# DENDROEREMAEIDAE N. FAM., FROM FOREST TREES IN WESTERN NORTH AMERICA (ACARI: ORIBATIDA: LICNEREMAEOIDEA)

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SUMMARY: A new family of oribatid mites, Dendroeremaeidae, is described on the basis of material collected from bark and twigs of coniferous and deciduous trees in northwestern North America. *Dendroeremaeus* n. gen. is described as the type genus of the family, with *Dendroeremaeus krantzi* n. sp as type species. A second species, *Dendroeremaeus foveolatus* n. sp. is described also. The characteristics and relationships of this family to others of the poronotic Brachypylina are discussed, and the family is included in the early-derivative poronotic taxon Licneremaeoidea, and may be most closely related to Lamellareidae or Passalozetidae. Adults of *Dendroeremaeus krantzi* and *D. foveolatus* have the octotaxic system developed on the notogaster, and nymphs are unideficient and plicate. Scalps are retained by some tritonymphs.

ORIBATIDA, LICNEREMAEOIDEA, NOUVEAU GENRE, NOUVELLE ESPÈCE, AMÉRIQUE NORD OUEST, ARBORICOLE, CANOPÉE

RÉSUMÉ : La nouvelle famille d'Oribates, les Dendroeremaeidae, est décrite à partir de matériel récolté des ramilles et des écorces des habitats arboricoles du nord-ouest d'Amérique du Nord. Un nouveau genre, *Dendroeremaeus* n. gen., une nouvelle espèce, *D. krantzi* n. sp., sont décrits ainsi qu'une deuxième espèce, *D. foveolatus* n. sp. Les caractéristiques et relations de cette famille avec les autres Brachypylina poronotiques sont discutées. Nous plaçons cette famille dans la superfamille Licneremaeoidea, étroitement apparentée aux Lamellareidae ou Passalozetidae. Les adultes du *Dendroeremaeus krantzi* et *D. foveolatus* ont le système octotaxique, les immatures sont unidéficients et plissés. Quelques tritonymphes retiennent les scalps.

## INTRODUCTION

Licneremaeoidea is a diverse assemblage of oribatid mite families, none of which is species rich. All members have apheredermous immatures with plicate hysterosomal integument (GRANDJEAN 1954). Outside the superfamily these characters are shared by Cymbaeremaeidae (Cymbaeremaeoidea), Tectocepheidae (Tectocepheoidea), Ameronothridae (Ameronothroidea), Achipteriidae, Tegoribatidae

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(Achipterioidea) and Phenopelopidae (Phenopelopoidea). These, along with the licneremaeoid families Licneremaeidae, Scutoverticidae and Passalozetidae, were considered by GRANDJEAN (1954) to form a natural group bridging oribatid taxa lacking the octotaxic system, and those poronotic groups with the octotaxic system developed. Thus, the most early-derivative poronotic mites — taxa currently in the superfamilies Licneremaeoidea, Phenopelopoidea and Achipterioidea — are often referred to as the 'higher plicates,' in reference to the folded cuticle of their immatures (NORTON & ALBERTI 1997). The Licneremaeoidea seem the earliest derivative of these higher plicates, as members lack pteromorphs in the adult (NORTON & ALBERTI 1997).

Since the treatment of the world oribatid fauna by BALOGH & BALOGH (1992), a number of taxa have been added to the Licneremaeoidea, and the scope of the superfamily is in a state of flux. WALTER & BEHAN-PELLETIER (1993) included Adhaesozetidae based on character state analysis of adults and immatures. The families Micreremidae and Lamellareidae and the genus *Glanderemaeus* were transferred to Licneremaeoidea from Cymbaeremaeoidea, Oripodoidea, and Cymbaeremaeoidea, respectively, by NORTON & ALBERTI (1997). *Glanderemaeus* was subsequently included in the Micreremidae by WOAS (2002). The family Fenichelidae was moved from the Oripodoidea to Licneremaeoidea by SUBIAS (2004).

We describe a new family of Licneremaeoidea for which material representing one new genus and two new species is available for study. Adults of the new species share a number of apomorphic character states with Oripodoidea and without knowledge of immature morphology this species would have been included in the oripodoid family Oribatulidae. However, the immature cuticle is plicate, and the hysterosoma lacks the defining autapomorphy for Oripodoidea, the presence of excentrosclerites. The systematic relationships of this new family within the Licneremaeoidea is discussed following the descriptive part of the paper.

The herein described species are infrequent, and not abundant, on bark and twigs in arboreal habitats in western North America. Members of the families Camisiidae, Ceratozetidae, Scheloribatidae and Mycobatidae are the numerically dominant oribatid mites in these habitats (FAGAN & WINCHESTER 2000; SCHOWALTER & GANIO 1998; WINCHESTER *et al* 2000).

## MATERIAL AND METHODS

Measurements and descriptions are based on specimens mounted in temporary cavity slides and on permanent slides. Terminology used in this paper follows

F. GRANDJEAN (see TRAVÉ & VACHON (1975) for references), and MAHUNKA & ZOMBORI (1985). The following conventions of measurement and description are used: *Total length*: measured from tip of rostrum to posterior edge of notogaster. *Length of notogaster*: measured from anterior margin to posterior edge. *Width of notogaster*: refers to maximum notogastral width. *Distance between setae of prodorsum and notogaster*: measured as mutual distance between central points of insertion of setal pairs, or (for different setae) as mutual distance between central points of insertion of setae on same side. *Abbreviations for setae of prodorsum*: *ro*: rostral seta; *le*: lamellar seta; *in*: interlamellar seta; *ex*: exobothridial seta; *bo*: bothridial seta. *Leg and palp setal formulae*: famulus is included in tarsal setal count on leg I and solenidial counts are in parentheses. The unideficience nomenclature for notogastral setae is used herein as outlined by NORTON in BALOGH and BALOGH (1988).

Abbreviations for collections: CNC, Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada; PFC, collections of the Pacific Forestry Centre of the Canadian Forestry Service, Natural Resources Canada, Victoria, British Columbia, Canada; RNC, collections of Roy A. Norton, Syracuse, New York, USA; USNM: National Museum of Natural History, Washington, District of Columbia, USA.

Specimens for scanning electron microscopy were cleaned by soaking in Terg-a-zyme® solution for 6-12 h, followed by brief (1-2 s.) submersion in an ultrasonic bath. Specimens were critical point dried, mounted on Al-stubs with double sided sticky tape, and gold-coated in a Hummer sputter apparatus.

DENDROEREMAEIDAE new family

Type genus: *Dendroeremaeus* gen. nov.

Family based on one genus and two species and represented by specimens of both sexes and all immature instars.

*Diagnosis.* Adults and immatures of this family resemble those of other Licneremaeoidea as follows. *Adults*: Dorsophragmata and pleurophragmata present. Octotaxic system present. Pteromorphs absent. Discidium, custodium and circumpedal carina absent. Chelicerae chelate-dentate. *Immatures*: Apheredermous, plicate. Humeral organ absent.

Adults and immatures of Dendroeremaeidae are distinguished from those of other families of Licneremaeoidea by the following unique combination of character states. *Adult*: Prodorsum with genal notch present; lamella present; pedotecta I and II present; humerosejugal porose areas Am and Ah present; sublamellar porose area Al present; coxisternal setation 3-1-2-2; octotaxic system present, with four pairs of saccules; palpal eupathidium *acm* attached to solenidion along length; axillary saccule of subcapitulum present. Preanal organ apically cup-shaped, with long stalk. *Immatures*: Gastronotal setation unideficient, setae of *c*, *l*, and *h* series subequal in larva, dimorphic in nymphs; prodorsal, gastronotal, coxisternal, aggenital and adanal porose regions present; seta *ex* of immatures differing in size and shape from that of adult; seta *d* absent from genua and tibiae in all instars.

*Description. Adult:* Body and legs with weakly developed, tuberculate, non-birefringent cerotegument. Dorsophragmata and pleurophragmata present. Lamellae present. Genal notch present (FIG. 3). Bothridium large, widest distally, with anterior cusp overhanging base of lamella. Pedotecta I and II present, covering acetabular apertures I and II, respectively (FIGS. 3, 8). Pedotectum I extending dorsally to base of seta *ex* (FIG. 3). Epimeral borders absent. Coxisternal setation: 3-1-2-2 (FIG. 2). Discidium and custodium absent. Tracheal system normal. Genital setae 6 pairs. Aggenital setae 1 pair. Anal setae 2 pairs. Adanal setae 3 pairs. Lyrifissure *ian* absent. Preanal organ apically cup-shaped, with long stalk (FIG. 2). Humerosejugal porose areas Am and Ah, present. Sublamellar porose area Al present (FIG. 3). Octotaxic system present as four pairs of saccules. Ten pairs of notogastral setae present, positioned laterally, other than seta *lm,* seta $c_1$ close to anterior margin of notogaster, $c_2$, $c_3$, *da, dm, dp* absent (FIG. 1). Pteromorphs absent. Five pairs of lyrifissures present. Subcapitulum diarthric, small axillary saccule at base of palp. Rutellum pantelobasic. Chelicera chelate-dentate with 2 slender, barbed setae. Trägårdh's organ present. Palp with normal 5 segments and tarsal lyrifissure; setal formula: 0-2-1-3-9(1). Eupathidium *acm* fused with solenidion along length (FIGS. 9, 17).

Legs tridactylous, with claws subequal in size and shape (FIGS. 13-16). Femora I to IV and trochanters III and IV with porose areas. Famulus *(e)* rod-like, rounded distally. Seta *d* absent from tibiae I to IV and genua I to III. Solenidion $\omega_2$ present on tarsus II. Seta *ev'* absent from femora III and IV. Solenidia on tibiae and genua short, other than $\varphi_1$ on tibia I. Solenidia on tibia I borne on tubercle projecting over base of tarsus I (FIG. 13).

*Immatures.* Apheredermous, plicate, without hysterosomal macrosclerites or excentrosclerites. Prodorsal porose regions present (FIG. 18). Gastronotal setation unideficient; larva with 12, nymphs with 15 pairs (adult loses $c_1$, $c_3$, *da*, *dm*, *dp*). Gastronotal setae of *c*, *d*, and *l* series monomorphic in larva (FIGS. 20, 30), dimorphic in nymphs (FIG. 18, 29). Opisthonotal gland present in all instars. Coxisternal porose regions present in all nymphs. Porose regions present dorsally on hysterosoma, and lateral of genital region, in adanal region, and surrounding opening of opisthonotal gland in all nymphs (FIG. 19). Apodemato-acetabular tracheal system or porose homologues absent. Paraprocts atrichous in larva, protonymph and deutonymph. Genital and aggenital setal formula (larva to adult): 0-1-3-5-6 and 0-0-1-1-1, respectively. Cupule development normal. Bothridium, bothridial seta and seta *in* fully formed in all nymphs. Companion seta *d* absent from tibiae I to IV and genua I to III. Setation of protonymphal leg IV normal: 0-0-0-0-7. Scalps retained in some tritonymphs collected (FIG. 23).

*Etymology*. See under description of genus.

*Dendroeremaeus* new genus
Type-species: *Dendroeremaeus krantzi*, new species

Genus based on adult female, male and immature material representing two species.

*Etymology.* The generic prefix "Dendro" is from the Greek "dendron" meaning tree, and refers to the arboreal habitat of this genus; "eremaeus" is a common suffix for oribatid genera and is from the Greek "eremaeios' meaning quiet or still.

*Diagnosis.* With character states of the family and the following additional character states: rostrum rounded; prodorsum with translamella; bothridial seta capitate; lenticulus present; solenidia on genua I to III and tibiae III and IV baculiform.

*Description. Adult:* Integument microtuberculate, with strong, large reticulate or areolate or foveate sculpturing on all of body except leg segments (FIGS. 1, 5-8, 27). Body and legs with weakly developed, tuberculate, non-birefringent cerotegument. Rostrum with rounded margin. Translamella present. Bothridial seta capitate (FIGS. 1, 11). Apodemes $ap_1$, $ap_2$ and *apsj* reaching about halfway to midline; $ap_3$ weakly developed; $ap_4$ not developed. Genital setae $g_1$, $g_2$ positioned anteriorly on genital plate, $g_3$ to $g_6$ positioned medially on genital plate (FIGS. 2, 12). Adanal setae $ad_2$ and $ad_1$ positioned postanally (FIG. 2). Lyrifissure *iad* anterior to seta $ad_3$, parallel to anterolateral margin of anal plate. Notogaster slightly flattened, overhanging ventral plate (FIG. 6). Lenticulus present (FIG. 1). Subcapitular setae *a, m* and *h* barbed, relative length: $h > m > a$. External face of rutellum showing smooth, blade-like edge distally, with strong dorsal lobe and small ventral tooth formed by narrow incision; inner face with one moderate tooth below dorsal lobe. Claws of legs uniform in size and shape, each with minute scales dorsally. Setae (*tc*) of tarsi I to IV, and (*it*) of tarsi I to III curved distally, ending in minute knob (too small to be illustrated on figs. 13-16). Solenidia on genua I to III and tibiae III and IV baculiform.

*Immatures.* Gastronotal setae of *c*, *d* and *l* series all large, barbed, fusiform to phylliform in larva; dimorphic in nymphs with setae of *d* series short, minutely barbed, or spiniform; setae of *c, l* and *h* series and $p_1$ large, barbed, fusiform (FIGS. 18, 20). Hysterosomal dorsum of nymphs slightly flattened, without defined carinate border.

*Remarks:* The baculiform shape of the solenidia on genua I to III and tibiae III and IV is similar to that described for the licneremaeid *Huilicheremaeus michaii* Fernandez, Marcangeli and Eguaras, 1997 (FERNANDEZ *et al* 1997), and for the lamellareid *Tenuelamellarea argentinensis* Martinez, Velis, Eguaras and Fernandez, 1995 (MARTINEZ *et al* 1995).

*Dendroeremaeus krantzi* sp. nov.
FIGS. 1-26

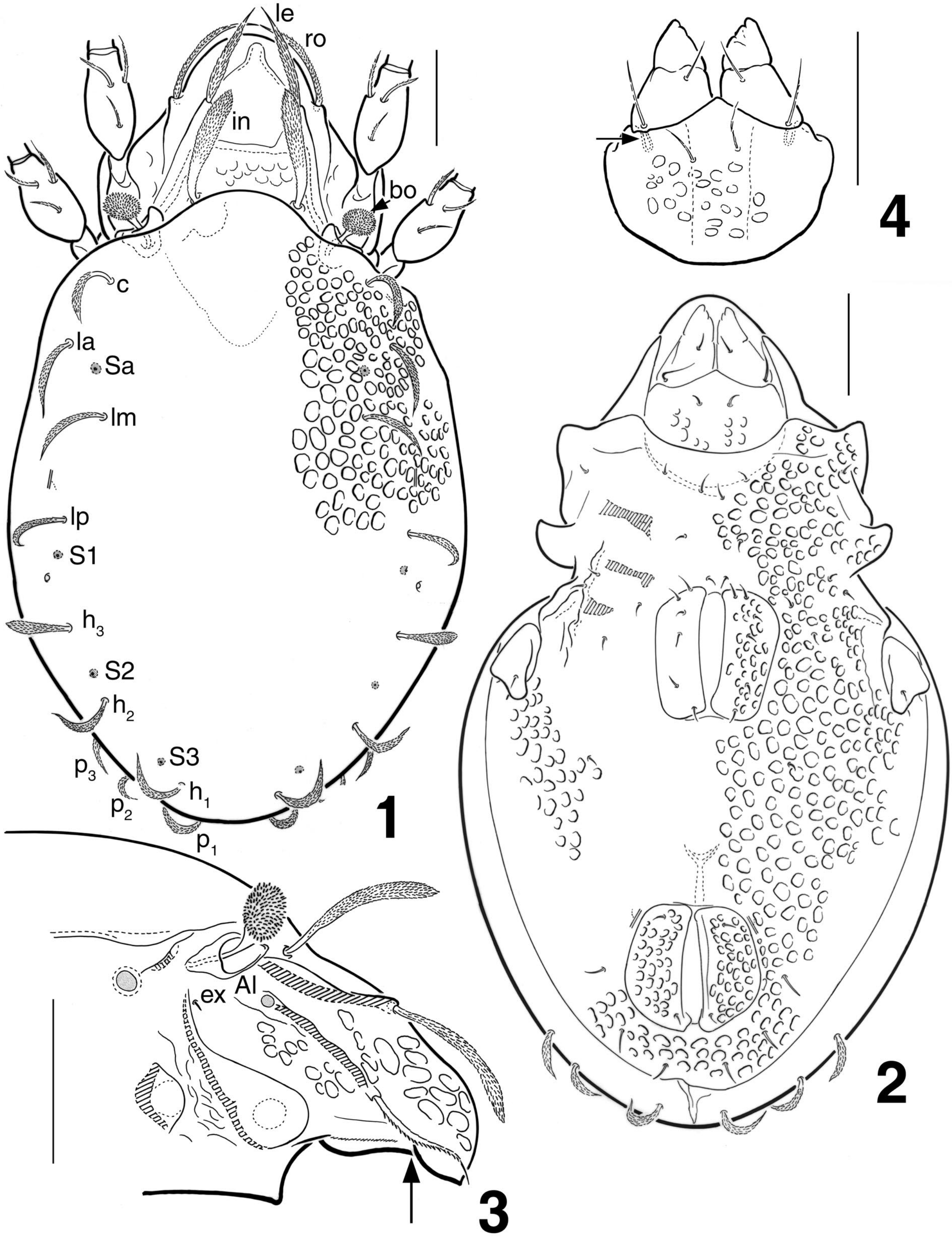
*Material examined.* **Holotype:** adult female. **Canada: British Columbia**: Vancouver Island, Campbell River, Montane Alternative Silvicultural Systems (MASS) site 49° 50' 53''N; 125° 26' 27''W, elevation 740-850m, 5 November 1996 (L.M. Humble and N.N. Winchester), from twig wash in *Abies amabilis* lower canopy; deposited in the CNC, type no. 23461. **Paratypes**: 20 with same data except 30 July-6 November 1996; **USA: Oregon**: Linn Co., January 1982 (D.E. Walter and P. Hansen) 3 adults, 1 nymph from lichen covered twigs of *Quercus garryiana* at ca. 50'; deposited in the CNC, USNM, PFC and the RNC.

*Etymology*: The specific epithet is in honour of the eminent acarologist Dr. Jerry KRANTZ who has introduced generations of students to the discipline of Acarology.

