

Phylogenetic relationships of *Paralamellobates*: immature characters of *P. misella* (Berlese) place the genus in Punctoribatidae (Acari, Oribatida)

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ABSTRACT — Species in the oribatid mite genus *Paralamellobates* are primarily tropical and subtropical, and are found in both arboreal and soil habitats. Herein, we describe all stages of *P. misella* (Berlese) collected from banana from the Philippines. We provide a revised and expanded diagnosis for *Paralamellobates*. *Paralamellobates striatus* Behan-Pelletier, described from Costa Rica, is considered a junior synonym of *P. misella* **new. syn.** We assess relationships of *Paralamellobates* using characters of adults and its apherodermous immatures. Based on morphology, the closest relatives are hypothesized to be among the Punctoribatidae (Ceratozetoidea) rather than among the Achipteriidae (Achipterioidea), and the Oribatellidae (Oribatelloidea) as suggested in previous classifications. However, molecular studies did not support our morphological analysis.

KEYWORDS — Oribatida; *Paralamellobates misella*; Punctoribatidae; Poronotic Brachypylina; morphology; molecular analysis

INTRODUCTION

The oribatid mite genus *Paralamellobates* has a checkered history. It was described as a subgenus of *Lamellobates* by Bhaduri and Raychaudhuri (1968), and considered a distinct genus by Behan-Pelletier (1998) and Norton and Ermilov (2014), although Subias (2004) retained subgeneric status. *Paralamellobates* includes 5 named species: the type species, *P. bengalensis* Bhaduri & Raychaudhuri, 1968, described from India, *P. misella* (Berlese, 1910) described as a species of *Oribatella* from Java, *P. ceylanicus* (Oudemans 1915) described as a species of *Oribatella* from Sri Lanka, *P. striatus* Behan-Pelletier, 1998 described from Costa Rica and *P. schoutedeni*

(Balogh 1959) described as a species of *Oribatella* from Angola. Of these, only the type species, and *P. schoutedeni* and *P. striatus* were illustrated in the original descriptions. Descriptions of Berlese's and Oudemans's species of *Paralamellobates* are short and lack illustration. Mahunka (1977), who examined the type specimen of Balogh's species, determined that *P. schoutedeni* is a junior synonym of *P. ceylanicus*, noting that it is "wholly identifiable with the well described and illustrated Oudemans's species". However, we are unaware of any illustrations of *P. ceylanicus* prior to Engelbrecht's (1986) re-description of this species based on material from Nigeria, Angola and South Africa. He accepted

Mahunka's synonymy and noted that this material corresponded "almost completely with Balogh's description of *P. schoutedeni*". He noted small variation between his specimens and the illustration of Balogh (1959), e.g., bothridial seta fusiform, not clavate, interlamellar setae more slender and glabrous, lamellar setae thinner and more glabrous and notogastral setae less prominent. He considered *P. ceylanicus* to have an almost cosmopolitan distribution. Hammer (1979) recorded *P. schoutedeni* from a number of habitats in Java, but provided no explanation for her species determination.

Mahunka (1991) who examined the type of *P. misella* considered, that it is "identical with or stands very near to" *P. ceylanicus*. Subías (2004, 2013) considered *P. ceylanicus* a junior synonym of *P. misella*, and this synonymy was accepted by Ermilov and Anichkin (2013) and Ermilov and Niedbala (2013), who recorded *P. misella* from Vietnam and Zambia, respectively. We follow Mahunka (1977, 1991) and Subías (2004) in their consideration that both *P. ceylanicus* and *P. schoutedeni* are junior synonyms of *P. misella*. Furthermore, we determined (see below) that *P. striatus* is also a junior synonym. *Paralamellobates misella* now has been recorded (under the names *misella*, *ceylanicus*, *schoutedeni*, *striatus*) from Java (Berlese 1910, Hammer 1979), Vietnam and Zambia (Ermilov and Anichkin 2013, Ermilov and Niedbala 2013), Saudi Arabia (Bayoumi and Al-Khalifa 1985), Angola (Balogh 1959, Engelbrecht 1986), Nigeria, South Africa (Engelbrecht 1986), the Philippines (Bayubay and Corpus-Raros 2006), Vietnam (Dao *et al.* 2010), China (Hong Kong) (Chen *et al.* 2010), Japan (Chinone and Ohmura 1981), Costa Rica (Behan-Pelletier 1998) and the Galapagos Islands (Baert 2011).

Collectively, species of *Paralamellobates* are primarily tropical and subtropical in distribution, though there are scattered, unidentified records from southern temperate regions in North America. Specimens have been collected from undisturbed forest with tree ferns and moss, from disturbed habitats such as rotting vegetation along roadsides, from secondary growth close to wet areas and from arboreal habitats.

The phylogenetic placement of *Paralamellobates* and *Lamellobates* has been the subject of some confusion. They were considered members of Oribatellidae by Oudemans (1915), Balogh (1959), Hammer (1979), Engelbrecht (1986) and Fujikawa (1991). They were placed in Austrachipteriidae by Behan-Pelletier (1998) and Subías (2004), which itself was placed in synonymy with Achipteriidae by Behan-Pelletier (2001) based on examination of adult and immature members of *Austrachipteria*. Behan-Pelletier (2001) hinted at possible relationship with Tegeribatidae, noting that immatures of *Lamellobates* and *Paralamellobates* lack the microsclerites of Oripodoidea, the macrosclerites of Ceratozetoidea and Galumnoidea, the apopheredermous condition of Oribatellidae and the strong plications of Phenopelopoidea and Achipteriidae. Schatz (2006) followed this idea, and included *Lamellobates* and *Paralamellobates* in Achipteriidae. *Paralamellobates* was placed in Anachipteriidae by Bayubay and Corpus-Raros (2006), a family without diagnosis and not recognized by Subías (2004) or Schatz *et al.* (2011). The two genera have been treated as unplaced genera in Ceratozetoidea (e.g. Balogh and Balogh 1992) and *Paralamellobates* was treated as an unplaced brachypylinae genus by Norton and Ermilov (2014). Recently, the genus has been placed in Punctoribatidae (=Mycobatidae) by Ermilov and Anichkin (2013) and Ermilov and Niedbala (2013), but without arguments.

In this paper we give a revised and expanded diagnosis of *Paralamellobates*, describe all stages of *Paralamellobates misella*, reared from four adults intercepted in New Zealand on banana imported from the Philippines, and give data on their biology. We support the inclusion of the genus in Punctoribatidae, based on the morphology of adults and immatures. However, evidence from molecular data does not support this placement.

MATERIALS AND METHODS

Terminology and Conventions

Morphological terminology used in this study follows that developed by Grandjean (see Trávě and

TABLE 1: Primers used for PCR amplification and sequencing of the 18S gene, the D2/D3 regions of the 28S rRNA gene and mitochondrial cytochrome oxidase I (COI) gene.

Gene	Primer name	Sequence (5'-3')	References
18S rRNA	1096F	GGTAATTCTGGAGCTAATAC	Holterman <i>et al.</i> 2006
	1912R	TTTACGGTCAGAACTAGGG	Holterman <i>et al.</i> 2006
	1813F	CTGCGTGAGAGGTGAAAT	Holterman <i>et al.</i> 2006
	2646R	GCTACCTTGTTACGACTTTT	Holterman <i>et al.</i> 2006
D2/D3 of 28S rRNA	D2A	ACAAGTACCGTGAGGGAAAGT	Nunn 1992
	D3B	TGCGAAGGAACCAGCTACTA	Nunn 1992
COI	CI-J-1718F	GGAGGATTTGGAAATTGATTAGTTCC	Simon <i>et al.</i> 1994
	COI-REVA	GATAAAACGTAATGAAAATGAGCTAC	Gotoh <i>et al.</i> 2009

Vachon 1975 for references, and Norton and Behan-Pelletier 2009 for overview). The following conventions of measurement and description are used: measurements are in micrometers; *prodorsal setae* measured on slide-mounted specimens (*ro*, rostral seta; *le*, lamellar seta; *in*, interlamellar seta; *ex*, exobothridial seta; *bo*, bothridial seta (sensillus)); *total length*, measured from tip of rostrum to posterior edge of notogaster on specimens in cavity slides, except when noted; *notogastral length to width ratio*, measured when viewed perpendicular to circumgastric scissure on specimens in cavity slides; *leg setal formula*, given as setal count on segments, with famulus included in tarsus I count, and solenidial counts given in parentheses. The inclusion of a single leg setal notation in parentheses denotes a pseudosymmetrical pair. The unideficiency nomenclature for notogastral setae is used herein; probable synonymies of this nomenclature with the holotrichous nomenclature of Grandjean were outlined by R. A. Norton in Balogh and Balogh (1988).

Imagery

Differential interference contrast images were obtained by a Nikon DS-Fi1 camera and any image stacks were combined (layered) with the aid of Helicon Focus Pro (v. 5.3) suite.

Specimens for scanning electron microscopy were cleaned by soaking in Terg-a-zyne® solution for 6-12h, 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.

DNA extraction, PCR and sequencing

Total DNA was extracted using the DNeasy for Blood and Tissue kit (Qiagen, Valencia, CA, USA) as per the manufacturer's instructions, with a slight modification as DNA was eluted twice with pre-warmed 50 µL AE buffer. Four individual mites were used for DNA extraction; two of them were treated destructively by physical disruption of the mite using micro-pestles, the other two were extracted non-destructively for retention as voucher specimens.

The primers used for PCR amplification and sequencing of the 18S, COI, D2/D3 regions of the 28S ribosomal RNA (rRNA) and mitochondrial cytochrome oxidase I (COI) genes are listed in Table 1. Briefly, two primer pairs, 1096F / 1912R and 1813F / 2646R (Holterman *et al.*, 2006), were used to amplify two fragments of the 18S rRNA gene. Primer pair D2A / D3B (Nunn, 1992) was used for a 800 bp fragment of the D2/D3 region of 28S rRNA gene, while the pair CI J-1718F / COIVERA (Simon *et al.*, 1994; Gotoh *et al.*, 2009) was used to amplify 1,000 bp of the COI. For all PCR reactions, each 20 µL volume consisted of 1x GoTaq master mix (Promega, Madison, WI), 250 nM of each primer, 0.04 µg/µL Bovine Serum Albumin (BSA, Sigma-Aldrich Co.), and 2 µL of DNA extract. Cycling conditions were: initial denaturation at 94°C for 2 min, 40 cycles of 94°C for 15 sec, 52°C for 30 sec and 72°C for 45 sec, followed by final extension

step of 7 min at 72°C. The amplicons were electrophoresed on 1.2 % agarose (in 1x TAE buffer) gels stained with SYBR® safe (Life Technologies™), and visualised using a Gel Doc Software system (BioRad, Hercules, CA, USA). Amplified products were sequenced bi-directionally using the amplification primers by EcoGene® (Auckland, New Zealand). The obtained DNA sequences were assembled, edited and aligned using Geneious Pro 7.1.5 (Biomatters, Auckland, New Zealand). The sequences were BLAST searched against the GenBank database (Altschul *et al.*, 1990). The obtained sequences were submitted into GenBank under the Accession numbers: CO1, KT781156; 18S, KT781157; 28S, KT781158.

All other DNA sequences for the 18S, 28S and COI genes of species from the cohort Brachypylina (superfamilies Achipterioidea, Carabodoidea, Ceratozetoidea, Cymbaeremaeoidea, Eutegaeoidea, Hydrozetoidea, Licneremaeoidea, Oribatelloidea, Oripodoidea, Phenopelopoidea, Tectocephoeidea and Eremaezetoidea) were downloaded from GenBank.

All DNA sequences were aligned with Geneious alignment and then re-aligned with MUSLE in Geneious Pro 7.1.5 (Biomatters Ltd, Auckland, New Zealand) using default parameter values. The aligned sequences were manually checked and edited if necessary. The alignment used for phylogenetic analysis was performed using Maximum-Likelihood (PHYML) and MrBayes in Geneious Pro 7.1.5 under the default settings (Huelsenbeck and Ronquist 2001). The MrBayes tree was run using GTR model with an invgamma-shape parameter, the resulting trees were inspected for chain convergence in Tracer 1.4 (Rambaut and Drummond, 2007). The 18S trees were rooted using sequences of *Atropacarus striculus* (EF091416), *Hypochthonius rufulus* (EF093784) and *Trhypochthonius tectorum* (AF022041) as outgroups.

Rearing

Preliminary biological observation was carried out in a physical containment laboratory (Level 3, PC3, Auckland, New Zealand). Four adult mites were individually kept in plastic bottles (55 mm height,

42 mm diameter) each with the calyx end of banana fruit as habitat and food source. The bottles were sealed and put in the PC3 lab at $22 \pm 1^\circ\text{C}$, $42 \pm 5\%$ RH with a dim light source at the ceiling. Fruit ends were checked daily and life stages and number of mites were recorded. The fruit end provided ambient micro-environment and food source for the mites.

TAXONOMY

Paralamellobates Bhaduri & Raychaudhuri, 1968

Type species: *Paralamellobates bengalensis* Bhaduri & Raychaudhuri, 1968; p. 197

Diagnosis: Adult — Species comprising this genus are unique among poronotic Brachypylina (Grandjean 1953) in having the following combination of character states. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region. Rostrum rounded medially with pair of strongly developed teeth. Lamellae broad, converging, cusps with medial and lateral teeth subequal in length. Medial margins of cusps parallel. Humero-sejugal porose area Am long, oval; Ah present, poorly delimited. Genal tooth long, subtriangular, with carina extending along length. Tutorium narrow with pointed cusp. Pedotectum I convex dorsally; with dorsal margin ventral to insertion of seta *ex*. Pedotectum II present. Custodium triangular. Discidium triangular between acetabula III and IV. Dorsophragmata separate. Nine pairs of smooth, acuminate notogastral setae (setae *c1*, *c3*, *d* series and *p3* absent). Lenticulus absent. Octotaxic organs developed as saccules, dimorphic: Sa, S2 and S3 long, filiform tubules, S1 elongated saccule. Posterior tectum developed, divided medially, with overlapping lobes. Pteromorphs curved ventrally, immovable, without line of desclerotization. Epimeral setal formula 3-1-2-2; *1c* barbed, longest and thickest epimeral seta. Genital setae 6 pairs, with few barbs; *g1-g3* positioned on anterior margin of genital plate. One pair aggenital setae, 1 or 2 pairs of anal and adanal setae. Postanal porose present. Subcapitular mentum without tectum. Palp setal formula 0-2-1-3-

9(1); eupathidium *acm* subequal in length to solenidion, forming double horn with solenidion along length. Axillary saccule of subcapitulum present. Cheliceral digits toothed, chelicera with porose region abaxially. Tarsi monodactylous, without enlarged tarsal pulvillus. Solenidion absent from tibia IV. Solenidion $\omega 2$ absent from tarsus II. Genua I, II and IV with ventral spur. Seta *l''* on genua I and II spinous, and distinctly thicker than other setae on these segments. Dorsal knobs or spines absent from tibia I distally.

Diagnosis: Immatures — Apherodermous. Body colorless, cuticle without sclerites or plicae, bearing granular cerotegument. All or most gastronomic setae long, setiform; larval setation unidifferent, with 11 pairs (*h3* not developed until protonymph), protonymph, deutonymph and tritonymph with 14 pairs (*p3* not developed). Hysterosomal sclerites absent. Humeral organ absent from sejugal region. Without apodemato-acetabular tracheal system or porose homologues. Paraprocts atrichous in larva, protonymph and deutonymph. Epimeral setal formula (larva to tritonymph) 3-1-1, 3-1-2, 3-1-2, 3-1-2. Genital setal formula (larva to tritonymph): 0-1-3-5. Aggenital setal formula 0-0-1-1. Opisthonotal gland present in all instars. Cupule development normal. Bothridium and bothridial seta fully formed in all instars. