedeagus shorter than diameter of para-anal suckers. In nests of termites. *Australhypopus* Fain et Friend, 1984 (includes "*Acotyledon*" *formosani*, and other species)
- 35 Legs IV and/or III of both sexes strongly modified; empodial claws IV and/or III greatly enlarged, hook-like, opposable with structures at base of tarsus. Associated with Crustacea (Coenobitidae & Potamidae). 36
- Legs III–IV of female with tibiae-tarsi freely articulated; male as female or with legs III enlarged; empodial claws not opposable with structures on base of tibia. 39
- 36 Tibiae and tarsi III–IV not fused; leg III with tarsus normally developed, without empodial claw opposing structures at base of tarsus; male with fan-like projec-

- tions posteriorly. One species on gills of river crab, *Geothelphusa dehaani*; Japan...
*Kanekobia* Fain, Yunker, van Goethem et Johnston, 1982
 – Tibiae and tarsi III–IV fused; tibio-tarsi III–IV similarly developed, with empodial
 claw opposing structures at base of tarsus; male without fan-like posterior projections...37
 37 Empodial claws III–IV opposable to a large hypertrophied seta arising from
 the base of tibio-tarsus. On body setae behind gills of *Coenobita*; pantropical.....
*Askinasia* Yunker, 1970
 – Empodial claws III–IV opposable to a large, strong cuticular tubercle on the basal por-
 tion of tibio-tarsus; tubercle bearing 3 modified setae at its apex.....38
 38 Body globose, both sexes rounded posteriorly, cuticle smooth. One species attached
 to shaft of gills of *Coenobita clypeatus*; Neotropical.....*Ewingia* Pearse, 1929
 – Body somewhat dorso-ventrally flattened, female bilobed posteriorly, cuticle
 wrinkled. One species attached to gill lamellae of *Coenobita rugosus*; Afrotropical...
*Hoogstraalacarus* Yunker, 1970
 39 External vertical setae *ve* present on lateral sides of prodorsal shield approximately
 halfway between internal vertical setae *vi* and scapular setae, length of *ve* setae greater
 than 10 µm; tarsi I–II each with seta *ba* present, filiform, not associated with solenidion
 ω_140
 – External vertical setae *ve* absent, or, if present (some *Rhizoglyphus* and *Acarotalpa*), then
 10 µm long or less and tarsi I–II with seta *ba* spiniform and closely associated with solenidion
 ω_1 or *ba* absent.....45
 40 Tibiae I–II with 1 ventral seta; tibiae IV without ventral seta; prodorsal shield weakly
 developed. In nests of *Xylocopa* spp. (Apidae), 1 species, *H. longa*, in house dust or stored
 food products.....*Horstia* Oudemans, 1905
 – Tibiae I–II with 2 ventral setae; tibiae IV with 1 ventral seta; prodorsal shield well
 developed.....41
 41 Tarsi I–II with 2–3 foliate setae, seta *ra* always foliate and positioned posteroapically;
 tibial setae often spine-like; supracoxal seta *scx* of leg I unbarbed, sometimes greatly re-
 duced or absent.....*Sancassania* Oudemans, 1916
 (= *Caloglyphus* Berlese, 1923, = *Rhizoglyphoides* Volgin, 1978, = *Mycetosancassania* Klimov, 2000,
 = *Ctenocolletacarus* Fain, 1984 syn. nov.)
 – Tarsi I–II with one foliate seta (*f*) or none; seta *ra* filiform, positioned medially or api-
 cally; supracoxal setae *scx* variously formed.....42
 42 Tarsi I–II with seta *ra* posteroapical in position; supracoxal setae *scx* of leg I inflated
 basally and heavily barbed; tibial setae spiniform. In field and storage habitats, often
 associated with ants or termites.....*Cosmoglyphus* Oudemans,
 1932
 – Tarsi I–II with seta *ra* posteromedial in position; supracoxal setae *scx* variously
 formed, long or short, inflated basally or thin, nude or barbed; tibial setae filiform.....43
 43 Female with internal spermatheca large, bearing sclerotized ramifications, openings
 to oviducts widely separated; tarsi I–II with seta *f* thinly foliate or filiform; supracoxal seta
scx of leg I longer than 10 µm, thin or inflated basally. In vertebrate nests, tree holes and
 storage habitats.....*Acotyledon* Oudemans, 1903
 – Female with spermatheca simple, openings to oviducts close together.....44
 44 Supracoxal seta *scx* of leg I thin and nude or slightly barbed, length >20 µm; length of
 posterior hysterosomal setae less than or equal to hysterosomal width. One species, *N. rhizo-*
glyphoides, in stored products, insect and vertebrate nests; widespread.....
 Samsinak, 1980
 – Supracoxal seta *scx* of leg I a tiny spine < 5 µm long; posterior hysterosomal setae
 distinctly longer than maximum hysterosomal width. Two species from litter and a ro-