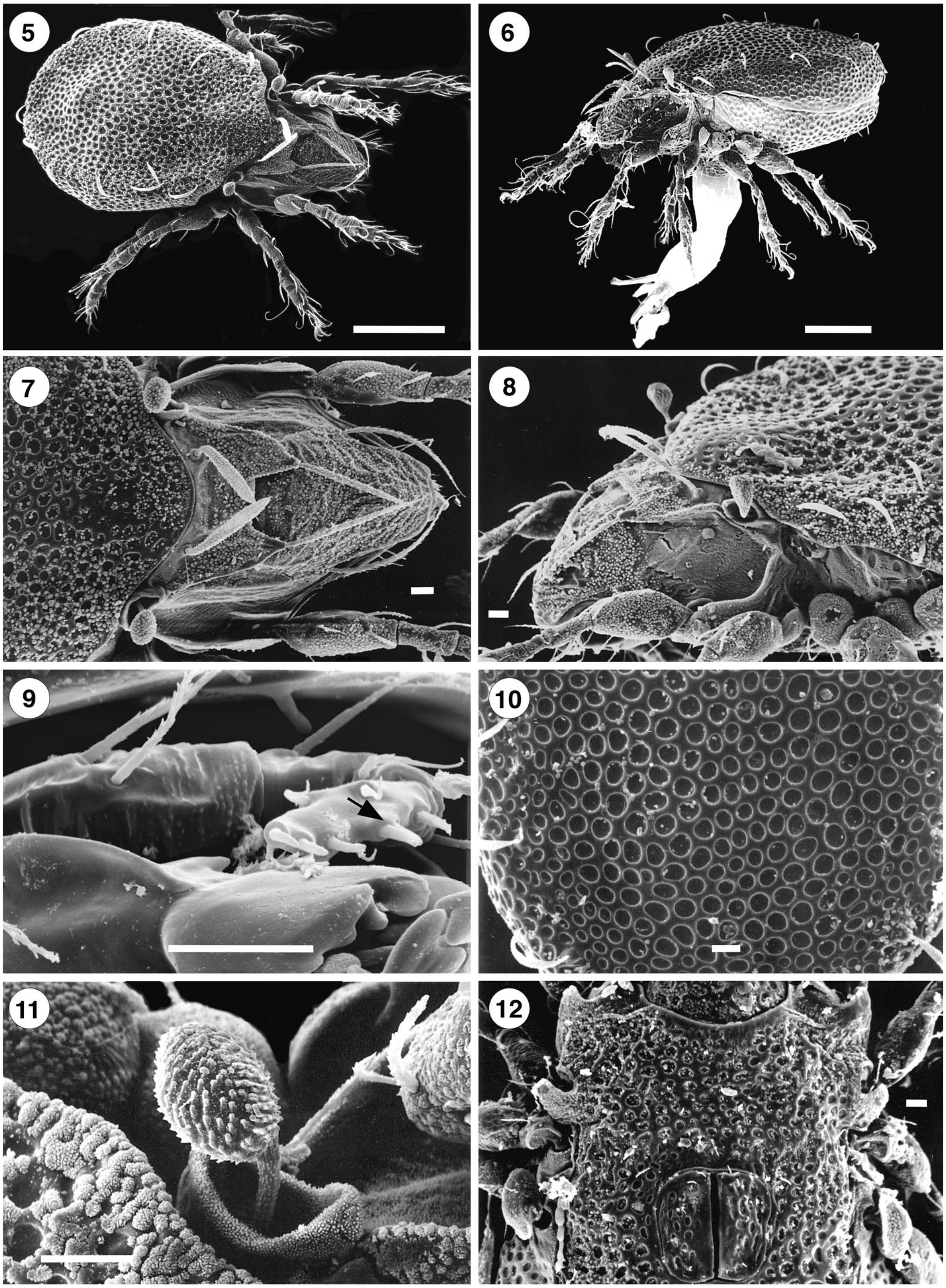
*Diagnosis.* Total length 375-435 μm; lamella 60-65 μm long; lateral carina present, about 57 μm long; bothridial seta 43-50 μm long, with finely barbed globular head subequal in length to narrow stalk; notogaster with reticulate sculpturing; lenticulus weakly developed; with reticulations less well-developed in lenticular area; notogastral setae about 40μm long, thick, fusiform, heavily barbed along length; postanal porose area present.

*Adult Measurements.* Female ($n$ = 10): total length 420 μm (400-435μm), notogastral length 329μm (325-340μm), notogastral width 247μm (235-260μm). **Male** ($n$ = 8): total length 388μm (375-405μm), notogastral length 305μm (300-310μm), notogastral width 240μm (235-250μm).

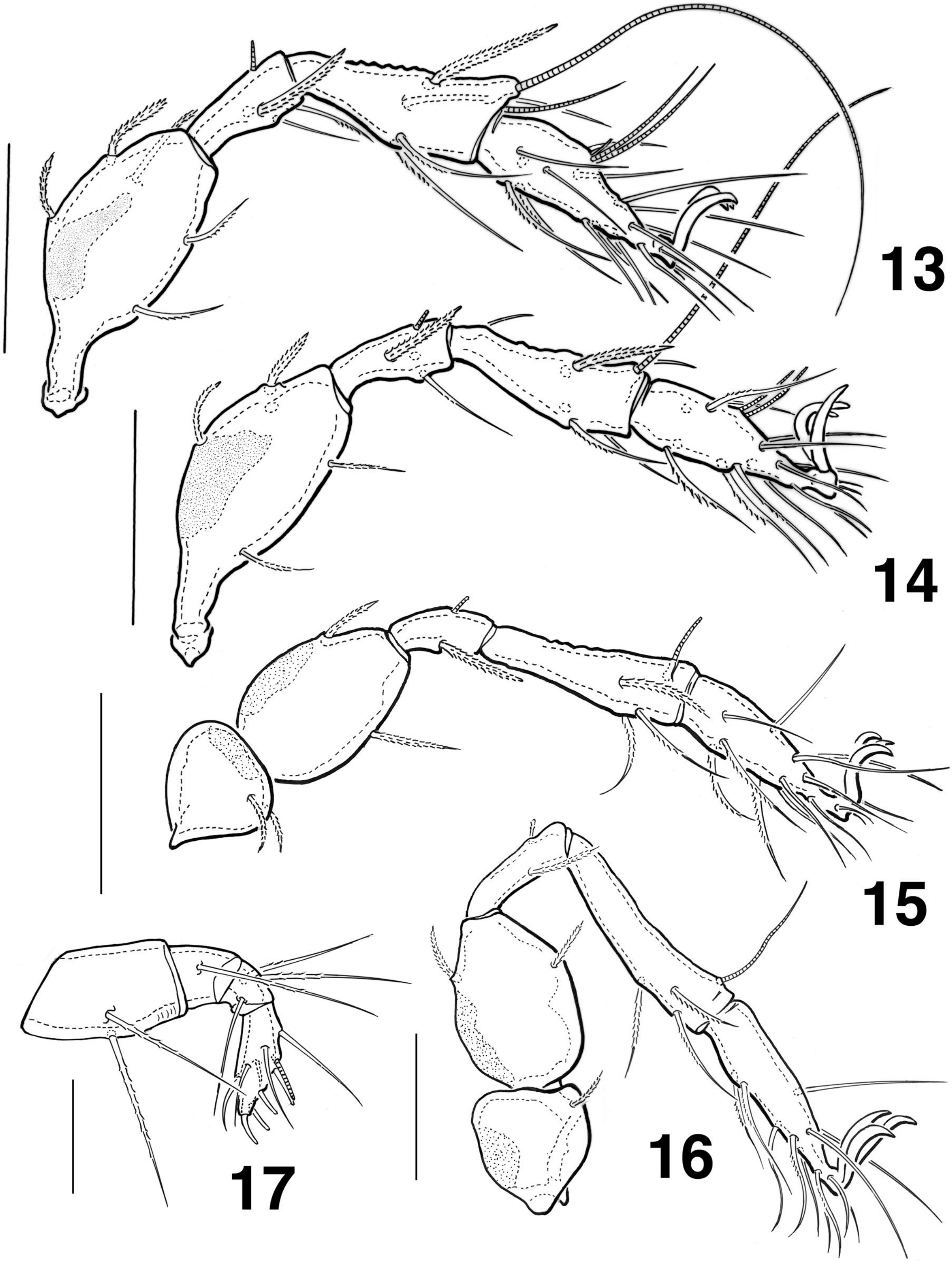
*Description. Adult. Integument.* Reticulations less well-developed in lenticular area (FIGS. 7, 8). Leg



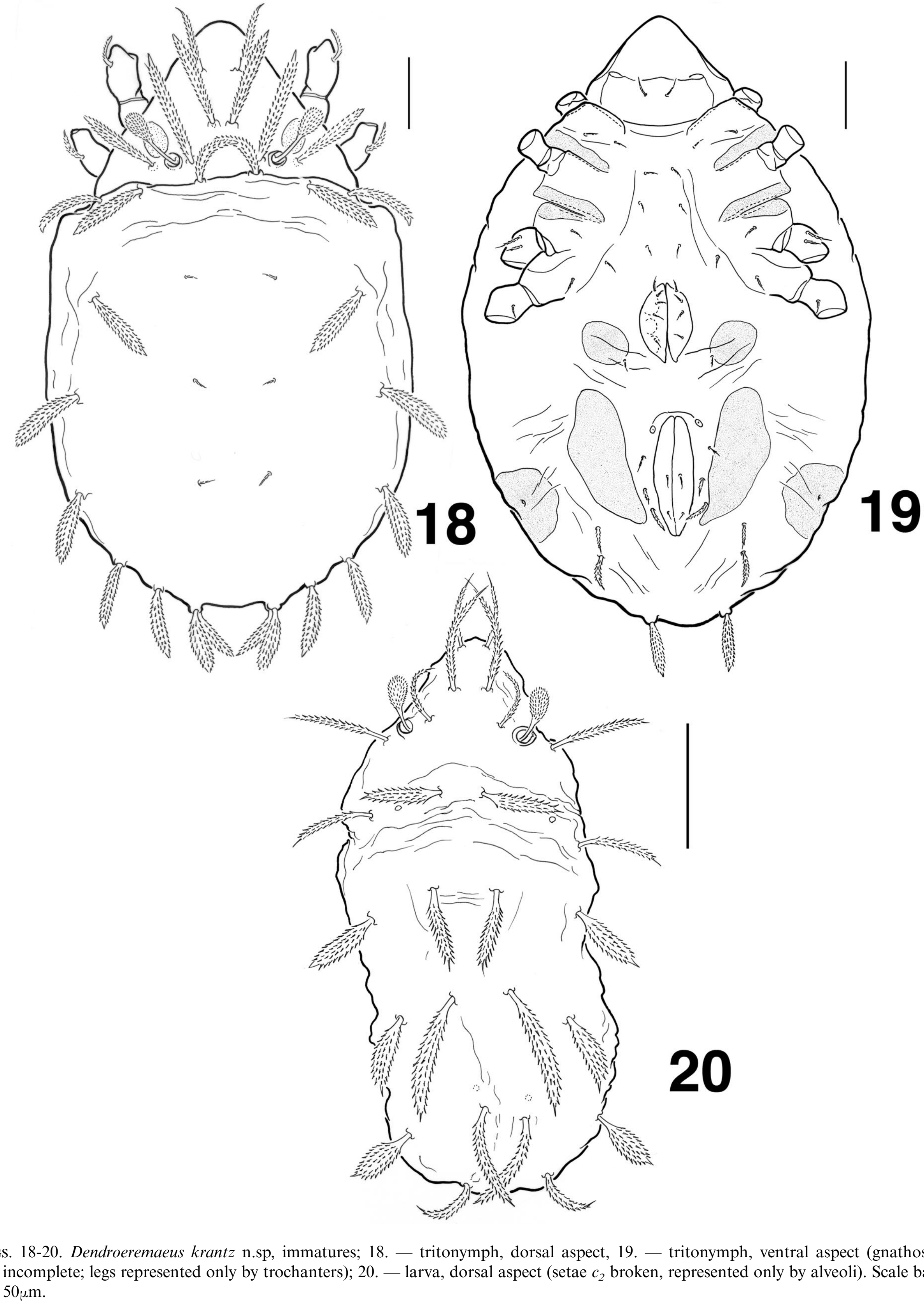

FIGS. 1-4. *Dendroeremaeus krantzi* n.sp., adult female: 1. — dorsal aspect; 2. — ventral aspect (legs removed); 3. — prodorsum, lateral aspect (gnathosoma and legs removed), genal notch indicated by arrow; 4. — subcapitulum, ventral view (palps removed), axillary saccule indicated by arrow. Scale bars: = 50$\mu$m.



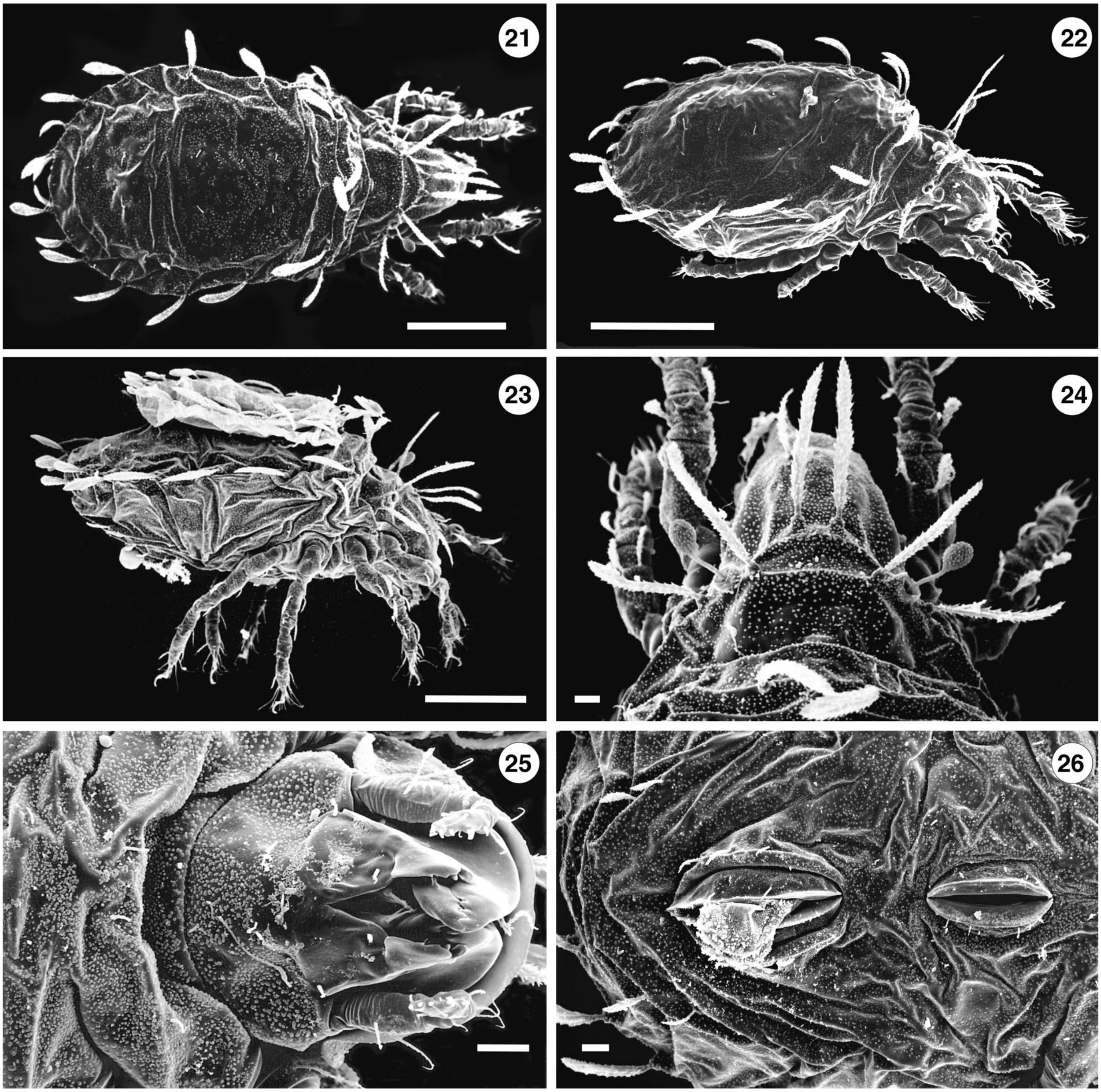

FIGS. 5-12. *Dendroeremaeus krantz* lorantzi n.sp, scanning electron micrographs of adult females: 5. — dorsal aspect; 6. — lateral aspect with ovipositor extended; 7. — anterior half, dorsal aspect; 8. — anterior half, lateral aspect; 9. — detail of palptarsus and rutellum, ventral aspect (fused eupathidium *acm* and solenidion indicated by arrow); 10. — detail of notogaster; 11. — bothridium and bothridial seta; 12. — coxisternal region. Scale bars: 5, 6 = 100µm; 7-12 = 10µm.




FIGS. 13-17. *Dendroeremaeus krantzi* n.sp, legs and palp of adult female, all abaxial aspect: 13. — leg I (trochanter removed); 14. — leg II (trochanter removed); 15. — leg III; 16. — leg IV; 17. — palp (trochanter removed). Scale bars: = 50μm.




FIGS. 18-20. *Dendroeremaeus krantz* n.sp, immatures; 18. — tritonymph, dorsal aspect, 19. — tritonymph, ventral aspect (gnathosoma incomplete; legs represented only by trochanters); 20. — larva, dorsal aspect (setae $c_2$ broken, represented only by alveoli). Scale bars = 50$\mu$m.




FIGS. 21-26. *Dendroeremaeus krantzi* n.sp, scanning electron micrographs of tritonymphs; 21. — dorsal aspect; 22. — dorsolateral aspect; 23. — lateral aspect, with scalps; 24. — anterior third, dorsal aspect; 25. — anterior third, ventral aspect; 26. — anogenital region. Scale bars: 22-24 = 100μm; 25-27 = 10μm.

segments with roughened integument. Body with granular cerotegument, easily removed (FIGS. 8, 10); cerotegument of bothridium microtuberculate (FIG. 11). Color medium brown.

*Prodorsum*. Integument reticulate posterior to translamella. Lamellae 60-65 μm long, slightly converging; translamella 30-35 μm long, depth 5-7 μm (FIGS. 1, 7). Lamellar cusps 17-20 μm long, narrowing anteriorly to width of lamellar setae (FIG. 7). Lateral carinae about 57 μm long. Setae *ro* 60-70 μm long, spinose along length, smooth basally, acuminate distally, arising anterior of lateral carina; mutual distance at base 75-80 μm. Setae *le* about 60-70 μm long, thick, heavily barbed along length, tapered distally, mutual distance at base 35-40 μm. Setae *in* about 55 μm long, thick, heavily barbed along length, abruptly tapered distally, extending anteriorly to base of lamellar setae; mutual distance at base 50-53 μm. Bothridial setae 43-50 μm long, with finely barbed globular head subequal in length to narrow stalk. Exobothridial setae about 12 μm long, finely barbed, tapered distally (FIG. 3).

*Lateral Region*. Pedotectum I covering acetabulum I, narrowing along length, and curving dorsally to level of seta *ex* (FIGS. 3, 8). Pedotectum II covering acetabulum II (FIG. 3). Sublamellar porose area Al small, about 5μm in diameter, positioned at proximal base of lateral carina (FIG. 3). Humerosejugal porose areas Am oval, Ah circular, each 8 μm wide (FIG. 3).

*Notogaster*. Longer than wide, ratio about 1.3:1.0. All ten pairs of notogastral setae about 40μm long, thick, heavily barbed along length, fusiform, tapered distally; setae *c, la* and *lp* curving posteriorly, *lp*, and $h_3$ curving laterally and $h_2$ and $h_1$ curving anterolaterally (FIG. 1). Saccules very small: Sa midway between setae *la* and *lm*, S1 midway between setae *lp* and $h_3$, S2 midway between setae $h_3$ and $h_2$, *and S3* between $h_2$ and $h_1$ (FIG. 1). Lyrifissures obscured by heavy sculpturing.

*Ventral Region*. Ventral region with alveolate sculpturing (FIG. 2). Apodemes obscured by heavy sculpturing of coxisternal region. Ridge present medial to acetabulum IV (FIG. 2). Epimeral, genital, aggenital and anal setae smooth, acuminate, about 10μm long. Adanal setae $ad_1$ and $ad_2$ about 10μm long, barbed, tapered distally, seta $ad_3$ about 10μm long, smooth, narrower than $ad_1$ and $ad_2$, tapered. Postanal porose area present, narrow, oval, about 16 μm long.

*Gnathosoma*. With character states of genus; axillary saccule about 5μm long (FIG. 4).

*Legs.* Paraxial porose area present on femora I to IV and trochanters III and IV. Leg setal formulae (trochanter to tarsus): leg I, 1-5-3(1)-4(2)-20(2); leg II, 1-5-3(1)-4(1)-15(2); leg III, 2-2-1(1)-3(1)-15; leg IV, 1-2-2-3(1)-12. Tibia III slightly longer than tarsus III; tibia IV subequal in length to tarsus IV. Setae *d* and *l′* of femora I and II, *l″* of genua and tibiae I and II thick, heavily barbed, tapered distally. Setae *l′* absent from tibiae IV in one adult. Genual solenidia σI to σIII short, about 6μm long, subequal in length to fastigial seta. Tarsal solenidia $\omega_1$I, $\omega_2$I, $\omega_1$II and $\omega_2$II shorter than segment; tarsal solenidia closely adjacent on segments (FIGS. 13, 14).

*Immatures. Measurements*. Mean length: larva (*n* = 1) 238 μm; protonymph (*n* = 2) 248 μm (238, 257); deutonymph (*n* = 1) 338 μm; tritonymph (*n* = 7) 425 μm (range 440-440).

*Integument*. Line of dehiscence (when observed) extending anteriorly to *seta* $c_2$. Cerotegument weakly developed, microtuberculate. Integument weakly microtuberculate.

*Tritonymph. Prodorsum*. Lateral porose areas present anterior of bothridia (FIG. 18). Setae *ro* thick, heavily barbed along length, acuminate distally, about 50 μm long. Seta *le* thick, fusiform, heavily barbed along length, tapered distally, about 70 μm long, subequal in shape to *c, l* and *h* setae of tritonymph. Setae *in* thick, heavily barbed along length, tapered distally, about 80 μm long. Mutual distance of setal pairs *ro, le* and *in* about 18, 10 and 40 μm, respectively. Setae *ex* thick, heavily barbed along length, tapered distally, about 58 μm long. Bothridial setae about 45 μm long, head clavate to capitate in shape, but less capitate than that of adult (compare figs. 8, 11 with FIG. 24). Bothridium cup-shaped.

*Gastronotal Region*. Three very weakly developed porose regions present, irregularly shaped, consisting of longitudinal pair between setae *da, dm* and *la, lm,* and single, transverse, U-shaped porose region lateral and posterior to setae *dp* (similar, but more weakly developed than that illustrated in FIG. 29). Porose regions each encompassing small non-porose regions. Gastronotal setae *c, l, h* series and $p_1$ thick, fusiform, heavily barbed along length, tapered distally; *c* and *l* series 55-60 μm long; *h* series about 45 μm long, and $p_1$ about 37 μm long. Gastronotal setae $p_2$ about 20 μm long, thick, heavily barbed; setae $p_3$ narrow, barbed, about 15 μm long, Gastronotal setae of *d* series short, thin, tapered, about 10μm long (FIGS. 18, 21).

*Ventral Region*. Medial margins of epimeral plates poorly defined; coxisternal porose areas present. Epimere I with narrow mentotectum overlying base of subcapitulum (FIG. 25). Epimeral, genital, aggenital and anal setae smooth, acuminate, about 12 μm long; seta $ad_3$ heavily barbed, tapered to blunt distally, about 14 μm long; setae $ad_1$ and $ad_2$ barbed, tapered, 6 μm and 10 μm long, respectively. Porose regions present lateral to aggenital and adanal setae. Development of epimeral setae (protonymph — adult): 3-1-2-1, 3-1-2-2, 3-1-2-2, 3-1-2-2. Development of genital, aggenital, anal and adanal setae (protonymph — adult): 1356, 0111, 0022, 0333, respectively.

*Legs.* Development of setae and solenidia given in TABLE 1. In protonymph, seta *d* of femora I to III, setae (*l*) of genua I and II, seta *l'* of genu III, seta *l'* of tibiae I and II all thick and heavily barbed. Solenidion $\omega_2$ about one-third length of $\omega_1$ on nymphal tarsus I; subequal to $\omega_1$ on tarsus II, as in adult. Solenidia on genua I to III and tibiae III and IV, and $\varphi_2$ on tibia I, about 6-10 μm long; solenidion on tibia II about 13 μm long, and $\varphi_1$ on tibia I about 57 μm long. Proral setae of tarsus I appear eupathidial in all nymphal instars. Subunguinal seta of tarsus I of normal form and inserted proximal to antelateral pair in all nymphs; becoming eupathidial in adult, and moving distal to antelateral pair. Porose areas on femora I to IV clearly present.

*Protonymph and Deutonymph.* Porose regions on prodorsum and hysterosoma developed in deutonymph as in tritonymph. Development of gastronotal porose regions not evident in protonymph or deutonymph. Porose areas on femora I to IV clearly present in deutonymph, not evident in protonymph. Tarsal pulvillus present, minute.

*Larva* (based on crushed, pharate specimen). Shape of prodorsal and gastronotal setae similar to that of tritonymph, except seta *ex* subequal in length and shape to setae *le* and *in.* Gastronotal setae of *c* series about 32 μm, of *d* series about 48 μm long, of *l* series about 26 μm long, and *h* series 16-20 μm long. Prodorsal and hysterosomal porose regions not evident. Porose areas on femora I to IV not evident. Tarsal pulvilli present.

*Remarks:* 1) *Scalps.:* The 2 protonymphs and 1 deutonymph of *D. krantzi* examined were apheredermous; 2 of the 7 tritonymphs examined carried scalps. 2) *Variation.* The carina lateral to the lamella is bilaterally absent from a specimen from the population from lichen covered twigs of *Quercus garryiana*, and is weakly developed in another specimen from this population. 3) *Sex ratios.* Available evidence indicates that adults of *Dendroeremaeus krantzi* reproduce sexually and have a normal 1:1 sex ratio. Although our material is not rich, males are known from all populations.

*Dendroeremaeus foveolatus* sp. nov.
FIGS. 27-30

*Material examined.* **Holotype: USA: Oregon**: Linn Co., January 1982 (D.E. Walter and P. Hansen) from lichen covered twigs of *Quercus garryiana* at ca. 50′; deposited in the CNC, type n° 23462. **Paratypes**: 6 adults and 3 nymphs with same data as holotype (adults mounted on same slide as holotype); **California**: Del Norte Co., Smith River N.W.A., Darlingtonia Trail on Rt. 199, 41° 55' 00''N; 123° 54′ 27''W, 21 March 2004 (V. Behan-Pelletier) 1 adult from twigs of evergreen shrub. Paratypes deposited in the CNC, and the RNC.

*Etymology*: The specific epithet refers to the foveate sculpturing of the notogaster of this species.

*Diagnosis.* Total length 380-425 μm; sculpturing of notogaster foveate; lenticulus well-developed, not covered with sculpturing; lamella 55-57 μm long; lateral carina absent; bothridial seta about 38 μm long, with finely barbed globular head subequal in length to barbed stalk; notogastral setae about 16-26μm long, thick, heavily barbed along length.

*Adult Measurements.* **Female** (*n* = 3): total length 397 μm (380-425μm), notogastral length (*n* = 2) 323μm (305, 340μm), notogastral width (*n* = 2) 223μm (220, 225μm). **Male** (*n* = 1): total length 385μm, notogastral length 305μm, notogastral width 200μm.

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

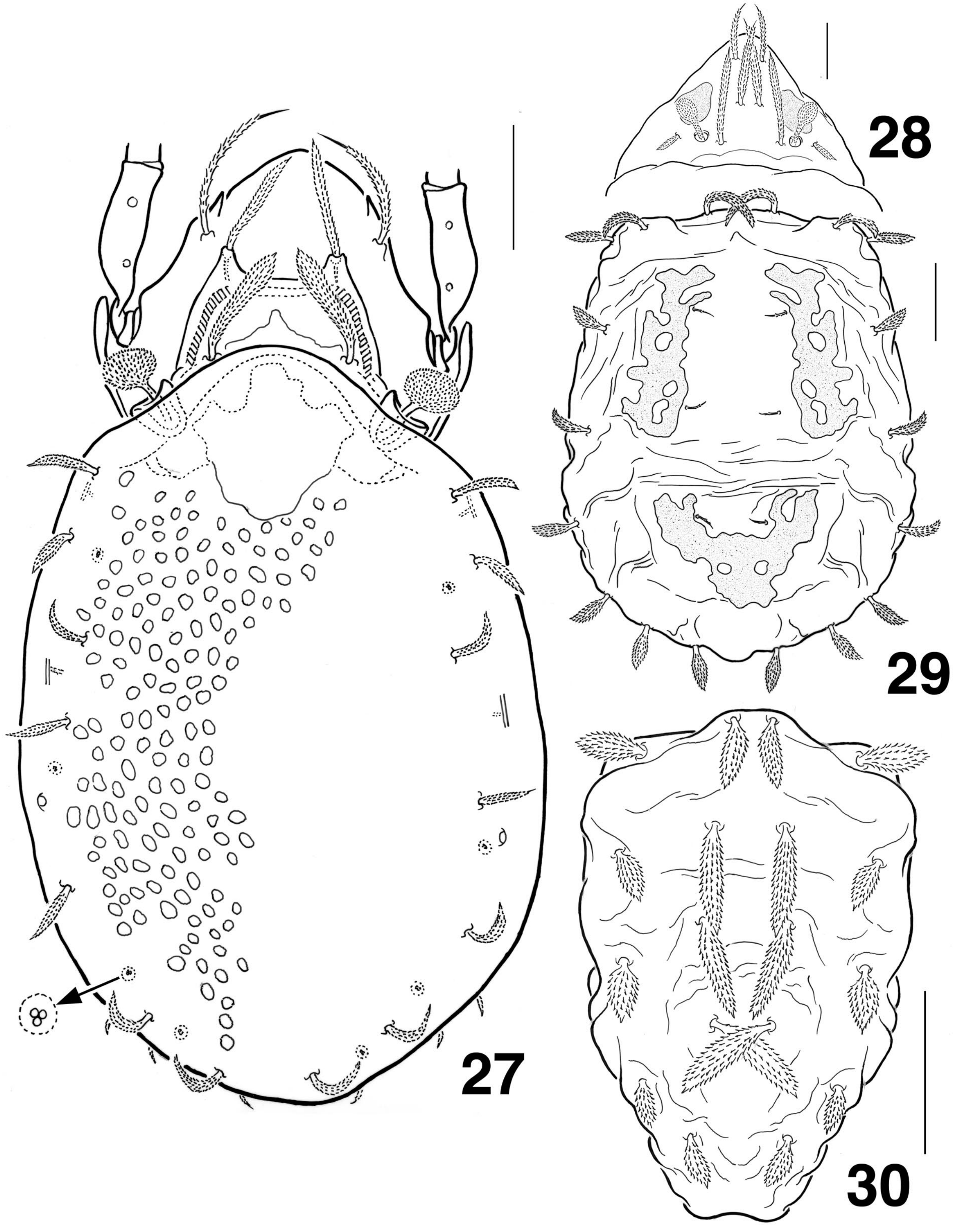
TABLE 1. Development of setiform organs in *Dendroeremaeus krantzi.* Setae (Roman) and solenidia (Greek) are listed opposite the instar in which they first appear; parentheses indicate pairs of setae.

