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ONTOGENY AND SYSTEMATICS OF THE GENUS *CEROPHAGUS* (ACARI: GAUDIPELLIDAE), MITES ASSOCIATED WITH BUMBLEBEESBarry M. O'Connor¹

ABSTRACT

Nymphs and adults of *Cerophagus nearcticus* n. sp. are described from the nest of *Bombus terricola occidentalis* in California and phoretic associations with *B. impatiens* in Michigan and New York. On the basis of adult morphology, the genus *Cerophagopsis* is removed from synonymy with *Cerophagus* and retained in the family Acaridae, while *Cerophagus* is transferred to the family Gaudiellidae. The genus *Rhytoglyphus* is considered a junior subjective synonym of *Cerophagopsis*. The genera of Gaudiellidae are noted and the genus *Trigonacoptes* is considered a junior subjective synonym of *Gaudiella*.

Descriptive taxonomy, systematics and phylogeny reconstruction for many groups of astigmatid mites have been hampered by their dimorphic life cycles. Deutonymphs are specialized for dispersal and/or surviving adverse conditions and typically have a morphology quite unlike that of the other instars. Taxa have usually been based on only the adult or the deutonymph but not often both. In order to positively correlate the heteromorphic life stages, it is best to rear the species in pure culture. A second method of absolute correlation is to obtain all instars of a species as pharate individuals through collection methods such as hand sorting or flotation of substrate materials. Simple association in the same habitat is not usually deemed sufficient to prove conspecificity following the experiences of early workers who incorrectly associated deutonymphs and adults in this fashion (e.g. Michael 1886, corrected by Fain 1969). Often, once one species in a genus has been positively associated through rearing or collection of pharate instars, subsequent associations of related taxa may be assumed through simple co-occurrence in the same habitat sample, however, these still do not prove conspecificity.

A second difficulty in studying the phylogeny of the Astigmata is the problem of convergent evolution. Most commonly, deutonymphs of unrelated taxa may converge in both progressive and regressive characters when they use similar hosts or other dispersal means (e.g. "inert" forms). The case described in this paper contains elements of all of these difficulties in dealing with systematics of the Astigmata.

The genus *Cerophagus* was established by Oudemans (1904) for the species *Glycyphagus bomborum* Oudemans, 1902, which had been described from deutonymphs collected from *Bombus terrestris* L. in the Netherlands. Vitzthum (1912) described *Cerophagus gracilis*, also from *B. terrestris*, in Germany. Zakhvatkin (1941) placed both nominal species names in synonymy

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with *Hypopus granulatus* Dujardin, 1849, originally described from *Bombus lapidarius* L. in France. He also reported specimens of this species from *Bombus argillaceus* (Scopoli), but without specific locality information. All of these descriptions dealt only with deutonymphal morphology; the post-deutonymphal instars have not been described for this species.

Fain and Heard (1987) described *Cerophagus trigona* from the nest of a meliponine bee, *Trigona carbonaria* Smith, in Australia. Numerous adults and nymphs were recovered along with one deutonymph that was assumed to belong to this species by association in the same habitat. This deutonymph was similar to those of the two species previously described in the genus *Cerophagopsis* Zakhvatkin, 1941: the type species, *C. skorikovi* Zakhvatkin, 1941, described from *Megachile döderleini* Friese (= *Chalicodoma sculpturalis* (Smith)) from Japan, and *C. furcata* Fain, 1974, described from a single specimen collected from *Bembex borrei* Handlirsch and later a second specimen from *Megachile* sp., both from Vietnam (Fain and Heard, 1987). On the basis of similarities in the deutonymphal morphology of their new species with *C. granulatus*, Fain and Heard placed *Cerophagopsis* in synonymy with *Cerophagus*.

Contemporaneous with the publication of Fain and Heard (1987), Potter and Olson (1987) described a new genus and species, *Rhyroglyphus indicus*, from adult mites collected in stored food products imported from India into the United States. On the basis of the similar adult morphologies of *R. indicus* and *C. trigona*, Fain (1988) placed *Rhyroglyphus* in synonymy with *Cerophagus*.

Over the past few years, I have examined a number of specimens which shed light on the ontogeny and systematics of this group of mites. Of particular importance are two collections which include pharate individuals belonging to a new species whose deutonymphal morphology is very close to *Cerophagus granulatus*, the type species of the genus. This positive correlation between adult and deutonymphal morphologies led me to hypothesize on the basis of the adult morphology, that the genus *Cerophagus* (*sensu stricto*) is more closely related to the family Gaudiellidae than the Acaridae (O'Connor, 1988). The purpose of this paper is to describe the known ontogeny of this new species, use detailed morphological comparisons to test the hypothesis of a relationship between *Cerophagus* (*s.s.*) and *Cerophagopsis*, and to discuss the phylogenetic relationships of these taxa. In the following description, signatures for idiosomal setae follow Griffiths et al. (1990). All measurements are given in micrometers (μm).

Cerophagus nearcticus new species

Female: (Figs. 1-12) Dorsum (Fig. 1). Body of single known female almost circular in outline, idiosomal length excluding copulatory tube 427, width 380. Except for prodorsal and supracoxal sclerites, cuticle unsclerotized, mammilated with raised rounded protuberances over entire surface except on and lateral to prodorsal sclerite. Prodorsal sclerite about as long as wide, with heavy ridges in posterior half. Sejugal furrow absent. Dorsal setae of moderate length, strongly bipectinate, on elevated tubercles bearing rounded mammillations, except setae *ve* evenly barbed and not elevated, and *scx* deeply bifurcate, with each fork bearing relatively long basal barb. Setae *ve* on anterior lateral corners of prodorsum, *vi* on anterior edge of prodorsal sclerite. External scapular setae (*sce*) somewhat more anterior than internal scapulars (*sci*). Notogastral setation complete; setae *h₃* situated on lateral margins of sclerotized copulatory tube. Measurements of idiosomal setae given in Table