- dent nest; Central Asia. *Apiacarus*
Volgin, 1974
- 45 Dorsal cuticle ornamented with raised protuberances; hysterosomal setae long and heavily barbed. In decaying wood; Holarctic. *Hortacarus* Mahunka, 1978 (= *Fagacarus* Fain & Norton, 1979 syn. nov.)
- Dorsal cuticle smooth; hysterosomal setae simple. 46
- 46 Tarsi I–II with seta *ba* absent, or, if present on tarsus I, then filiform. 47
- Tarsi I–II with seta *ba* in the form of a spine directly adjacent to solenidion ω_1 52
- 47 Tarsus I with *ba* present, filiform. 48
- Tarsus I with *ba* absent. 49
- 48 Body rounded; seta *ba* absent from tarsus II; tibiae I–II with 1 ventral seta; legs long, tarsi more than four times longer than wide; body rounded; male with para-anal suckers vestigial. Phytophagous or fungivorous in tree foliage; tropical and subtropical. *Neotropacarus*
Baker, 1985
- Body elongate; tarsi I–II with seta *ba* present; tarsi shorter, less than four times longer than wide; body elongate; male with para-anal suckers well developed. In polypore fungi; Holarctic. *Umakefeq* Klimov, 2000
- 49 Female with one pair of paraproctal setae situated in distinct ovoid pits anterior lateral to anus; male without sclerotized posterior projection. In nests of honey bees and ants; Palaearctic, Oriental. *Lasioacarus* Kadzhaya et Sevastianov, 1967
- Female lacking ovoid pits bearing paraproctal setae; male with sclerotized projection extending from posterior opisthosoma. 50
- 50 Inner scapular setae *si* and hysterosomal setae c_1 , c_2 , and d_1 present, long, filiform; male with posterior opisthosomal sclerotization bilobed. *Horstiella* Turk, 1949
- Inner scapular setae *si* and hysterosomal setae c_1 , c_2 , and d_1 present as microsetae or absent; male with not bilobed posterior opisthosomal sclerotization. 51
- 51 Hysterosomal setae c_1 , c_2 , and d_1 present as microsetae; seta f_2 present; male with posterior opisthosomal sclerotization narrow, setae h_1 not on sclerite, bases of setae h_2 , h_3 and ps_1 closely associated on edge of posterior sclerotized projection. Associated with subcortical habitats and fungal fruiting bodies; Holarctic. *Reckiacarus*
Kadzhaya, 1972
- Hysterosomal setae c_1 , c_2 , and d_1 absent; seta f_2 absent; male with posterior opisthosomal sclerotization broad, setae h_1 on sclerite; bases of setae h_2 , h_3 and ps_1 arranged in a triangle on ventral surface of posterior sclerotized projection. Often associated with dead insects, subcortical habitats, fungi, plant habitats or stored products; widespread. *Thyreophagus* Rondani, 1874 (= *Fumouzea* Zachvatkin, 1953, = *Michaelopus* Fain et Johnston, 1974, = *Moniziella* Berlese, 1897)
- 52 Both sexes with posterior hysterosoma sclerotized or tanned; supracoxal seta *scx* elongate and filiform; tibiae I–II with only one ventral seta (*hT* absent); all males homeomorphic with legs III normally developed. In spore tubes of woody bracket fungi (Polyporaceae). 53
- Female lacking posterior hysterosomal sclerite male often with posterior hysterosomal sclerite but female always without; supracoxal seta *scx* often very short or absent; tibiae I–II with one or two ventral setae. 54
- 53 Body elongate 2.5–3 times longer than wide; setae *si* short, much shorter than setae *se*; female epigynal apodeme Y-shaped; tarsi I–II with setae *wa* present; Palaearctic, Nearctic, Oriental, Australian. *Boletoglyphus* Volgin, 1953 (= *Fantovia* Samsinak, 1957, = *Ellipsopus* Fain et Ide, 1976, = *Lindquistia* Mahunka, 1977)

- Body approximately twice as long as wide; setae *si* long, equal in length to *se*; female epigynal apodeme straight, transverse; tarsi I–II with setae *wa* absent; Eastern Palaearctic, Oriental. *Capillaroglyphus* Klimov, 1999
- 54 Hysterosoma with maximum complement of dorsal setae (12 pairs); internal scapular setae *si* present although usually short (absent in 1 species).55
 - Hysterosoma with at most 7 pairs of dorsal setae; setae *c*₁ and *f*₂ always absent; internal scapular setae *si* and setae *c*₂ and *d*₁ usually absent.58
- 55 Tarsus I with seta *aa* present in the form of a large, recurved spine. In soil; Europe. *Acarotalpa* Volgin, 1966
 - Tarsus I with seta *aa* absent.56
- 56 Body globose; prodorsal shield extending posteriorly beyond insertions of external scapular setae *se*; genital papillae elongate. In fungal fruiting bodies. *Mezorhizoglyphus* Kadzhaya, 1966 (= *Bolletacarus* Volgin et Mironov, 1980)
 - Body ovoid; prodorsal shield extending posteriorly at most to level of external scapular setae *se*; genital papillae rounded.57
- 57 Male with sclerotized extension of posterior opisthosomal sclerite, sometimes bearing modified setae with enlarged, flattened bases. Associated with epiphytic Bromeliaceae; Neotropical. *Bromeliaglyphus* Nesbitt, 1985
 - Male with posterior opisthosoma without sclerotized extension; all posterior setae unmodified. Widespread in soil, decaying vegetable material, or in intact bulbs and corms. *Rhizoglyphus* Claparède, 1869
- 58 Tarsi less than twice as long as wide; hysterosomal setae short, not usually longer than the distance to the next posterior seta; male without posterior projection.59
 - Tarsi longer than 2 times the basal width; most dorsal hysterosomal setae longer than the distance to the next posterior seta; in phytotelmata.60
- 59 Male with posterior opisthosomal sclerite extending posteriorly and bearing 4 modified fan-like setae. Associated with wood-boring insects, 1 species, *H. carpio*, occasionally in stored products and fermented beverages. *Histiogaster* Berlese, 1883
 - Male without a terminal posterior expansion of posterior opisthosomal sclerite, all posterior setae filiform. Associated with phytotelmata. *Naiadacarus* Fashing, 1974 (= *Naiacus* Nesbitt, 1990)
- 60 Dorsal surface entirely sclerotized, without distinct prodorsal sclerite; anterior hysterosomal cupules *ia* greatly enlarged into dorsolateral lyriform organs; legs I–II short, stout; tarsal setae *ba* and *e* I–II greatly enlarged spines; tarsi I–II with only 2 filiform/foliate setae (*d*, *ra*—setae *la* short, spiniform); only homeomorphic males known. In caves and decaying organic matter. *Stereoglyphus* Berlese, 1923 (= *Troglocoptes* Fain, 1966)
 - Dorsal surface usually unsclerotized except for prodorsal sclerite (rarely totally sclerotized); anterior hysterosomal cupules *ia* small, rounded; legs I–II variable in form; tarsi I–II with 3 filiform/foliate setae (*d*, *ra*, *la*); heteromorphic males common. In soil, litter, decaying wood, fungi, tree holes, or in semiaquatic to aquatic habitats. *Schwiebea* Oudemans 1916