*Description. Adult. Integument.* Fovea absent on lenticular area, present or not at edge. Leg segments with roughened integument. Body with granular cerotegument, easily removed. Color medium brown.

*Prodorsum.* Integument irregularly rugose posterior to translamella. Lamellae, including cusps, 55-57 μm long, slightly converging; translamella 25-29 μm long, depth 5-7 μm (FIG. 27). Lamellar cusps 13-16 μm long, narrowing anteriorly to width of lamellar setae (FIG. 27). Lateral carinae absent. Setae *ro* 62-70 μm long, spinose along length, smooth basally, acuminate distally; mutual distance at base about 67 μm. Setae *le* about 59-63 μm long, thick, heavily barbed along length, tapered distally, mutual distance at base 35-38 μm. Setae *in* about 51-60 μm long, thick, slightly fusiform in shape, heavily barbed along length, abruptly tapered distally, extending anteriorly to base of lamellar setae; mutual distance at base 49-58 μm. Bothridial setae about 39 μm long, with barbed globular head subequal in length to barbed stalk. Exobothridial setae about 13 μm long, spiniform.

*Lateral Region.* Pedotectum I covering acetabulum I, narrowing to width of carina and curving dorsally to level of seta *ex*. Pedotectum II covering acetabulum II. Sublamellar porose area Al small, about 2μm in diameter; humerosejugal porose areas Am oval, about 5μm at widest, Ah circular, about 5μm in diameter.

*Notogaster.* Longer than wide, ratio about 1.4:1.0. Lenticulus clearly developed. Notogastral setae of *c*, *l*, and *h* series about 22-26μm long; setae of *p* series about 17μm long. All notogastral setae thick, fusiform to phylliform in shape, heavily barbed along length, tapered distally; arranged laterally on notogaster, except *lm* positioned more medially; setae *lp*, and $h_3$ curving laterally and $h_2$ and $h_1$ curving anterolaterally (FIG. 27). Saccules small, composite, with 2 to 5 canals: Sa between setae *la* and *lm*, and closer to *la*, S1 midway between setae *lp* and $h_3$, and closer to *lp*, S2 midway between setae $h_3$ and $h_2$, and closer to $h_2$, and *S3* between $h_2$ and $h_1$ (FIG. 27).




FIGS. 27-30. *Dendroeremaeus foveolatus* n.sp: 27. — dorsal aspect of adult female (detail of sacculus indicated at arrow); 28. — tritonymph, prodorsum; 29. — tritonymph, detail of gastronotal region (illustrated separately from prodorsum because of distortion of slide-mounted specimen; 30. — larval scalp. Scale bars: = 50$\mu$m.

*Ventral Region*. Apodemes obscured by heavy areolate sculpturing of coxisternal region (as for *D. krantzi*, in FIG. 2). Ridge present medial to acetabulum IV. Epimeral, genital, aggenital and anal setae smooth, acuminate; epimeral and genital setae about 17μm long, aggenital and anal setae about 11μm long. Adanal setae $ad_1$ and $ad_2$ about 10μm long, thick, barbed, ensiform, seta $ad_3$ about 10μm long, barbed, narrower than $ad_1$ and $ad_2$, tapered.

*Gnathosoma*. With character states of genus. Mentum with weakly areolate integument. Axillary saccule about 8μm long.

*Legs.* Paraxial porose area present on femora I to IV and trochanters III and IV; porose area on femur III positioned dorsally. Leg setal formulae (trochanter to tarsus): leg I, 1-5-3(1)-4(2)-20(2); leg II, 1-5-3(1)-4(1)-15(2); leg III, 2-2-1(1)-3(1)-15; leg IV, 1-2-2-3(1)-12. Tibia III slightly longer than tarsus III; tibia IV subequal in length to tarsus IV. Setae *d* and *l'* of femora I and II, *(l)* of genua I and II, and *l"* of tibiae I and II thick, heavily barbed, tapered distally. Genual solenidia σI to σIII short, about 6μm long, subequal in length to fastigial seta. Tarsal solenidia $\omega_1$I, $\omega_2$I, $\omega_1$II and $\omega_2$II shorter than segment; tarsal solenidia closely adjacent on segments.

*Immatures. Measurements*. Mean length: deutonymph ($n$ = 1) 300 μm; tritonymph ($n$ = 1) 375 μm.

*Integument*. Line of dehiscence, where evident, extends anteriorly to *seta* $c_2$. Cerotegument weakly developed, microtuberculate. Integument weakly microtuberculate.

*Tritonymph. Prodorsum*. Lateral porose areas present anterior of bothridia (FIG. 28). Setae *ro* thick, heavily barbed along length, acuminate distally, about 44 μm long. Seta *le* thick, heavily barbed along length, tapered distally, about 69 μm long, subequal in shape to setae $c_1$. Setae *in* thick, heavily barbed along length, tapered distally, about 67 μm long. Mutual distance of setal pairs *ro, le* and *in* about 21, 13 and 46 μm, respectively. Setae *ex* thick, heavily barbed along length, fusiform to phylliform, about 21 μm long. Bothridial setae about 36 μm long, head barbed, capitate, subequal in length to barbed stalk (FIG. 28). Bothridium cup-shaped.

*Gastronotal Region*. Three porose regions present, irregularly shaped, consisting of longitudinal pair between setae *da, dm* and *la, lm,* which extends anteriorly almost midway between setae *la* and $c_1$, and single, transverse, U-shaped porose region lateral and posterior to setae *dp* (FIG. 29). Longitudinal porose areas each encompassing three small semi-circular non-porose regions; transverse porose area encompassing pair of semi-circular non-porose regions (FIG. 29). Gastronotal setae *c, l, h* series and $p_1$ thick, narrowly cymbiform, heavily barbed along length, tapered distally; $c_1$, $c_2$ and $c_3$, about 66, 49, 36 μm long, respectively; *la* about 43 μm, *lm* about 38 μm, *lp* and *h* series about 39 μm long, and $p_1$ about 16 μm long. Gastronotal setae $p_2$ about 13 μm long, heavily barbed; setae $p_3$ narrow, barbed, about 13 μm long, Gastronotal setae of *d* series short, thin, tapered, about 13μm long (FIG. 29).

*Ventral Region*. Medial margins of epimeral plates poorly defined; coxisternal porose areas present. Epimere I with narrow mentotectum overlying base of subcapitulum. Epimeral, genital, aggenital and anal setae smooth, acuminate, about 10 μm long; seta $ad_3$ heavily barbed, tapered to blunt distally, about 11 μm long; setae $ad_1$ and $ad_2$ barbed, tapered, about 11 μm long. Porose regions present lateral to aggenital and adanal setae.

*Deutonymph.* Shape of prodorsal and gastronotal setae similar to that of tritonymph. Porose areas on femora I to IV clearly present in deutonymph, as in tritonymph.

*Larva*. Scalp of larva, carried with other scalps by tritonymph, illustrated (FIG. 30).

*Remarks:*

*Scalps.:* The deutonymph of *D. foveolatus* examined was apheredermous, whereas 1 of 3 tritonymphs examined carried scalps.

*Sex ratios.* Available evidence indicates that adults of *Dendroeremaeus foveolatus* reproduce sexually, as a single male was collected in the Oregon population.

*Sacculi*. The octotaxic organs generally have a composite form in this species, with 2 to 5 canals, similar to those illustrated for species of *Scheloribates* (Scheloribatidae) by NORTON *et al* (1997; their FIG. 5e).

*Identification.* Adults of the two species are easily distinguished by the following differences. Notogastral integument: reticulate in *D. krantzi*, foveate in *D. foveolatus.* Lenticulus: weakly developed in *D.*

*krantzi*, integument of lenticular area with reticulations; well-developed in *D. foveolatus*, integument of lenticulus without fovea. Carina lateral to lamella: present in *D. krantzi*, absent in *D. foveolatus*. Tritonymphs of the two species are easily distinguished by the following differences. Exobothridial seta: longer than bothridial seta in *D. krantzi*, much shorter than bothridial seta in *D. foveolatus*. Gastronotal setae of *c*, *l* and *h* series: subequal in length in *D. krantzi*; $c_1$ clearly longest seta in *D. foveolatus* and *lm* subequal in length to $c_3$.

## Discussion

The Licneremaeoidea has not been subject to formal cladistic analysis; such an analysis is beyond the scope of our study, and is possibly premature as immatures of Fenichelidae are unknown, as are those of Eremellidae, Papillonotidae and *Tuberemaeus*, considered possible relatives by Woas (2002). However, the following remarks on systematic relationships of Dendroeremaeidae are presented in a cladistic context.

*Character Analysis: Immatures.* Nymphs of Dendroeremaeidae have plicate hysterosomal integument and are mainly apheredermous, as are immatures of Tectocepheoidea (Tectocepheidae), Ameronothroidea (Ameronothridae, Fortuyniidae, Selenoribatidae, Tegeocranellidae), Cymbaeremaeoidea (Cymbaeremaeidae), Licneremaeoidea (Licneremaeidae, Passalozetidae, Scutoverticidae, Micreremidae, Adhaesozetidae, Lamellareidae, Fenichelidae), Achipterioidea (Achipteriidae, Tegoribatidae), Phenopelopoidea (Phenopelopidae) and the Eremaeozetidae, postulated a close relative of Cymbaeremaeidae by Schatz (2000). Below, we consider these superfamilies and families to help determine character state polarities in Dendroeremaeidae. Among Brachypylina the plicate condition of the hysterosomal integument is considered plesiomorphic, as this character state is found in brachypyline ancestors, the Desmonomata (Norton & Behan-Pelletier 1986, Norton 1998). The polarity of apheredermy is not so clear, as, other than Hermanniellidae, the most basal families in Brachypylina, i.e., Neoliodidae and Plasmobatidae, are eupheredermous (Woas 2002). Apheredermes and Eupheredermes are two of several groups in Grandjean's (1954) classification of brachypyline families, which was based on immature instars. He recognized that immatures of Brachypylina have a more conserved morphology than do adults, and therefore developmental traits might justifiably be weighed more heavily when studying relationships. Placement of Dendroeremaeidae in Grandjean's classification of nymphal types is not straightforward as three of the ten tritonymphs of *Dendroeremaeus* examined in this study are eupheredermous, and have all scalps of previous instars attached: scalps are flattened to the opisthonotum, and are easily removed. Although the line of dehiscence in the cuticle of all *Dendroeremaeus* immatures we have examined is incomplete, it must have been effectively complete in these eupheredermous tritonymphs (Fig. 23). Eupheredermy is often interpreted as a clear presence or absence character, but as Grandjean (1947, 1958, 1960) noted similar examples of temporary scalp carrying in several apheredermous plicate taxa (*Cymbaeremaeus, Ameronothrus, Peloptulus, Tectocepheus*), and in the apheredermous, unrelated oppioid genus *Autogneta* (Autognetidae). Grandjean (1958) recorded collections of *Ameronothrus maculatus* (Michael) among which most adults carried tritonymphal scalps. Furthermore, Grandjean (1958) considered Charassobatidae as closely related to *Licneremaeus*, with which it shares a large pedotectum I, absence of pedotectum II, corrosion of the bothridial seta in lactic acid, and anal plates smaller than genital plates; but unlike Licneremaeidae, its nymphs carry scalps [1]. He established a separate category — eupheredermes with centrodorsal setae present in nymphs — for this species, considering it distinct from the apopheredermous condition found in Oribatellidae, where centrodorsal setae of nymphs are large and the octotaxic system is present in adults.

Immatures of *Dendroeremaeus* are unideficient and the gastronotal setae of *Dendroeremaeus* nymphs are strongly dimorphic, with centrodorsal setae much smaller and less barbed than the *c*, *l* and *h* series setae.

1. In his description, Grandjean (1958) noted that scalps were removed from tritonymphs he illustrated (his Fig. 4), and that all nymphs in his collection carried scalps.

All gastronotal setae are similar in size and shape in known immatures of Passalozetidae, Adhaesozetidae, Licneremaeidae, and Achipteriidae. But dimorphy is found in the Eremaeozetidae (SCHATZ 2000), the micreremid *Micreremus brevipes* (Michael, 1888) (MICHAEL 1888), the scutoverticid *Argentinovertex coineaui* Fernandez and Cleva, 2002, the lamellareid *Tenuelamellarea argentinensis* (MARTINEZ *et al* 1995), the tegoribatid *Tegoribates americanus* Hammer, 1958 (BEHAN-PELLETIER 2001) [1], and in Phenopelopidae (HAMMEN 1952).

Distinct prodorsal, aggenital, and adanal porose regions and porose regions surrounding the opening of the opisthonotal gland and in the coxisternal region are found in some immatures of both ameronothroid and cymbaeremaeoid species. Among Licneremaeoidea they occur in larval and nymphal Adhaesozetidae (WALTER & BEHAN-PELLETIER 1993), and adanal porose areas are present in nymphal Micreremidae (WALTER & BEHAN-PELLETIER 1993), so their presence in Dendroeremaeidae must be considered plesiomorphic. However, porose regions on the gastronotal region of tritonymphs of Dendroeremaeidae are unique in Licneremaeoidea. These porose regions lack pigment, and are weakly developed in one species, but are as extensive as those described in immatures of the ameronothroids *Podacarus auberti* Grandjean, 1955 (GRANDJEAN 1955), *Alaskozetes antarcticus* (Michael) and *Halozetes* spp. (WALLWORK 1964). Porose sclerites in these latter taxa were one of the character states GRANDJEAN (1955) used to establish the family Podacaridae, and numbers of these sclerites help distinguish among species in this family (WALLWORK 1964). Although Podacaridae was subsequently synonymized with Ameronothridae by WEIGMANN & SCHULTE (1977), gastronotal porose sclerites are not known for immatures of other ameronothrid genera. The porose regions in Dendroeremaeidae are distinct from those developed in Ameronothroidea — they form three porose regions, rather than distinct sclerites — and appear independently derived.

Seta *d* on the genua and tibiae is retained to the tritonymph in all licneremaeoid families, except Micreremidae, Adhaesozetidae and Dendroeremaeidae, where it is absent from all instars. This loss is a possible synapomorphy of these families. Among other higher plicates retention of this seta to the tritonymph (DDC n3, *sensu* GRANDJEAN 1954) is found in Achipterioidea. This seta is retained to the adult (DDC Ad, *sensu* GRANDJEAN 1954) on tibia IV of adults of Phenopelopinae, which NORTON & BEHAN-PELLETIER (1986).considered a possibly atavistic reversal associated with the need for at least some sensory capacity in the dorsal area of tibia IV.

Within both 'lower plicates' and 'higher plicates', Dendroeremaeidae is unique in the different expression of the exobothridial setae in immatures (fusiform and heavily barbed) and adults (short, spinate). Within Licneremaeoidea, Dendroeremaeidae retains the plesiomorphic unideficient gastronotal setation, i.e., lacking setae $f_1$. Nymphs of Licneremaeidae and Lamellareidae are bideficient (lacking setae $f_1$, $p_3$) (MARTINEZ *et al* 1995), and those of Adhaesozetidae are trideficient (lacking setae $c_3$, $f_1$, $p_3$) (WALTER & BEHAN-PELLETIER 1993).

*Character Analysis: Adults*

The octotaxic system, the feature defining the poronotic Brachypylina, is absent in Ameronothroidea and Cymbaeremaeoidea, but is present in Licneremaeoidea. Among the Licneremaeoidea the complete system of 4 pairs occurs only in Passalozetidae, Fenichelidae (some genera) and Dendroeremaeidae; adults of Micreremidae and Scutoverticidae have 0 to 3 pairs, adults of Licneremaeidae and Lamellareidae have 2 pairs, and adults of Adhaesozetidae have 1 pair (NORTON & ALBERTI 1997). Whether the 4 pairs in Dendroeremaeidae is plesiomorphic or apomorphic is unclear as expression of the octotaxic system is quite varied throughout the poronotic Brachypylina (NORTON & ALBERTI 1997).

Among Licneremaeoidea, only Dendroeremaeidae express two character states that are common in nonplicate poronotic taxa — a genal notch on the prodorsum, and presence of the sublamellar porose area Al — and these are possible apomorphies for Dendroeremaeidae within the superfamily. The genal notch is generally present in the higher plicate super-

1. *Tegoribates americanus* was described as apopheredermous in BEHAN-PELLETIER (2001), a paper which overlooked the study of GRANDJEAN (1958); this species is more correctly described as being eupheredermous with centrodorsal setae present in nymphs.

family Phenopelopoidea, and in the achipterioid family Achipteriidae, but is absent from the achipterioid family Tegoribatidae (BEHAN-PELLETIER 2001). It is also expressed in the Tectocepheidae, a family usually considered a 'lower plicate' (BALOGH & BALOGH 1992), but which clusters close to the higher plicate genus *Eupelops* (Phenopelopidae) in a molecular analysis of Oribatida (MARAUN *et al* 2004). Among higher plicates the sublamellar porose area Al is only known from the Phenopelopoidea and Achipterioidea, although both it and the genal notch are widespread in the pronotic group Ceratozetoidea.

Among Licneremaeoidea, only *Dendroeremaeus krantzi* has a postanal porose area on the ventral plate. Among higher plicate families this character state is only found in the Tegoribatidae (BEHAN-PELLETIER 2001).

The typical, adult brachypyline coxisternal setation of 3-1-3-3 is reduced to 3-1-2-2 in the Dendroeremaeidae and in other licneremaeoid families, other than Lamellareidae, Passalozetidae and some members of the Scutoverticidae. However, this character state is present in Ameronothroidea and Cymbaeremaeoidea and it is possibly homoplastic in plicate apheredermous taxa.

Dendroeremaeidae has a small, but distinct axillary saccule at the base of the palp. This structure has a rather mosaic distribution in Brachypylina (NORTON & BEHAN-PELLETIER 1986, NORTON & ALBERTI 1997, CHEN *et al* 2004). It is common in poronotic taxa, including the licneremaeoid families Scutoverticidae and Adhaesozetidae, the Phenopelopoidea and the achipterioid family Tegoribatidae, but is absent from another achipterioid family, Achipteriidae, and members of the poronotic taxa Oripodoidea, and most non-poronotic Brachypylina, other than some species of *Eremaeus*, *Amerus,* and *Gymnodampia* (CHEN *et al* 2004).

In Dendroeremaeidae, as in all poronotic Brachypylina, with the exception of Licneremaeidae and Scutoverticidae, eupathidium *acm* is fused with the palp tarsal solenidion. This character is one of many with more than one state expressed in Licneremaeoidea, supporting the contention of NORTON & ALBERTI (1997) that the superfamily is paraphyletic. For example, pedotectum II is absent in Licneremaeidae, a character state this family shares with Charassobatidae (GRANDJEAN 1958), but is present in all other licneremaeoid families, in Cymbaeremaeoidea and Tectocepheoidea.