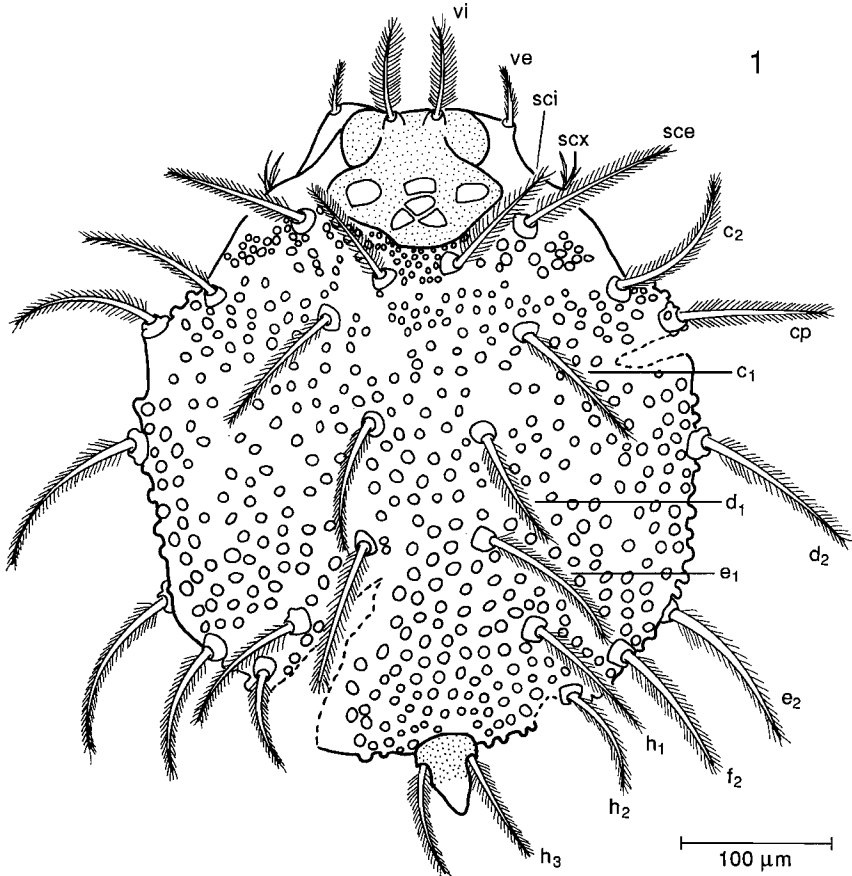


Figure 1. *Cerophagus nearcticus*, female, dorsum.

1. Due to complex cuticular structure, cupules could not be observed. Opisthotal gland openings (*gla*) ventro-lateral to setae e_2 .

Venter (Fig. 2). Ventral surface partially obscured by folded posterior legs (legs reconstructed in lateral view in Fig. 2). Cuticle mammilated laterally and posteriorly, smooth in coxal area and between legs IV and anus. Coxal apodemes I broadly fused medially; anterior apodemes of coxal fields II broad, posterior apodemes more narrow, fused medially with transverse sejugal apodemes; apodemes of coxal fields III-IV arched. All ventral body setae of coxal ($1a$, $3a$, $3b$, $4a$) and genital (g) origin strongly barbed. Ovipore positioned between coxal fields II-IV; due to obscuring structures, genital papillae were not observed. Notogastral setae c_3 similar in form to dorsal setae and likewise with elevated alveoli, positioned between and lateral to coxal fields II-III. Anus displaced anteriorly from posterior edge of body by a distance greater than the length of the anus. Paraproctal setation consisting of six pairs of

Table 1. — Measurements (in mm) of idiosomal setae in *Cerophagus nearcticus*.

Seta	Female	Protonymph
<i>vi</i>	49	33
<i>ve</i>	30	18
<i>sci</i>	85	40
<i>sce</i>	103	40
<i>scx</i>	28	15
<i>c₁</i>	87	40
<i>c₂</i>	93	40
<i>cp</i>	99	37
<i>c₃</i>	48	21
<i>d₁</i>	89	42
<i>d₂</i>	117	46
<i>e₁</i>	100	53
<i>e₂</i>	115	42
<i>f₂</i>	87	42
<i>h₁</i>	90	40
<i>h₂</i>	73	40
<i>h₃</i>	67	18
<i>ps₁</i>	63	11
<i>ps₂</i>	88	11
<i>ps₃</i>	44	11
<i>ad₁</i>	43	—
<i>ad₂</i>	40	—
<i>ad₃</i>	39	—
<i>1a</i>	46	22
<i>3a</i>	35	16
<i>3b</i>	30	—
<i>4a</i>	27	—
<i>g</i>	23	6

setae, four pairs of thin, bipectinate setae flanking anus (*ps₃* and *ad₁₋₃*), and two pairs of setae (*ps₁₋₂*) similar in form to dorsal setae positioned on mammilated tubercles posteriorly and laterally from anus. Posterior end of body with a sclerotized copulatory tube bearing copulatory opening subapically on ventral surface.

Gnathosoma. Chelicerae (Fig. 3) chelate, fixed digit with three teeth, moveable digit with one median and one apical tooth; paraxial face with globose seta above base of moveable digit and short, pointed process and broadly rounded process more proximal on cheliceral shaft. Subcapitulum (Fig. 4) broadly trapezoidal, ventral subcapitular setae filiform; palpal supracoxal setae short and somewhat spinelike. Rutella rounded apically, dorsoapical teeth not visible. Palps (Fig. 4) with unique structure: basal palpal segment very wide basally, bearing 1 dorsal and 1 ventral filiform setae; distal palpal segment attenuated into blunt process bearing 1 dorsal seta and very elongate solenidion. The elongate process may be hollow and possibly homologous with button-shaped ventral eupathidium at apex of palp in other acaroid mites.

Legs (Figs. 5–12). All legs stout, well-sclerotized; legs I–II with sclerotized ridges on femora, genua and tibiae. Setation as follows: Trochanters I–III each with a strongly barbed seta (*pR*, *sR*); femora I, II and IV with a strongly bipectinate seta (*vF*, *wF*), *vF* I–II situated on tubercles; genua I–II with setae *cG* and *mG* and genu III with seta *nG* bipectinate; tibiae I–II with setae *gT* and *hT* and tibiae III–IV with setae *kT* bipectinate; tarsi with 12–12–10–10