Notes: Adults of the following genera are unknown: *Armacarus* Mahunka, 1979, *Bembidioglyphus* Klimov, 1998, *Calvoliella* Samsinak, 1969, *Carabidobius* Volgin, 1953, *Froriepia* Vitzthum, 1919, *Garsaultia* Oudemans, 1916, *Ghanacarus* Mahunka, 1973, *Halictacarus* Mahunka, 1975, *Irianopus* Fain, 1986, *Kadzhajania* Sevastianov, 1969, *Konoglyphus* Delfinado

et Baker, 1974, *Lackerbaueria* Zachvatkin, 1941, *Lamtoglyphus* Fain, 1975, *Lowreyacarus* Fain, 1986, *Machadoglyphus* Mahunka, 1963, *Mahunkallinia* Eraky, 1999, *Neohorstia* Zachvatkin, 1941, *Notiopsyllopus* Fain, 1977, *Paraceroglyphus* Fain et Beaucournu, 1973, *Passaloglyphus* Mahunka et Samsinak, 1972, *Pinoglyphus* Mahunka, 1978, *Psyllopus* Fain et Beaucournu, 1993, *Schulzea* Zachvatkin, 1941, *Spinacaropus* Fain et Camerik, 1978, *Terglyphus* Samsinak, 1965, *Thectochloracarus* Fain, Engel, Flechtman et OConnor, 1999, *Trichopsyllopus* Fain et Baker, 1983, *Meliponopus* Fain and Flechtman, 1985

Notes: Genera *Heteroglyphus* Foa, 1897, *Podoglyphus* Oudemans, 1937, *Valmontia* Oudemans, 1923 described very superficially, their position in the family is unknown.

3.7. Key to Genus of Phoretic Deutonymphs Acaroidea

- 1 Legs I–II without pretarsi; coxal apodemes II–IV end freely.....
.....*Sapracarus* Fain and Philips, 1978 (Suidasiidae)
– Pretarsal ambulacrum and/or empodial claw present on legs I–II; coxal apodemes II–IV end freely or fuse with other apodematal elements.....2
- 2 Leg IV with empodial claw absent; leg IV often shorter than leg III, with some fusion of segments and usually with one or more long apical setae.....3
– Leg IV with empodial claw present, or, if absent, then empodial claw III also absent, but claws I–II present; leg IV generally similar in form to leg III.....4
- 3 Empodial claws I–III borne on membranous ambulacra.....
.....*Lardoglyphus* Oudemans, 1927 (Lardoglyphidae)
– Empodial claws I–III arising directly from tarsal apices, or some or all claws absent. Phoretic on Coleoptera and Hymenoptera; cosmopolitan.....*Tortonia* Oudemans, 1911 (Suidasiidae)
- 4 Coxal apodemes III–IV ending freely; all coxal fields completely open; propodosomal ocelli absent. Associates of social bees; Holarctic, Neotropical, Oriental.....5
– Coxal apodemes III–IV usually fused medially; if unfused (some Acaridae), then posterior apodemes II contiguous or fused with apodemes III, or propodosomal ocelli present.....6
- 5 Dorsal sclerites strongly punctate; empodial claws I–IV well developed, strongly hooked, with basal flange. Associated with *Bombus*; Holarctic.....
.....*Cerophagus* Oudemans, 1903
– Dorsal sclerites smooth; empodial claws I–II small and thin; claws III IV absent. Associated with meliponine bees; Neotropical.....*Meliponopus* Fain and Flechtman, 1985
- 6 Posterior apodeme of coxal field II fused with anterior apodeme of coxal field III or running parallel for much of its length, or divided, with medial element parallel to coxal field III; empodial claws often enlarged and hook-like; genital papillae often elongate and tapering to a fine point, rarely rounded; coxal setae I, III filiform or absent. Associates of bees and wasps (Hymenoptera).....7
– Posterior apodeme of coxal field II free posteriorly, although it may end near the anterior apodeme of coxal field III (if fused with apodeme III, then coxal setae conoidal); empodial claws small; if enlarged then not hook-like; genital papillae short, broadly rounded apically; coxal setae often conoidal. Most genera not associated with bees and wasps (exceptions occur).....12
- 7 Tarsus IV with 2 or 3 long setae, each longer than the length of leg IV.....8
– Tarsus IV with at most one seta longer than the length of leg IV.....10
- 8 Empodial claws I–IV large, twisted, and hook-like; claws I–III distinctly larger than claws IV. Associated with *Anthidium* and related genera of bees (Megachilidae).....
.....*Sennertionyx* Zachvatkin, 1941
– Empodial claws variously formed, but never twisted.....9

- 9 Empodial claws I–IV short, strong, barely hooked apically; posterior apodeme of coxal field II entire, running obliquely along anterior apodeme III; tibiae I–II with 1 ventral seta. Associated with *Xylocopa* bees (Apidae). **Horstia** Oudemans, 1900
- Empodial claws I–IV with distinct apical hook; posterior apodeme of coxal field II divided, with only medial portion parallel to anterior apodeme III; tibiae I–II with 2 ventral setae. Associated with *Diadasia* and *Anthophora* bees (Apidae). **Diadasiopus** OConnor, 1997
- 10 Coxal setae *3a* and *4a* present, filiform, setae *4b* absent; posterior apodeme of coxal field II divided; posterior dorsum with well-developed longitudinal apodemes. Associated with *Anthophora* and *Diadasia* (Apidae); Holarctic. **Medeus** Volgin, 1974
- Coxal setae *3a* and *4a* absent, setae *4b* present, filiform; posterior apodeme of coxal field II continuous; posterior dorsum without longitudinal apodemes; associated with *Megachile* (*Chalicodoma*) (Megachilidae). 11
- 11 Empodial claws I–IV with a rounded basal flange. Cosmopolitan. **Cerophagopsis** Zachvatakin, 1941
- Empodial claws I–IV simply claw-like. Afrotropical. **Megachilopus** Fain, 1974
- 12 Propodosoma with a pair of pigmented eye-spots, with or without distinct lenses. 13
- Propodosoma without eye-spots. 22
- 13 Propodosoma with unpaired eye-spot on anterior part of propodosoma; genu I with 2 solenidia (σ'' and σ'). 14
- Propodosoma with paired eye-spots on anterior or lateral part of propodosoma; genu I with 1 solenidion. 15
- 14 Palp supracoxal setae *elcp* present; lanceolate; supracoxal seta *scx* not bifurcate apically; tarsal seta *aa* I present; solenidia σ'' and σ' approximately the same size. Associated with *Ips typographus* (Coleoptera: Curculionidae: Scolytinae), one species **Ipsoglyphus** Klimov & Khaustov, 2018
- Palp supracoxal setae *elcp* absent; supracoxal seta *scx* bifurcate apically; tarsal seta *aa* I absent; solenidion σ' longer than σ'' , σ'' very short. Associated with *Mycetina marginalis* (Coleoptera: Endomychidae), one species **Mycetinopus** Klimov & Kolesnikov, 2023
- 15 Eyes widely separated in middle of propodosoma. 16
- Eyes contiguous or closely separated on anterior edge of propodosoma. 20
- 16 Eyes without distinct lenses; conoidal setae *ps₁* and *ps₂* of attachment organ in a transverse row or external conoids *ps₂* only slightly anterior to internal conoids *ps₁*. 17
- Eyes with distinct lenses; conoidal setae *ps₁* and *ps₂* of attachment organ in a concave pattern, external conoids *ps₂* distinctly anterior to internal conoids *ps₁*. 18
- 17 Propodosomal shield with rostrum; gnathosomal solenidia not longer than gnathosoma; setae *sup* spiniform or knife-like; famulus clavate; setae *e* I–II, *p* and *q* I–IV short, spiniform; attachment organ not shifted from posterior edge of body (distance between them much shorter than attachment organ length). In polypore fungi, phoretic on Bolitophagini (Tenebrionidae) and Ciidae **Capillaroglyphus** Klimov, 1998
- Propodosomal shield rounded, without rostrum; gnathosomal solenidia distinct longer than gnathosoma; setae *sup* filiform; famulus solenidion-like, with rounded tip, not clavate; setae *e* I–II, *p* and *q* I–IV filiform; attachment organ shifted from posterior edge of body (distance between them equal or more the attachment organ length). In polypore fungi, phoretic on Bolitophagini (Tenebrionidae) and Ciidae. . . **Boletoglyphus** Volgin, 1953

- 18 Coxal apodemes III–IV ending freely, median apodeme absent. Often on wood-associated insects. *Thyreophagus* Rondani, 1874
- Coxal apodemes fused to each other medially and to posterior median apodeme. 19
- 19 Sternal apodeme ending freely far anterior to ends of coxal apodemes II. Palaearctic, Afrotropical. *Lamtoglyphus* Fain, 1974
- Sternal apodeme extending to ends of coxal apodemes II and fused with them. One species, *G. endroedii*, from undetermined Coleoptera. *Ghanacarus* Mahunka, 1973
- 20 Coxal apodemes III–IV ending freely, not fused to each other medially. *Histiogaster* Berlese, 1883
- Coxal apodemes III–IV fused to each other medially. 21
- 21 Dorsal hysterosomal setae c_1 present. Associated with subcortical insects, Holarctic, Oriental. *Calvoliella* Samšňák, 1969
- Dorsal hysterosomal setae c_1 absent. Associated with polypore fungi; Holarctic. *Umakefeq* Klimov, 1999
- 22 Attachment organ vestigial, with 1 pair of suckers; gnathosomal solenidia long. *Acotyledon* Oudemans, 1903
- Attachment organ well developed with 2 pairs of suckers and 2 pairs of conoidal setae, or, if vestigial (“inert” deutonymphs), then gnathosomal solenidia vestigial. 23
- 23 Coxal setae $4a$ in the form of large striate conoids; supracoxal setae scx absent. Associated with *Epicharis* bees (Apidae); Neotropical. *Horstiella* Turk, 1948
- Coxal setae $4a$ not large, if there are conoids, then not striate; supracoxal setae scx present. 24
- 24 External conoidal setae ps_2 of attachment organ completely anterior to median sucker ad_{1+2} 25
- External conoidal setae ps_2 of attachment organ lateral or posterior to median sucker ad_{1+2} 30
- 25 Coxal apodemes I fused into a shorter sternal apodeme that does not extend as far posteriorly as apodemes II. 26
- Coxal apodemes I fused into a sternal apodeme that extends posteriorly approximately as far as coxal apodemes II. 27
- 26 Body elongate, oval; attachment organ shifted anteriorly such that distance from posterior end of organ to posterior end of body greater than length of attachment organ; anterior and posterior coxal apodemes II elongate, fused to each other posteriorly; some dorsal setae may be elongate. Associated with termites; Palaearctic. New Genus for “*Acotyledon*” *lamiai* and similar species
- Body rounded or ovoid, not elongate; attachment organ positioned near posterior end of body; coxal apodemes II variously developed but not extremely elongate; associated with bees and wasps. *Schulzea* Zachvatkin, 1941
- 27 Attachment organ displaced anteriorly from end of body by a distance greater than its length; a distinct median apodeme present posterior to attachment organ. Associated with ants; Holarctic. *Garsaultia* Oudemans, 1916
- Attachment organ normally positioned near posterior end of body; without median apodeme posterior to attachment organ. 28
- 28 Dorsal body setae elongate and pectinate or stiffened and spineform; tarsus III with 1 and tarsus IV with 2 setae longer than their respective legs. Associated with Sphecidae wasps. *Sphecacarus* Klimov, 2011 (includes some *Lackerbaueria* Zachvatkin, 1941)

- Dorsal body setae simple; tarsus III and IV with no setae longer than legs. . .29
- 29 Coxal setae 4a in the form of clearly bilobed conoids. Associated with ants. . .
- *Forcellinia* Oudemans, 1924 (= *Dorylacarus* Mahunka, 1979, = *Ocellacarus* Mahunka, 1979) and *Tyrophagus* Oudemans, 1924 (these genera are not separable morphologically)
- Coxal setae 4a in the form of simple conoids. In soil, decaying wood and stored products. *Mycetoglyphus* Oudemans, 1932
- 30 Coxal apodemes I fused to form sternum, which extends along with anterior apodemes II to level of coxal apodemes III.31
- Coxal apodemes I and anterior apodemes II not extending to level of coxal apodemes III.37
- 31 Legs I–II short, tarsi very short, only slightly longer than wide.36
- Legs I–II longer, tarsi at least 3 times longer than basal width.32
- 32 Coxal fields heavily sclerotized, with rounded fovea or scale-like reticulation; coxal apodemes weakly developed beneath coxal sclerites.33
- Coxal fields not as heavily sclerotized, usually simply punctate; coxal apodemes distinct.35
- 33 Coxal fields I–II heavily sclerotized only in medial area (sclerotization is shaped like a “bottle”—wide at the base and narrowing towards the gnathosoma). Afrotropical. . .
- *Sandoroglyphus* nom. nov. pro *Fainoglyphus* Mahunka, 1979 (preoc.)
- urn:lsid:zoobank.org:act:07025D27-E4A1-49CC-A386-B9D782167E01
- Coxal fields I–II entirely heavily sclerotized. Associated with ants.34
- 34 Propodosoma very long and broad, extending anteriorly approximately as far as tips of legs I; at least some dorsal hysterosomal setae very long and heavily pectinate; coxal fields with scale-like reticulation; subcapitular remnant elongate, at least 4 times longer than basal width; associated with army ants; Neotropical.
- *Pinoglyphus* Mahunka, 1978
- Propodosoma extending anteriorly over gnathosomal remnant but not to tips of legs I; dorsal hysterosomal setae very short and simple; coxal fields with rounded fovea; subcapitular remnant about as long as wide. Associated with ants; Nearctic, Neotropical. *Armacarus* Mahunka, 1979
- 35 Posterior lateral cuticular suckers of attachment organ laterally displaced, much closer to conoidal setae ps_2 than to ps_1 ; associated with termites; widespread.
- *Australhypopus* Fain & Friend, 1984 (including “*Acotyledon*” *formosani* and related species)
- Posterior lateral cuticular suckers of attachment organ normally positioned between conoidal setae ps_1 and ps_2 . Associated with termites; Palearctic, Nearctic, Neotropical. *Mahunkallinia* Eraky, 1999
- 36 Tarsus I with 3–4 setae thin and attenuate, longer than tarsus I; empodial claws I–II very elongate or not distinct. Associated with ants and termites; Palearctic, Nearctic, Neotropical. *Froriepiea* Vitzthum, 1919
- Tarsus I with some foliate setae very broad, no setae attenuate; empodial claws large. Associated with termites; Afrotropical, Australian.
- *Machadoglyphus* Mahunka, 1963
- 37 Attachment organ with all 4 conoidal setae in a transverse row completely posterior to median suckers.38
- Attachment organ with lateral conoidal setae more anterior than posterior conoidal setae, not completely posterior to median suckers.39

- 38 Coxal setae *1a*, *3a*, *4a*, *4b* represented by vestigial alveoli; external and internal scapular setae similar in length. In stored products, vertebrate nests; often phoretic in fur of mammals; widespread. *Neoacotyledon* Samsinak, 1980
- Coxal setae *1a*, *3a*, *4a* in the form of conoids, *4b* filiform; external scapular setae at least 5 times longer than internal scapulars. Associated with passalid beetles; Afrotropical, Neotropical. *Passaloglyphus* Mahunka & Samsinak, 1972
- 39 Genua III–IV distinctly longer than tibiae III–IV; tarsi III–IV often projecting at an angle from tibiae III–IV. *Cosmoglyphus* Oudemans, 1932 (= *Stunkardacarus* Fain, 1979, = *Rettacarus* Mahunka, 1978)
- Genua III–IV subequal to or shorter than tibiae III–IV; tarsi III–IV not projecting at an angle from tibiae III–IV. 40
- 40 Genu III with a short dorsal solenidion (σ) in addition to lateral seta. 41
- Genu III without solenidion. 45
- 41 Tibiae I–II much longer than corresponding genua. Holarctic.
..... *Viedebanttia* Oudemans, 1929 (Lycoglyphidae fam. nov.)
- Tibiae I–II similar in length or only slightly longer than corresponding genua. 42
- 42 Genu I with 2 solenidia, one long, the other very short. One species, *T. neotropicalis*. Associated with *Thectochlora* bees (Halictidae); Neotropical.
..... *Thectochloracarus* Fain, Engel, Flechtmann & OConnor, 1999
- Genu I with only 1 solenidion. 43
- 43 Coxal fields III closed, nearly contiguous medially; tarsi at least three times longer than wide; subcapitular remnant of gnathosoma at least twice as long as wide. Associated with phytotelmata, often phoretic on Syrphidae flies; Nearctic, Neotropical, Palearctic, Australian. *Naiadacarus* Fashing, 1974
- Coxal fields closed but widely separated medially; tarsi at most twice as long as wide; subcapitular remnant shorter, about as wide as long. Associated with Hymenoptera.
..... 44
- 44 Conoidal setae *ps*₂ of attachment organ positioned anterior to median suckers; posterior apodemes of coxal fields II well developed, connecting laterally with transverse median groove; dorsal and ventral body surfaces heavily sclerotized, smooth or with fine punctations. Associated with *Bombus* bees (Apidae); widespread.
..... *Kuzinia* Zachvatkin, 1941
- Conoidal setae *ps*₂ of attachment organ positioned lateral to median suckers; posterior apodemes of coxal fields II absent; without transverse median ventral groove; body weakly sclerotized, dorsum with rounded fovea. One species, *S. brasiliensis*; Neotropical. *Spinacaropus* Fain & Camerik, 1978
- 45 Empodial claws of pretarsi IV much smaller than claws of pretarsi I–III. One species associated with *Halictus* bees (Halictidae); South Africa.
..... *Halictacarus* Mahunka, 1975
- Empodial claws of pretarsi I–IV similar in form. 46
- 46 Propodosoma with external scapular setae *se* at least 4 times longer than internal scapular setae. Associated with termites; Palaearctic. *Terglyphus* Samšiňák, 1965 (= *Mahunkaglyphus* Eraky, 1998)
- External scapular setae *se* no more than 3 times longer than internal scapular setae; associations varied. 47

- 47 Solenidion ω_2 of tarsus I absent; posterior ventral setae gT of tibiae I–II and sometimes genua cG I–II usually filiform and distinctly barbed; internal vertical setae si usually long and barbed. Phoretic on fleas or carrion or grain insects.48
- Solenidion ω_2 of tarsus I present; posterior setae gT of tibiae I–II and genua cG I–II stout and spineform, smooth or barbed, or thin and unbarbed, never both filiform and barbed; internal vertical setae si unbarbed.53
- 48 Setae of coxal fields I and III in the form of conoids.50
- Setae of coxal fields I and III very fine and short or absent.49
- 49 Dorsal body surface with rounded depressions; setae of coxal fields I and III present but very short; solenidion ω_3 of tarsus I situated in middle of tarsus. On fleas, grain and carrion beetles, in grain, cosmopolitan.*Acarus* Linnaeus, 1758
- Dorsal body surface finely punctate, without rounded depressions; setae of coxal fields I & III absent; solenidion ω_3 positioned in basal third of tarsus. One species, *P. gerbilicola*, phoretic on fleas; North Africa.*Psyllopus* Fain & Beaucournu, 1993
- 50 Coxal apodemes III–IV ending freely; coxal fields III widely open medially; no posterior median longitudinal apodeme anterior to genital region. One species, *T. oregonensis* from fleas associated with mountain beavers; western Nearctic.*Trichopsyllopus* Fain & Baker, 1981
- Coxal apodemes III–IV fused to each other on both sides, closing coxal fields III; posterior median apodeme present anterior to genital opening.51
- 51 Dorsal idiosomal setae somewhat elongate and flattened; opisthonotal gland openings situated laterally at level of setae d_1 . One species, *B. acinacisetosus*, from a carabid beetle; far eastern Palaearctic.*Bembidioglyphus* Klimov, 1998
- Dorsal idiosomal setae very short, filiform; opisthonotal gland openings situated laterally at level of setae e_152
- 52 Dorsal surface smooth. Phoretic on fleas; Palaearctic, Nearctic, Afrotropical.*Paraceroglyphus* Fain & Beaucournu, 1973
- Dorsal surface with distinct punctations. One species associated with Crabronidae wasps, *Ectemnius* spp.; Palaearctic.*Lackerbaueria* Zachvatkin, 1941
- 53 External vertical setae ve present; bases of internal vertical setae vi usually separate, rarely contiguous.54
- External vertical setae ve absent; bases of internal vertical setae vi usually contiguous, rarely separate.63
- 54 Tarsus I with 9 setae (aa present at level of solenidion ω_2 or more apical).58
- Tarsus I with 8 setae (aa absent).55
- 55 Internal vertical setae vi elongate, at least 4 times longer than external verticals ve ; propodosomal shield with larger punctations at apex than posteriorly; coxal apodemes III meet in midline.56
- Internal vertical setae vi very short, only slightly longer than external verticals ve ; propodosomal shield with uniform small punctations; coxal apodemes III fused with apodemes IV, widely separate medially. One species, *I. brevis*, from small marsupial; New Guinea.*Irianopus* Fain, 1986
- 56 Seta ba II absent.*Reckiacarus* Kадzhaya, 1972
- Seta ba II present.57
- 57 Gnathosomal remnant elongate, more than 2.5 times longer than basal width; distance between trochanters I more than twice the maximum width of the gnathosomal remnant.*Rhizoglyphus* Claparede, 1869

- Gnathosomal remnant wider, not more than 1.5 times longer than wide; distance between trochanters I only slightly greater than maximum width of the gnathosomal remnant. *Mezorhizoglyphus* Kadzhaya, 1966 (= *Boletacarus* Volgin et Mironov, 1980)
- 58 Seta *e* of tarsus I simply foliate, similar in form to seta *f*; anterior cuticular suckers of attachment organ vestigial. One species, *N. segermanae*, phoretic on fleas; subantarctic islands. *Notiopsyllopus* Fain, 1977
- Seta *e* of tarsus I cylindrical with sucker-like apex, different in form from simply foliate seta *f*; anterior suckers of attachment organ normally developed. 59
- 59 Tarsus I attenuate, at least 6 times longer than basal width; proral setae (*p*, *q*), and ventral setae *la* and *ra* very thinly foliate; gnathosomal remnant elongate, subcapitular remnant longer than femur I. One species, *L. longipes*, from caves; Australia. *Lowreyacarus* Fain, 1986
- Tarsus I normally developed, less than 5 times longer than basal width; proral setae and setae *la* and *ra* more broadly foliate (or proral setae small spines); gnathosomal remnant not elongate, subcapitular remnant generally shorter than femur I. 60
- 60 Coxal apodemes III–IV completely fused with median apodeme; attachment organ large, with striated posterior membrane; tarsus I with seta *aa* positioned between levels of solenidia ω_2 and ω_3 . Palearctic. *Carabidobius* Volgin, 1953
- Coxal apodemes III–IV fused with each other but usually slightly separated medially; attachment organ without striated posterior membrane. 61
- 61 Proral setae (*p*, *q*) on all legs are small spines. *Lycoglyphus* gen. nov. (Lycoglyphidae fam. nov.)
- Proral setae (*p*, *q*) on all legs foliate, long. 62
- 62 Seta *aa* on tarsus I more apical than solenidion ω_2 , positioned approximately at level of solenidion ω_3 (exception *S. geotruporum*); fields of solenidia ω_1 and ω_3 are separated; seta *ba* II distant from ω_1 , filiform. Widespread in many habitats. *Sancassania* Oudemans, 1916 (= *Caloglyphus* Berlese, 1923), *Psyllacarus* Fain, Bartholomaeus, Cooke & Beaucournu, 1990 (= *Ctenocolletacarus* Fain, 1984 syn. nov., = *Dynastopus* Fain, 1978 syn. nov. and = *Omentopus* Fain, 1978 syn. nov.)
- Seta *aa* on tarsus I at level of solenidion ω_2 ; fields of solenidia ω_1 and ω_3 connected; seta *ba* II closed to ω_1 , spiniform. *Obelacarus* gen. nov. (Lycoglyphidae fam. nov.)
- 63 Dorsal hysterosomal setae in the form of very large spines or long and somewhat lanceolate; conoidal coxal setae large and somewhat elongate. Associated with bees. 64
- Dorsal hysterosomal setae usually short and filiform, rarely elongate and filiform; coxal setae small, rounded conoids or filiform. 65
- 64 Gnathosoma deeply cleft into a V-shape; dorsal setae in the form of very large spines. One species, *K. mexicanus*, from Hymenoptera; Mexico. *Konoglyphus* Delfinado & Baker, 1974
- Gnathosomal remnant small, not cleft into a V-shape; scapular setae and anterior hysterosomal setae long and somewhat lanceolate. One species, *N. mammilata*, associated with *Archianthidium* (Megachilidae); SE Europe, W Asia. *Neohorstia* Zachvatkin, 1941
- 65 Supracoxal seta *scx* of leg I thick, bifurcate apically; spoon-like seta *e* of tarsus I greatly expanded apically, wider than tarsal apex; tarsus I less than 4 times longer than wide. 66

– Supracoxal seta of leg I simple, filiform, not bifurcate apically; seta *e* of tarsus I usually only slightly expanded apically, or, if wider than tarsal apex, then tarsus 4–5 times longer than basal width.67

66 Coxal apodemes III fused with apodemes IV and with median apodeme; empodial claws short, at most equal to 1/5 length of tarsus I; seta *e* of tarsus II short, filiform; tibiae I–II with 2 ventral setae. In decaying wood, phoretic on Coleoptera; Holarctic.*Hortacarus* Mahunka, 1978 (= *Fagacarus* Fain & Norton, 1979 syn. nov.)

– Coxal apodemes III fused with apodemes IV on each side but not fused together medially; empodial claws long, at least half the length of tarsus I; seta *e* of tarsus II foliate or spoon-like; tibiae I–II with 1 ventral seta. Associated with honeybees (*Apis* spp.); Old World.*Lasioacarus* Kadzhaya & Sevastianov, 1969

67 Tarsus I 4–5 times longer than wide, with ventral seta *wa* strongly thickened, heavily barbed and extending to tarsal apex; seta *hT* of tibiae I–II also strongly thickened, and heavily barbed; on temperate forest insects and myriapods; Holarctic.*Kadzhajania* Sevastianov, 1969

– Tarsus I less than 4 times longer than wide, with ventral seta *wa* short, simple, unbarbed; seta *hT* of tibiae I–II also simple, unbarbed; widespread in many habitats.*Schwiebea* Oudemans, 1916 (probably = *Aellenella* Manunka, 1977, = *Mauracarus* Mahunka, 1978, = *Robinisca* Zachvatkin, 1941, = *Rodionovia* Zachvatkin, 1941, = *Setoglyphus* Mahunka, 1979, = *Troupeauia* Zachvatkin, 1941)

Notes: “Inert” deutonymphs of *Acarus* and *Stereoglyphus* not included in key.

Deutonymphs are unknown in the genera *Acarotalpa* Volgin, 1966, *Aleuroglyphus* Zachvatkin, 1940, *Apiacarus* Volgin, 1974, *Askinasia* Yunker, 1970, *Bromeliaglyphus* Nesbitt, 1985, *Diphtheroglyphus* Nesbitt, 1950, *Ewingia* Pearse, 1929, *Hoogstraalacarus* Yunker, 1970, *Kanekobia* Fain, Yunker, van Goethem et Johnston, 1982, *Madaglyphus* Fain, 1971, *Neotropacarus* Baker, 1985, *Paulacarellus* Fain, 1976, *Pontoppidania* Oudemans, 1923, *Tyroborus* Oudemans, 1924, *Tyrolichus* Oudemans, 1924, *Volginia* Kadzhaya, 1969, *Platyglyphus* Kurosa, 1976, *Gaudiella* Atyeo, Baker and Delfinado, 1974, *Partamonacoptes* Fain and Rosa, 1983, *Bulacarus* Fan and Zhao, 2024, *Suidasia* Oudemans, 1905, *Namibacarus* Fain, Coineau and André, 1993, *Neosuidasia* Ranganath and ChannaBasavanna, 1983, *Glycacarus* Griffiths, 1977, *Scatoglyphus* Berlese, 1913.

The genus *Troxocoptes* Fain & Philips, 1983, originally described in the Acaridae, warrants separate family placement.

Fainoglyphus Mahunka, 1979 is a junior homonym of *Fainoglyphus* Atyeo & Gaud, 1977 and is replaced here by *Sandoroglyphus* nom. nov. The new name is derived from the original author name Sándor Mahunka.

4. Discussion

Phylogeny-based classification provides more than a practical framework for organizing biological diversity into delimited and diagnosable units; when grounded in a robust methodology, it seeks to recognize monophyletic groups that reflect natural evolutionary relationships [114–117]. Such natural groups are especially valuable because biologically meaningful traits—ranging from host associations and vector capacity to habitat preferences [118–125], suitability for biocontrol [126–129] or as factitious prey for mass rearing of predatory mites [84], and tolerance to environmental stressors [130–133]—tend to be distributed non-randomly across lineages. Consequently, sound classification enhances

the predictive power of comparative analyses and depends critically on representative taxon sampling.

Our results reinforce the growing consensus that several central lineages of Astigmata, most notably the superfamily Acaroidea and the traditionally delimited family Acaridae, do not represent monophyletic units [6,8,10,11]. Families historically grouped within Acaroidea on morphological grounds, including Lardoglyphidae, Suidasiidae, and Gaudiellidae, appear in disparate regions of molecular phylogenetic trees, indicating that the similarities used to unite them are likely convergent or plesiomorphic. Likewise, Acaridae is consistently recovered as polyphyletic, resolving into two major well-supported clades corresponding to Rhizoglyphidae *sensu novo* (traditional Rhizoglyphidae excluding Acotyledonini) and Acaridae *sensu novo* (Acarini together with Tyrophagini and Acotyledonini). It should be noted, however, that some published phylogenies [11,49] rely on mitochondrial and 18S rRNA sequences of *Sancassania* or *Cosmoglyphus* that were misidentified as *Rhizoglyphus* (see Results); topological inferences involving these taxa should therefore be interpreted accordingly. Several additional lineages, such as Horstiinae and Cerophagini, are also recovered as distinct entities. Notably, highly divergent crab-associated mites traditionally treated as “Ewingidae” [134,135] are consistently nested within Rhizoglyphinae, in agreement with morphology-based phylogenetic interpretations, despite their striking autapomorphies [5]. Our phylogeny recovered Lycoglyphidae within a large well-supported cluster (100/100) that also includes Acaridae *sensu novo*, Rhizoglyphidae *sensu novo* (including Ewingidae), Pontoppidaniidae *sensu novo* (*Pontoppidania* and *Paulacarellus*), Cerophagidae *sensu novo* (including *Cerophagus*, *Sennertionyx*, and *Cerophagopsis*), Bulacaridae, Horstiidae stat. nov., Chortoglyphidae (formerly in Glycypagoidea), Echimyopodidae (formerly in Glycypagoidea), Histiotomatidae (formerly in Histiotomatoidea), and Canestriniidae (formerly in Canestrinioidea). A few genera (*Neotropacarus* and *Umakefeq*) were placed outside their traditionally expected relationships. Hereafter, we refer to this assemblage as the AR cluster, representing the core families Acaridae and Rhizoglyphidae, together with additional related lineages (Figure 1). One of the more counterintuitive outcomes of molecular analyses is that Acaridae *sensu novo*—a lineage that is strongly supported by molecular data—is diagnosed largely by character states long regarded as plesiomorphic, such as the presence of setae *aa* on tarsus I (Figure 1). This pattern highlights the limitations of inferring phylogenetic relationships solely from perceived character polarity and highlights the necessity of reassessing morphological evidence in the light of independent molecular hypotheses.