On the notogaster of Dendroeremaeidae dorsolateral setae *lm* and *lp* remain in a lateral position and the central region of the notogaster is glabrous. Usually in apheredermous taxa that lack dorsocentral setae in adults, one or more dorsolateral setae shift medially to occupy the central space, as is found in Passalozetidae. This plesiomorphic lateral positioning of *lm* and *lp* is also found in Lamellareidae (COETZEE 1987).

In the licneremaeoid families Dendroeremaeidae, Passalozetidae and Lamellareidae, and in Phenopelopoidea and Achipterioidea, the preanal apodeme is a goblet-shaped structure, with a narrow neck, in contrast to the small, narrow, caecum-shaped apodeme in those other licneremaeoid families for which the structure of this apodeme is known.

*Systematic Relationships.*

Among Brachypylina having both apheredermous plicate immatures and the octotaxic system of porose organs (higher plicates), only Dendroeremaeidae share a sublamellar porose area Al with Phenopelopoidea and Achipterioidea, and a genal notch on the prodorsum with Phenopelopoidea and Achipteriidae. However, members of Achipterioidea and Phenopelopoidea have pteromorphs, custodia and circumpedal carinae, character states absent in Dendroeremaeidae. Furthermore, Dendroeremaeidae lacks the autapomorphy for Phenopelopoidea — blocky, birefringent cerotegument. Similarities in a number of character states support a relationship between Dendroeremaeidae and families within the Licneremaeoidea: (1) octotaxic system expressed as 4 pairs, shared with Passalozetidae; (2) coxisternal setation 3-1-2-2, shared with Micreremidae, Adhaesozetidae, Scutoverticidae and Licneremaeidae; (3) seta *d* absent from tibiae and genua of both immatures and adults, shared with Micreremidae and Adhaesozetidae; (4) eupathidium *acm* fused to palptarsal solenidion, shared with Micreremidae, Adhaesozetidae, Passalozetidae and Lamellareidae; (5) preanal sclerite goblet shaped with narrow neck, shared with Passalozetidae and Lamellareidae; (6) immatures with adanal porose regions shared with Micreremidae; (7) immatures with prodorsal porose areas, shared with Adhaesozetidae; (8) immatures with dimorphic gastronotal setae *c, l,* and *h* series, shared with some species of Micreremidae, Scutoverticidae and Lamellareidae. Of these character states only 4 and 5 are considered to have evolved only once within the Oribatida. Lee (1991) used the shape of the preanal apodeme (among other characters) to develop a classification of Oripodoidea, with Licneremaeoidea as outgroup. He considered Lamellareidae as basal in Oripodoidea, and included Lamellareidae with Crassoribatulidae (a family recently synonymized with Oribatulidae (Subias 2004)) and the oribatulid subfamily Fovoribatulinae in the "crassoribatulid complex", a complex he considered primitive in the Oripodoidea. It is possible that some species included in the "crassoribatulid complex" may prove to have plicate nymphs. Certainly, as already noted, without knowledge of immatures, Dendroeremaeidae would have been placed in the Oribatulidae.

Within Licneremaeoidea, Dendroeremaeidae appears most closely related to Passalozetidae and Lamellareidae. However, the possible paraphyly of Licneremaeoidea (Norton & Alberti 1997), and the character states Dendroeremaeidae share with Tectocepheoidea and Ameronothroidea indicate the need for detailed phylogenetic analysis of all apheredermous plicate Brachypylina, one that incorporates morphological and molecular character states.

## Aknowledgements

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## References

Balogh (J.) & Balogh (P.), 1988. — Oribatid Mites of the Neotropical Region I. — In: Balogh (J.) & Mahunka (S.) (eds.): The Soil Mites of the World. Vol. 2. Akademiai Kiadó, Budapest. 335 pp.

Balogh (J.) & Balogh (P.), 1992. — The Oribatid Mites Genera of the World. Volume 1. — The Hungarian National Museum Press, Budapest, **4**: 263 pp.

Behan-Pelletier (V.M.) 2001. — Phylogenetic relationships of *Hypozetes* (Acari: Tegoribatidae). — In: Halliday (R.B.), Walter (D.E.), Proctor (H.C.), Norton (R.A.) & Colloff (M.J.) (eds.): Acarology: Proceedings of the 10th International Congress. CSIRO Publishing, Melbourne, Australia: 50-57.

Chen (J.), Behan-Pelletier (V. M.), Norton (R. A.) & Wang (H. F.), 2004. — Analysis of *Gymnodampia* (Acari: Oribatida), with redescription of *G. setata* Jacot and description of two new species from North America. — Can. Ent. **136**: 793-822.

Coetzee (L.), 1987. — The South African Lamellareidae Balogh, 1972 (Acari, Oribatei). — Navors. Nas. Mus., Bloemfontein, **5**(13): 326-353.

Fagan (L.L.) & Winchester (N.N.), 1999. — Arboreal arthropods: diversity and rates of colonization in a temperate montane forest. — Selbyana 20: 171178.

Fernandez (N.A.) & Cleva (R.), 2002. — Contribution à la connaisance des Oribates d'Argentine I. *Argentinovertex coineaui* n. gen. n. sp. — Acarologia, **42**(1): 89-103.

Grandjean, (F.), 1947. — Observations sur les Oribates (18e série). — Bull. Mus. nat. Hist. natur. (2), **19**: 395-402.

Grandjean, (F.), 1954. — Essai de classification des Oribates (Acariens). — Bull. Soc. zool. France, **78** (1953): 421-446.

Grandjean, (F.), 1955. — Sur un Acarien des iles Kerguelen. *Podacarus Auberti* (Oribate). — Mém. Mus. nat. Hist. natur. (n.s.), sér. A, Zool., **8**: 109-150.

Grandjean, (F.), 1958. — *Charassobates cavernosus* Grandjean 1929 (Acarien, Oribate). — Mém. Mus. nat. Hist. natur. (n.s.), sér. A, Zool., **16**: 121-140.

Grandjean, (F.), 1960. — Les Autognetidae n.fam. (Oribates). — Acarologia, **2**: 575-609.

Hammen, (L.) van der, 1952. — The Oribatei (Acari) of the Netherlands. — Zool. Verh., Leiden, **17**: 1-139.

Lee, (D.C.), 1991. — A modified classification of the Oripodoidea (Acarida: Cryptostigmata) based on a preliminary phylogenetic model. — In: Dusbabek (F.) & Bukva (V.) (eds.): Modern Acarology. Academia, Prague, vol. 2: 233-238.

Mahunka (S.) & Zombori (L.) 1985. — The variability of some morphological features in Oribatid mites. — Folia Entomol. Hung., S.N., **46**(1): 115-128.

MARAUN (M.), HEETHOFF (M.), SCHNEIDER (K.), SCHEU (S.), WEIGMANN (G.), CIANCIOLO, (J.), THOMAS (R.H.), & NORTON (R.A.), 2004. — Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. — Expt. Appl. Acar. **33**: 183—201.

MARTINEZ (P.A.), VELIS (G.J.), EGUARAS (M.J.) & FERNANDEZ (N.A.), 1995. — La famille Lamellareidae dans la République Argentine. *Tenuelamellarea argentinensis* n.sp. — Acarologia, **36**(4): 355-361.

MICHAEL (A.D.), 1888. — British Oribatidae. vol. II. — Ray Society, London: 337-657.

NORTON (R.A.), 1998. — Morphological evidence for the evolutionary origin of Astigmata (Acari: Acariformes). — Exp. Appl. Acar., **22**: 559-594.

NORTON (R.A.) & ALBERTI (G.), 1997. — Porose integumental organs of oribatid mites (Acari, Oribatida). 3. Evolutionary and ecological aspects. — Zoologica. **146:**115-143.

NORTON (R.A.) & BEHAN-PELLETIER (V.M.), 1986. — Systematic relationships of *Propelops*, with a modification of family-group taxa in Phenopelopoidea (Acari: Oribatida). — Can. J. Zool. **64**: 2370-2383.

NORTON (R.A.) ALBERTI (G.), WEIGMANN (G.) & WOAS (S.), 1997. — Porose integumental organs of oribatid mites (Acari, Oribatida). 1. Overview of types and distribution. — Zoologica **146**: 1-31.

SCHATZ (H.), 2000. — *Eremaeozetes sabinae* sp. nov. (Acari: Oribatida) from the Hawaiian Islands. — Internat. J. Acarol. **26**: 155-159.

SCHOWALTER (T. D.) & GANIO (L.M.), 1998. — Vertical and seasonal variation in canopy arthropod communities in an oldgrowth conifer forest in southwestern WA, USA. — Bull. Ent. Res. **88**: 633640.

SUBIAS (L.S.), 2004. — Listado sistemático, sinonímico y biogeográfico de los ácaros oribátidos (Acariformes, Oribatida) de mundo (1758-2002). — Graellsia **60**: 3-305.

TRAVÉ (J.) & VACHON (M.), 1975. — François GRANDJEAN 1882-1975 (Notice biographique et bibliographique). — Acarologia, **17**(1): 1-19.

WALLWORK (J.A.), 1964. — A revison of the family Podacaridae Grandj. (Acari: Oribatei). — Acarologia, **6**(2): 387-399.

WALTER (D.E.) & BEHAN-PELLETIER (V.M.), 1993. — Systematics and ecology of *Adhaesozetes polyphyllos* sp.nov. (Acari: Oribatida: Licneremaeoidea), a leaf inhabiting mite from Australian rainforests. — Can. J. Zool., **71**: 1024-1040.

WEIGMANN (G.) & SCHULTE (G.), 1977. — The evolution of the family Ameronothridae (Acari: Oribatei). I. Morphological aspects. — Acarologia, **19**(1): 161-166.

WINCHESTER (N.N.), BEHAN-PELLETIER (V.), & RING (R.A.), 2000. — Arboreal specificity, diversity and abundance of canopy-dwelling oribatid mites (Acari: Oribatida). — Pedobiologia **43**:391-400.

WOAS (S.), 2002. — Acari: Oribatida. — In ADIS, J. (Ed.), Amazonian Arachnida and Myriapoda. Sofia-Moscow: Pensoft Publishers: 21-291.