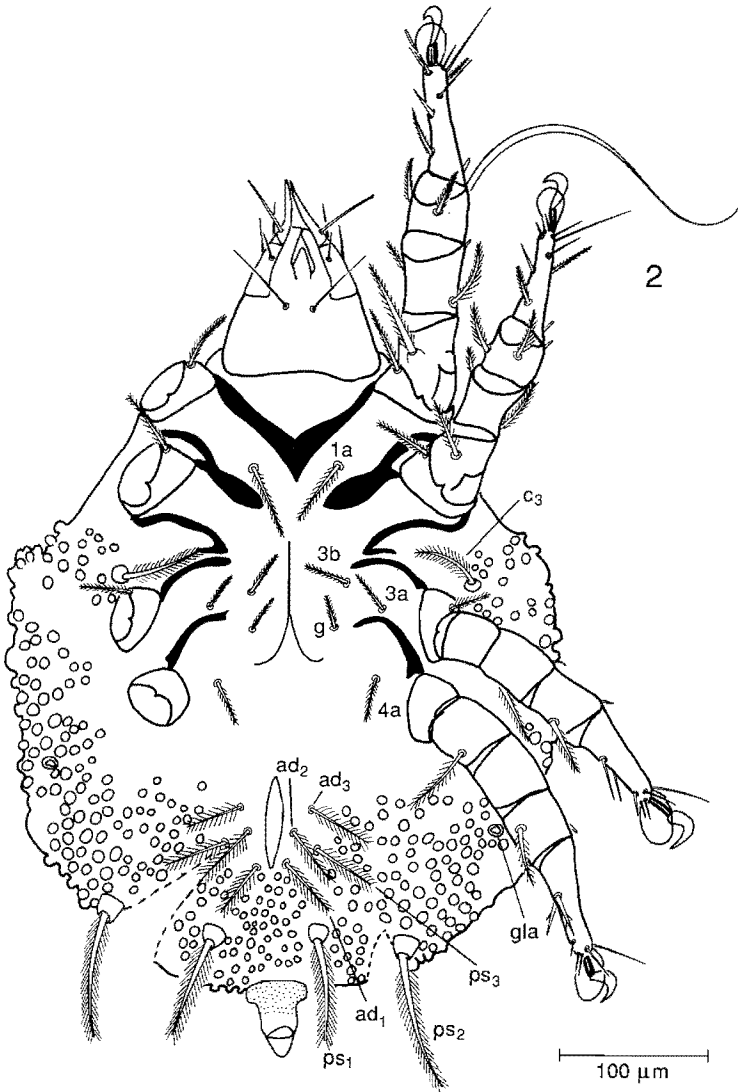
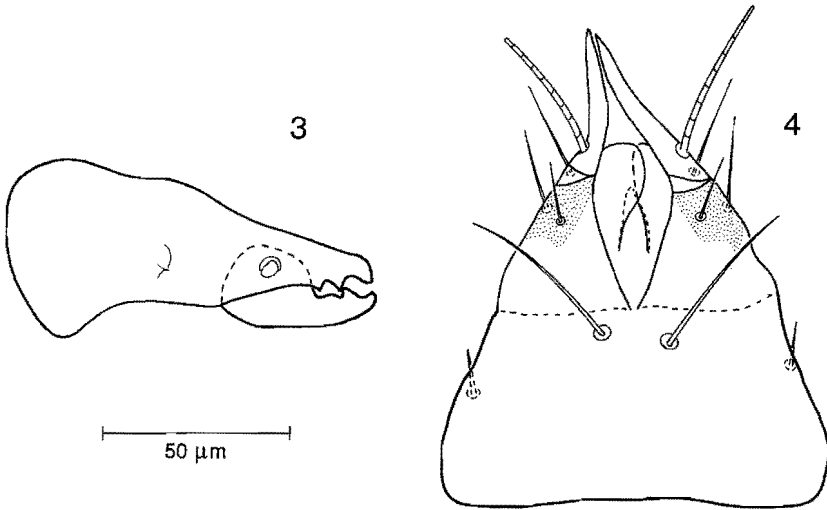


Figure 2. *Cerophagus nearcticus*, female, venter.

setae respectively, seta *aa* absent from tarsus I; setae of tarsi I-II generally similar in form and position, setae *wa* and *ba* bipectinate, other setae filiform or spine-like; tectal setae (*e* and *f*) similar in length and form; proral setae (*p* and *q*) larger than unguinal setae (*u* and *v*); seta *ba* II stouter than *ba* I; setae of tarsi III-IV generally similar in form and position except setae *r* and *w* IV stouter, bearing few barbs while those of tarsus III thinner, smooth. Soleni-



Figures 3-4. *Cerophagus nearcticus*, female. 3. Chelicera. 4. Gnathosoma, ventral.

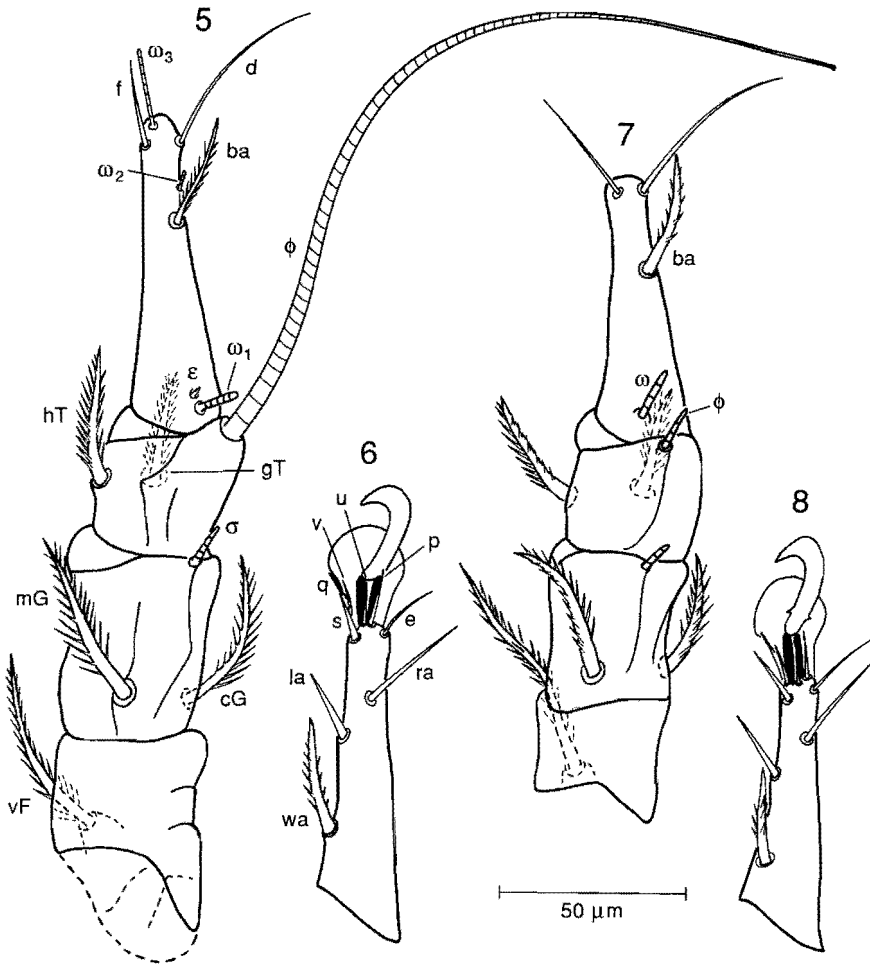
dia: genua I-III each with one solenidion σ , posterior σ absent from genu I; tibiae I-IV each with solenidion ϕ , ϕ I extremely elongate (length 209) and positioned on tubercle, other tibial solenidia very short (lengths 8-11); tarsus I with solenidion ω_1 basal, ω_2 very short, in apical $\frac{1}{5}$ of tarsus distal to seta *ba*, ω_3 apical; tarsus II with solenidion ω basal. Tarsus I with famulus ϵ small and spinelike, adjacent to solenidion ω_1 . Pretarsi I-IV similar, consisting of large, stout empodial claw connected to tarsal tendons by stout condylophores; ambulacrum consisting of broadly rounded stalk and ventrally directed disc below empodial claw.

Male: One male specimen examined, in very poor condition, with all dorsal setae missing except *vi*; legs I-II broken and positioned away from body on slide; legs III-IV crushed against ventral surface, obscuring most details of ventral surface and legs.

Body almost circular in outline, idiosomal length 272, width 252. Dorsal body cuticle entirely sclerotized and darkly tanned, with mammillations as in female. Form of setae *vi* as in female; tubercles bearing setal alveoli and few broken setal remnants suggest other dorsal setae similar to female's. Ventral surface largely obscured, coxal setae *1a* barbed, other ventral setae not visible; genital region not visible. Legs I-II similar to female's in form and setation; legs III-IV may be stouter than in female; tarsus IV distinctly shorter and stouter than female's, bearing two expanded, sucker-like setae (presumably *d* and *e*) on lateral face.

Tritonymph: One specimen observed, pharate within deutonymphal cuticle. Body form, cuticle, notogastral setae and legs as in female. Genital papillae visible, short, two-segmented, with rounded apices. Paraproctal setation consisting of three pairs of setae, 1 pair (*ps₃*) thin, bipectinate, and flanking anus, 2 pairs (*ps₁₋₂*) enlarged, flattened, almost palmate in form, positioned as in female. Coxal and genital setae filiform, unbarbed.

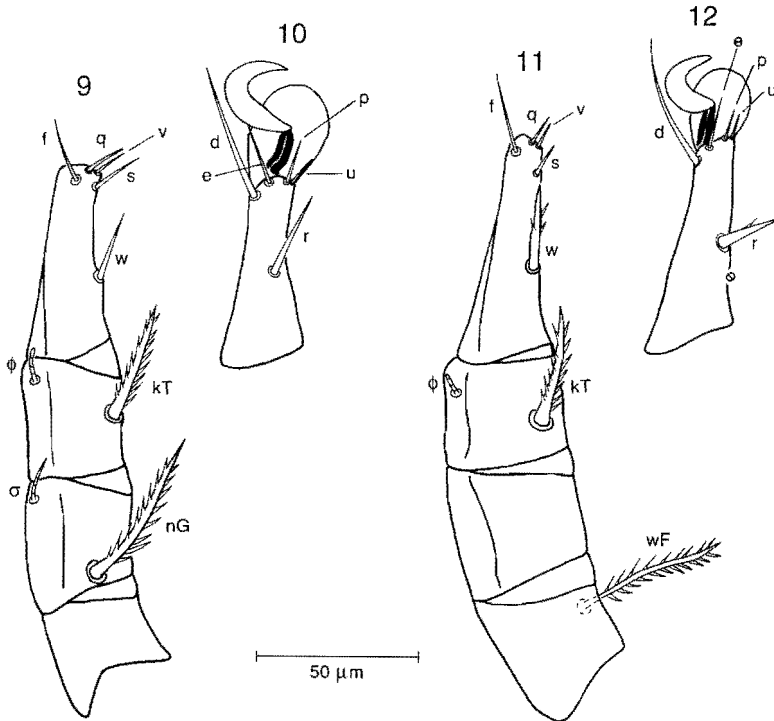
Deutonymph: (Figs. 13-22). Body length of holotype, mean and range of 6 specimens 229, 231 (227-235); width 173, 175 (173-180). Gnathosoma consist-



Figures 5-8. *Cerophagus nearcticus*, female, legs. 5. Leg I, dorso-lateral. 6. Tarsus I, ventro-lateral. 7. Leg II, dorsal. 8. Tarsus II, ventral.

ing of deeply cleft subcapitulum bearing palpal supracoxal setae dorsally; palps distinct, each bearing dorsal seta and elongate, terminal solenidion.

Dorsum (Fig. 13). Propodosoma and hysterosoma each covered by large sclerite bearing pattern of deep punctations; sclerites separated by sejugal furrow. Propodosoma bearing short, filiform scapular setae (*sci*, *sce*); vertical setae not on sclerite, visible ventrally. Supracoxal setae (*scx*) of legs I similar to other dorsal setae. Hysterosomal sclerite with complete set of short, filiform, notogastral setae (except *c₃*, positioned ventrally). Cupules *ia* visible between setae *c₁* and *cp*, other cupules ventrally positioned. A strong longitudinal dorsal apodeme underlies hysterosomal sclerite posteriorly.



Figures 9-12. *Cerophagus nearcticus*, female, legs. 9. Leg III, dorso-lateral. 10. Tarsus III, ventro-lateral. 11. Leg IV, dorso-lateral. 12. Tarsus IV, ventro-lateral.

Venter (Fig. 14). Cuticle unsclerotized except where dorsal hysterosomal sclerite extends ventrally along posterior margin. Coxal apodemes well developed, all connected except posterior apodemes of coxal fields IV. Anterior apodemes of coxal fields I extend dorsally around gnathosoma to body apex. Internal vertical setae (*vi*) positioned apically, external vertical setae (*ve*) positioned lateral to gnathosoma, above extensions of coxal apodemes I. Coxal setae *1a* and *3b* filiform; setae *3a* and *4a* absent, represented by vestigial alveoli. Genital setae *g* short and filiform, flanking genital opening. Genital papillae two segmented, apical segment attenuate. Attachment organ relatively small, bearing well developed anterior and median suckers, two pairs of conoidal setae and five weakly developed cuticular suckers; pair of vestigial alveoli visible anterior to median suckers. Pair of cupules (probably *im*) positioned laterally between bases of legs III-IV; cupules *ih* positioned on lateral margins of attachment organ.

Legs (Figs. 15-22). Legs I-IV equally developed, segmental proportions similar to other stages. Setation unusual in that tarsal setae *s* I-II and *ba* I are retained. Setae: tarsi 9-9-8-8, setae of tarsi I-II similar in form and position: *ba* filiform, anterior dorsal in middle of segment; *d* relatively short and filiform, posterior dorsal in apical third of segment; pair *e* and *f* foliate, dorso-apical; *wa* filiform, midventral in proximal third of segment; *la* and *ra* foliate,

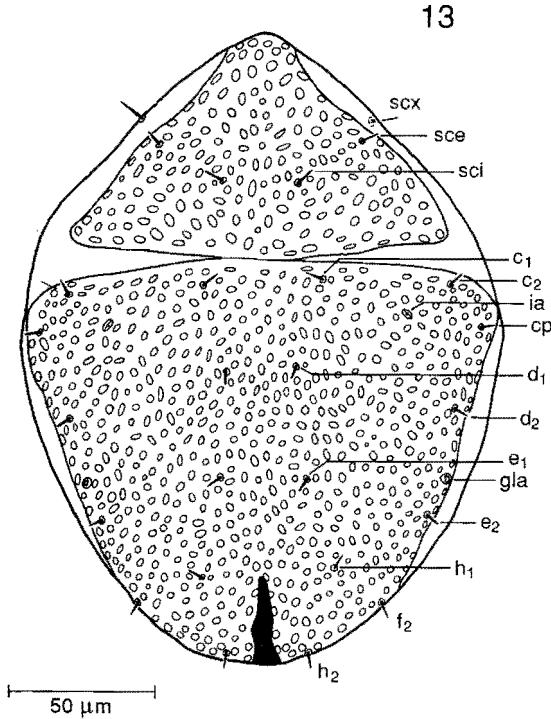


Figure 13. *Cerophagus nearcticus*, deutonymph, dorsum.

somewhat anterior to *wa*; seta *q* short and foliate, anterior ventral at apex of segment; seta *p* represented by vestigial alveolus paired with seta *q*; seta *s* filiform, midventral, slightly subapical. Tarsus III with 3 dorsal setae: *d* filiform, *e* and *f* foliate; ventrally with five setae: foliate setae *r* and *w* in basal half of segment, foliate setae *p* and *q* apical, and filiform seta *s* subapical. Tarsus IV similar to tarsus III except setae *r* and *w* filiform. Tibiae 2-2-1-1, setae *gT* and *hT* I-II and *kT* III-IV filiform. Genua 2-2-1-0, setae *mG* and *cG* I-II and *nG* III filiform. Femora 1-1-0-1, setae *vF* I-II and *wF* IV filiform. Trochanters 1-1-1-0, setae *pR* I-II and *sR* III filiform. Solenidia: tarsi 3-1-0-0, tarsus I with ω_1 basal, ω_2 and ω_3 in apical half of segment; tibiae 1-1-1-1, ϕ I greatly elongate, ϕ II-IV much shorter; genua 1-1-1-0, solenidia σ becoming progressively shorter posteriorly. Famulus ϵ short, spine-like, adjacent to solenidion ω_1 on tarsus I.

Pretarsi with empodial claws strongly hooked, base of claw with flattened medial expansion; ambulacral stalks relatively short but distinct, no obvious ambulacral discs; paired condylophores short and strongly developed, visible within each ambulacrum.

Protonymph: Two specimens observed, one in poor condition, containing a parate deutonymph. Body form, cuticle and notogastral setae (except h_3) as in female. Setae h_3 positioned ventrally, shorter and thinner than in female

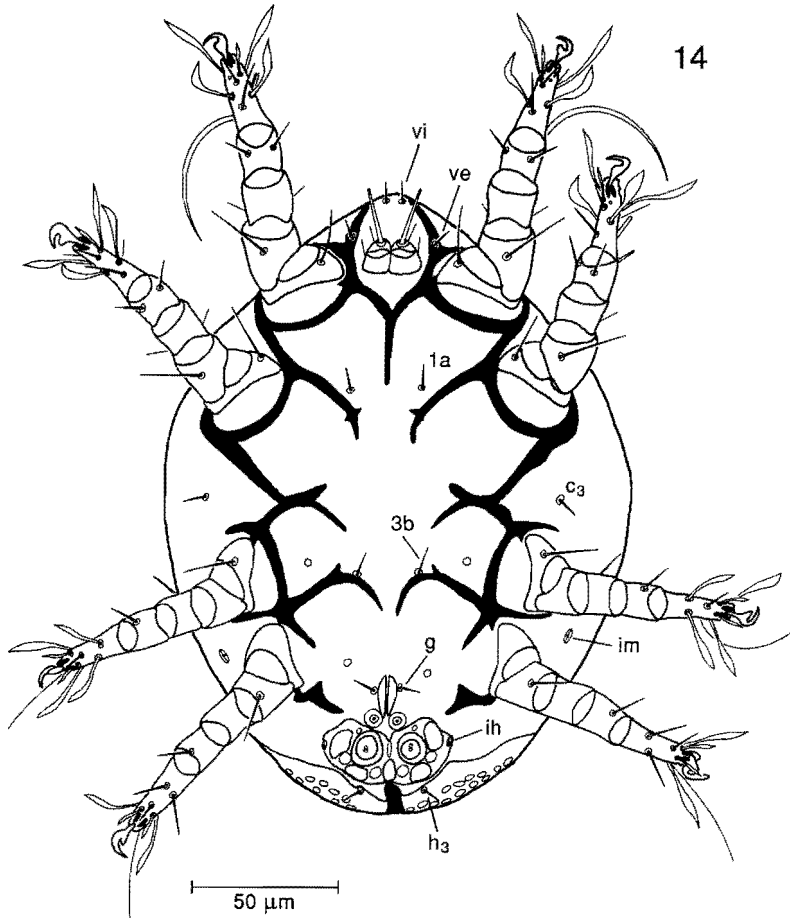
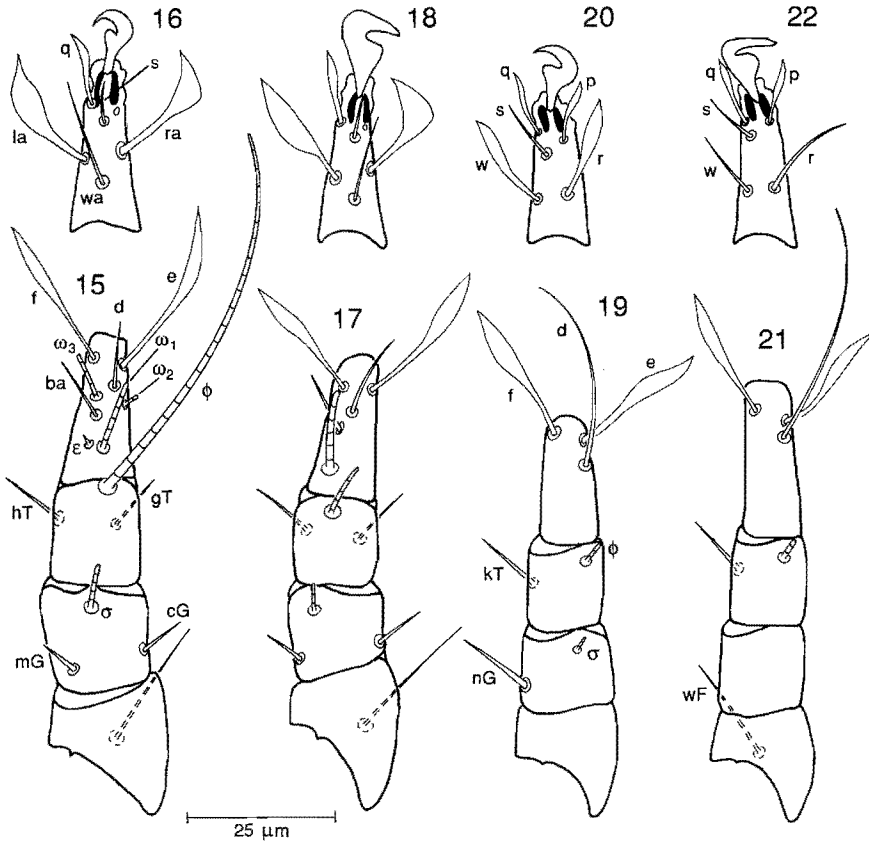


Figure 14. *Cerophagus nearcticus*, deutenymph, venter.

and tritonymph. Paraproctal setation consisting of 3 pairs of PS setae, all thin, bipectinate and flanking anus. Coxal setae *1a* and *3a* and genital setae *g* filiform. Measurements of idiosomal setae given in Table 1. Legs generally similar to those of female and tritonymph, but setae and solenidia having typical protonymphal pattern (i.e. lacking setae *pR* I-II and *sR* III; *wF*, *kT*, *s*, *e* and *f* IV; and solenidia ω_3 I and ϕ IV).

Larva: Not observed.

Material Examined: Holotype and five paratype deutenymphs (one containing a pharate tritonymph) from *Bombus (Pyrobombus) impatiens* Cresson, 1863 (Hymenoptera: Apidae); USA, MICHIGAN, Washtenaw Co., 23 May 1935. Mite specimens labelled: "BMOC #86-0131-1". Host bee in collection of University of Michigan Museum of Zoology (UMMZ) labelled: "Mites



Figures 15-22. *Cerophagus nearcticus*, deutonymph, legs. 15. Leg I, dorsal. 16. Tarsus I, ventral. 17. Leg II, dorsal. 18. Tarsus II, ventral. 19. Leg III, dorsal. 20. Tarsus III, ventral. 21. Leg IV, dorsal. 22. Tarsus IV, ventral.

removed, B. M. OConnor #86-0131-1". One paratype deutonymph from *B. impatiens*; USA, NEW YORK, Tompkins Co., Ithaca, Cornell University Campus, 21 May 1974, B. M. OConnor; slide labelled: "BMOC 74-0521-1a". One paratype female, one paratype male, two paratype protonymphs (one containing a pharate deutonymph) from nest of *Bombus (Bombus) terricola occidentalis* Greene, 1858; USA, CALIFORNIA, San Mateo Co., San Bruno Mts., 9 July 1960, R. W. Thorp (slides labelled "*Bombus occid. nigroscutatus*", a junior synonym of *B. terricola occidentalis* [Hurd, 1979]), these specimens from the Canadian National Collection of Insects, Ottawa.

Type Deposition: Holotype and 4 paratype deutonymphs deposited in the University of Michigan Museum of Zoology; 1 paratype deutonymph deposited in the Cornell University Insect Collection, Ithaca, New York; adults,

protonymphs and one deutonymph deposited in the Canadian National Collection of Insects, Ottawa, Ontario.

SYSTEMATIC RELATIONSHIP OF *CEROPHAGUS NEARCTICUS*

The three collections of *Cerophagus nearcticus* described above appear to be conspecific based upon the essentially identical morphology of the deutonymphs in each series. The deutonymph collected along with the adults and protonymphs in the nest of *Bombus terricola* is pharate within a protonymphal cuticle and is broken and somewhat distorted. However, I was able to locate and compare all structures with those in the free, undistorted deutonymphs collected from *B. impatiens*. Correlation of protonymph and adult is based only upon their similar morphologies and collection in the same habitat. The one tritonymph obtained was surprisingly pharate within the deutonymphal cuticle while still attached to the host bee. I have also observed this phenomenon of tritonymphal development within the deutonymphal cuticle on a host in several collections of the chaetodactylid genus *Sennertia* associated with carpenter bees, *Xylocopa* spp.

Deutonymphs of *Cerophagus nearcticus* share a large suite of character states with *C. granulatus* as most recently redescribed and figured by Zakhvatkin (1941). The deeply pitted dorsal sclerites, configuration of coxal apodemes, form and position of the attachment organ structures, general form of the legs and pretarsi are all identical in the two species. I have not been able to examine specimens of the European species to check the accuracy of the earlier descriptions. Some differences were noted between *C. nearcticus* and Zakhvatkin's description and figures of *C. granulatus*. Zakhvatkin mentioned 13 setae on tarsus I of which 5 were noted as foliate. This number agrees with the total number of sensilla (setae, solenidia and famulus) and foliate setae on tarsus I of *C. nearcticus*. However, in his figure 695, Zakhvatkin illustrated seta *wa* I as foliate, whereas it is filiform in *C. nearcticus*. He also illustrated three non-foliate setae at the ventral apex of tarsus I. In *C. nearcticus*, only setae *s* and *q* are present in this region (*p* is absent) and *q* is foliate. In *C. granulatus*, solenidium ϕ I was illustrated as only slightly longer than ϕ II, while in *C. nearcticus*, ϕ I is approximately 7 times longer than ϕ II. Although the fine details of the tarsal chaetotaxy should be checked in *C. granulatus* to determine if the above differences are real, I regard the differences in tibial solenidial length in the two species as distinctive and not likely to have been figured incorrectly by Zakhvatkin (1941).

PHYLOGENETIC RELATIONSHIPS OF THE GENUS *CEROPHAGUS*

Testing hypotheses of phylogenetic relationships of the genus *Cerophagus* is complicated by prior nomenclature. For the sake of clarity in the following discussion, I will use the following generic names in their original conception: *Cerophagus*, to include the deutonymphal characters of *C. granulatus* and *C. nearcticus* and adult characters of *C. nearcticus*; *Cerophagopsis* to include the deutonymphal characters of *C. skorikovi*, *C. furcata*, *Cerophagus trigona* and three undescribed species I have examined; and *Rhyphoglyphus* to include adult characteristics of *R. indicus*, *C. trigona* and one undescribed species.

In placing the genus *Cerophagopsis* in synonymy with *Cerophagus*, Fain and Heard (1987) diagnosed the taxon with the following character states of the deutonymphs: "(1) Dorsum either pitted or striated. (2) Claws of tarsi I-IV

equal, rather long, non-pedunculate and strongly modified in shape, they are abruptly bent in their middle at 90 to 110°, the basal part being inflated while the apical half is narrow and blade-like. These claws are not twisted spirally. (3) Condylphores relatively long, especially the posterior ones. (4) Tarsi I-IV with 10-9-8-8 setae of which 7-7-6-4 are foliate, most of them very narrowly so. (5) Palposoma strongly reduced, the palpi being either very short or completely lacking."

Of these characters, (1) is not diagnostic, with the two states mentioned being characteristic of *Cerophagus* and *Cerophagopsis* respectively. Character state (2) is an apparent synapomorphy; the form of the pretarsus in the two nominal taxa is essentially identical; I have observed a similar but smaller basal flange in the empodial claw in an undescribed genus associated with certain euglossine Apidae. The form of the condylphores (3) is similar in the two taxa, however, a similar form also occurs in other bee-associated Acaridae such as *Megachilopus*, *Sennertionyx* and an unnamed genus. Character (4) requires more detailed analysis as follows. In *Cerophagus nearcticus*, the tarsal setation is 9-9-8-8, while in *Cerophagopsis* it is 10-9-8-8 as stated or 9-8-8-8 in one unnamed species. However, all of the setae of tarsi I-II are not homologous in the two taxa. In *Cerophagus*, setae *aa* I and *p* I-II are absent while *s* I-II are present. In *Cerophagopsis*, *aa* is present on tarsus I and *p* is usually present on tarsi I-II (absent in one unnamed species) while *s* I-II are absent. Seta *ba* is present on both tarsi I and II in both taxa. Some differences in form and position of tarsal setae and solenidia are also apparent: setae *d* of tarsi I-II are foliate in *Cerophagopsis*, filiform in *Cerophagus*; solenidion ω_2 is positioned in the distal half of tarsus I more apically than seta *ba* in *Cerophagus*, while in *Cerophagopsis*, ω_2 is in the basal half of the segment, more basal than seta *ba*. Character (5) also requires more detailed analysis. The gnathosomal remnants (=palposoma) of *C. nearcticus* are much more developed than those of *Cerophagopsis*. Both taxa retain all three pairs of sensilla ancestrally present in acaroid mites (the palpal tarsal solenidion, distal dorsal palpal seta and palpal supracoxal seta). In *C. nearcticus*, the palpi themselves are conspicuously present although short and are borne on a short, medially cleft subcapitular remnant. Zakhvatkin (1941) also mentioned the presence of palpal remnants in *C. granulatus* although he did not mention setae other than what are clearly the solenidia. In *Cerophagopsis*, the gnathosoma is reduced to a sclerotized plate bearing the setae and solenidia. Distinct palpal remnants are not discernable.

Of the character states mentioned by Fain and Heard (1987), I regard only one as a potential unique synapomorphy of *Cerophagus* and *Cerophagopsis*: the form of the pretarsal empodial claws. Certain other deutonymphal character states, however, are shared between *Cerophagus*, *Cerophagopsis* and three genera of bee-associated Acaridae belonging to the subfamily Horstiinae *sensu* O'Connor (1988), *Megachilopus*, *Sennertionyx* and an unnamed genus. These include the form of the pretarsal condylphores, loss of coxal setae *3a* and *4a* and the presence of seta *ba* on tarsus I. Tarsal setae *p* I-II are also absent in all of these genera except *Cerophagopsis* where they are present in some but not all species. The presence of seta *ba* I in these taxa is an example of paedomorphosis. Early in the evolution of the Astigmata, an ontogenetic modification evolved in that seta *ba* of tarsus I, which was ancestrally present throughout ontogeny, was not expressed in the deutonymphal instar. This first derived pattern occurs in most Astigmata in which the deutonymph is retained in the life cycle. The failure of this seta to regress in the deutonymph is here interpreted as a further derivative condition resulting from the reversal of the earlier ontogenetic pattern of deletion and reappearance. A simpler paedomorphic condition involves coxal seta *4a*. This seta ancestrally appears first in the deutonymphal instar in acariform mites. Its delayed appearance

until the tritonymphal instar in these mites is a case of simple ontogenetic retardation. Using only deutonymphal characters, a case can be made for a relationship between *Cerophagus* and certain genera of Horstiinae, notably *Cerophagopsis*.

Adult morphology is potentially more informative in formulating hypotheses of relationship for these taxa. Positive correlation of the deutonymph with the protonymph and tritonymph in *C. nearcticus* has been accomplished, with the adult collected with the protonymphs so similar as to invite little question of conspecificity. The case of *Cerophagus trigona* is much less certain, with the correlation made only by the collection of a single deutonymph in the same habitat as the adults. However, I have recently received a series of specimens from Dr. Lynn Royce of Oregon State University that had been collected from a nest of *Apis mellifera* L. in Thailand. Like the collection of *C. trigona*, this material contains a number of males and females and a single deutonymph. Both the adults and deutonymph strongly resemble *C. trigona* although minor differences suggest they are not conspecific. This second habitat association between a *Cerophagopsis* type deutonymph with a *Rhypoglyphus* type adult is still not conclusive evidence, but I will accept the proposed correlation of ontogenetic stages until more definitive evidence can be obtained.

Adults of both the *Cerophagus* and *Rhypoglyphus* types belong to the superfamily Acaroidea as diagnosed by OConnor (1982) in that they possess ventral sejugal apodemes and modified sucker-like setae on tarsi IV of the male. Adults with the *Rhypoglyphus* morphology possess the two diagnostic characteristics of the family Acaridae: asymmetry of setae *e* and *f* of the tarsi, with *f* longer than *e* (although only slightly in these species), and enlargement of ventral tarsal setae *u* and *v* such that they are larger than the more lateral setae *p* and *q* (OConnor, 1982)². Adults of *C. nearcticus* do not possess these two diagnostic character states of the Acaridae; setae *e* and *f* are the same length and setae *p* and *q* are larger than *u* and *v*. Thus, there is no direct evidence that *Cerophagus* belongs to the family Acaridae.

On the other hand, *Cerophagus* adults share a number of derived character states with taxa comprising the family Gaudiellidae. This family had been proposed for a single species, *Gaudiella minuta*, collected from a nest of *Melipona quadrifasciata* Lep. in Brazil (Atyeo et al., 1974). Two other small families, Platyglyphidae and Partamonacoptidae, species of which had also been collected from the nests of social bees, were placed in synonymy with Gaudiellidae by OConnor (1988). The monospecific family Platyglyphidae (*Platyglyphus malayanus*) was described by Kurosa (1976) from an unidentified bee nest from Malaysia. Possibly unaware of the description of *Gaudiella minuta*, Fain and Rosa (1983) proposed the new family Partamonacoptidae for two species placed in two new genera (*Partamonacoptes* and *Trigonacoptes*) from neotropical meliponine nests. *Trigonacoptes* and *Gaudiella* are morphologically very similar, and I have previously indicated their probable synonymy (OConnor, 1988). I have had the opportunity to study the holotype of *Gaudiella minuta* and observed that in addition to the very similar overall morphology, it shares a similar pattern of enlarged, barbed dorsal setae with *Trigonacoptes camargoi* that is not apparent from the original figures of *G. minuta*. The two pairs of longer simple setae in the posterior central quarter of the body are actually barbed rather than smooth as originally illustrated

²Setae *e* I-II are not mentioned or illustrated for *C. trigona*; I have verified the presence of these setae on paratypes kindly provided by Dr. Fain. The adult tarsal setal counts for this species should thus be 13-12-10-10 as in *R. indicus*.

(Atyeo et al, 1974, fig. 1). The two species are clearly distinct but I consider *Trigonacoptes* to be a junior subjective synonym of *Gaudiella* (NEW SYNONYMY).

Although it is beyond the scope of this paper to provide a complete phylogenetic analysis of relationships among the gaudiellid genera, certain derived character states shared among *Cerophagus* and the Gaudiellidae suggest a closer relationship than either has with the Acaridae. The most conspicuous of these are the round body form and loss of the sejugal furrow shared among all taxa. *Cerophagus* also shares the heavily barbed form of some dorsal setae with the New World Gaudiellidae (not *Platyglyphus*) and the cuticular mammilation with *Partamonacoptes*. Unlike *Gaudiella* and *Partamonacoptes*, however, the opisthosoma is not as abbreviated in *Cerophagus* and the female ovipore is more anterior in position, ancestral states also retained in *Platyglyphus*. Among the Gaudiellidae, *Cerophagus* is unique in the form of the palpi, the bipectinate dorsal setae, ridged leg segments and the presence of a sclerotized copulatory tube in the female.

Deutonymphal morphology cannot be used to test this hypothesis of relationship since deutonymphs have not been positively correlated with species in the Gaudiellidae. Fain and Flechtmann (1985) described an unusual deutonymph, *Meliponopus palpifer*, from a single damaged specimen collected from *Melipona seminigra* and suggested the possibility that it could represent the deutonymph of one of the previously described nidicolous species. Those authors conservatively declined to assign this taxon to a family. O'Connor (1988) noted similarities in the gnathosomal structures of *Meliponopus* and *Cerophagus* deutonymphs and considered both in the Gaudiellidae. Closer inspection of the gnathosoma in *Cerophagus* indicates that the subcapitular remnant is much more reduced in this taxon (although not as reduced as in *Cerophagopsis* and related Acaridae). *Meliponopus* retains a more plesiomorphic form of the deutonymphal gnathosoma. As I have not examined the specimen of *M. palpifer*, I now believe it was premature to assign this taxon to the Gaudiellidae.

In summary, the evidence from the adult morphology of *Cerophagus nearcticus* suggests that *Cerophagus* is more closely related to the Gaudiellidae than to the Acaridae. The genus *Cerophagopsis* is removed from synonymy with *Cerophagus*, and the generic name *Rhyphoglyphus* is considered a junior subjective synonym of *Cerophagopsis* rather than *Cerophagus*. The character states which originally suggested a close phylogenetic relationship between deutonymphs of these taxa are presumed to be convergent. It is worth noting that another, even more extreme modification of deutonymphal pretarsal empodia has arisen independently in several different taxa. The enlarged, spirally twisted claws which characterize deutonymphs of the family Chaetodactylidae also occur in the genera *Sennertionyx* (Acaridae) and *Macroharpa* (Winterschmidtidae). Similarly, paedomorphic modifications of leg setation occur sporadically throughout the Astigmata, such as in the Carpolyphidae and Lardoglyphidae. With the description and correlation of ontogenetic stages of additional taxa in the Acaroidea, a thorough analysis of morphological and ontogenetic characters using a parsimony approach may be possible. At that point, relationships among the families and genera in this large group may be hypothesized with more confidence.

On the basis of the above arguments, I present the following diagnosis for the genus *Cerophagus*:

Cerophagus Oudemans, 1904

Family Gaudiellidae. Adults with circular body outline; dorsal, latero-ventral and postero-ventral cuticle with raised mammilations; sejugal furrow absent. Gnathosoma triangular, palpi attenuated distally. Body chaetome complete. Dorsal setae bipectinate, borne on tubercles. Prodorsal sclerite well

developed. Supracoxal seta of leg I bifurcate with basal barbs. Legs strongly sclerotized, bearing longitudinal and transverse ridges on segments. Leg setation complete except seta *aa* absent from tarsus I. Solenidion ω_2 distally positioned on tarsus I. Female with ovipore between coxal fields III-IV, and a terminal sclerotized copulatory tube bearing setae h_3 . Male more strongly sclerotized than female, setae *d* and *e* of tarsus IV modified into suckers.

Deutonymph with gnathosomal remnant well developed. Dorsal propodosomal and hysterosomal sclerites strongly pitted. Dorsal setation complete, ventral setation lacking coxal field setae *3a* and *4a*. Leg setation complete for astigmatid mite deutonymph except tarsal setae *aa* I, *p* I-II absent, and setae *s* I-II and *ba* I present. Pretarsal empodia consisting of a strongly hooked claw bearing a flattened basal projection.

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