The position of Histiotomatoidea remains another major point of uncertainty. Some molecular phylogenies support this primarily filter feeding lineage as sister to the remaining non-schizoglyphid Astigmata [55,57,58], whereas others recover histiotomatoids as a derived group that originated within the AR cluster [6,9,53] or sister group to the AR cluster [8,10,11]. In our analyses, Histiotomatidae is recovered within the AR cluster but exhibits a conspicuously long branch (Figure 1). This raises the possibility that some of the character-state incongruences and its unusual placement reflect long-branch effects rather than true phylogenetic affinity, suggesting that genome-scale data combined with analytical approaches designed to mitigate long-branch attraction will be essential for resolving its position. Within the AR cluster, two lineages—Acaridae *sensu novo* and Histiotomatidae—exhibit pronounced long branches. In Histiotomatidae, this pattern is accompanied by character-state incongruences and an unusual phylogenetic placement, which may reflect long-branch artifacts. These results suggest that the position of Histiotomatidae could shift with denser taxon sampling, genome-scale data, and analytical approaches specifically designed to mitigate long-branch attraction. In contrast, although Acaridae *sensu novo* also forms a long branch, its monophyly is strongly and consistently supported, even if its

precise placement within the AR cluster remains sensitive to additional data. In our phylogeny, two previously unrecognized lineages exhibit pronounced ecological specialization: Pontoppidaniidae, occurring in intertidal seaweed wrack, and Cerophagidae, associated with bees. The strong ecological restriction of each group is consistent with, and lends additional support to, their recovery as monophyletic lineages. Lycoglyphidae were recovered in a cluster with Chortoglyphidae and Horstiidae, albeit with low to moderate support. Within Lycoglyphidae, the two sampled genera, *Obelacarus* and *Viedebanttia*, were inferred as closely related but did not form a monophyletic group. This apparent non-monophyly is most plausibly explained by missing data, specifically the absence of EF1 α sequences for *Viedebanttia*. Importantly, the presence of two cheliceral setae in Lycoglyphidae, rather than representing a plesiomorphic retention from ancestral Oribatida, is more plausibly interpreted as a derived synapomorphy that arose through character-state reversal. This interpretation indicates the need to consider both homology and convergent or reversed evolution when evaluating morphological traits in light of molecular phylogenies.

Within the AR cluster, all the family-level lineages exhibit retroconjugate (reverse) mating, with the sole exception of Histiostomatidae. This exception further emphasizes the distinctive evolutionary trajectory of histiostomatids and may reflect both their semi-aquatic ecology and the influence of long-branch artifacts. Outside the AR cluster, taxa with proconjugate mating form two groups: a large assemblage comprising Hemisarcopitoidea + Glycyphagidae and a smaller independent cluster including Rosensteiniidae and Aeroglyphidae. All the remaining astigmatan lineages, including Psoroptidia, exhibit retroconjugate mating. Collectively, these results indicate that mating position is a phylogenetically structured character and may represent a fundamental trait that is useful for defining higher-level groups within Astigmata. However, further work—particularly expanded taxon sampling and genome-scale phylogenetic analyses—is required to assess the robustness of this pattern and to achieve a more natural classification of the group.

5. Conclusions

Our detailed morphological description and phylogenetic analyses provide an up-to-date reassessment of the relationships within Astigmata, integrating densely sampled molecular data with morphological and ecological information. The results confirm that several historically recognized lineages, including Acaroidea and Acaridae, are not monophyletic, potentially indicating the limitations of morphology-based classifications alone. Molecular data reveal well-supported clades corresponding to Acaridae *sensu novo*, Rhizoglyphidae *sensu novo*, and several smaller lineages, including Horstiidae and Cerophagidae, while highly divergent taxa such as “Ewingidae” are consistently placed within Rhizoglyphinae *sensu novo*, corroborating some morphology-based hypotheses despite their extreme autapomorphies. Our analysis further resolves the position of Lycoglyphidae, recovered within a well-supported cluster—the AR cluster—together with Acaridae *sensu novo*, Rhizoglyphidae *sensu novo*, and several other families. The ecological specialization of lineages such as Pontoppidaniidae (intertidal seaweed wrack) and Cerophagidae (bee-associated) reinforces their monophyly and demonstrates the predictive value of ecological traits in phylogenetic inference (albeit with limitations). Within Lycoglyphidae, the presence of two cheliceral setae is better interpreted as a derived synapomorphy arising via character-state reversal rather than ancestral retention. Furthermore, based on our tree, mating position emerges as a phylogenetically structured character, with retroconjugate (reverse) mating pervasive in the AR cluster and proconjugate mating restricted to certain external lineages.

Collectively, these results demonstrate the power of integrating molecular, morphological, and ecological evidence to redefine higher-level relationships in Astigmata, support

the recognition of novel lineages, and clarify patterns of trait evolution. Future studies incorporating denser taxon sampling, complete genomic datasets, and rigorous analytical methods are essential to resolve the remaining uncertainties, particularly concerning long-branch lineages, and to achieve a robust natural classification of this ecologically and economically important group.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/taxonomy6010018/s1>, Figure S1: Maximum likelihood tree of astigmatid mites (Astigmata) and outgroups (Oribatida s. str.) inferred in IQ-TREE.

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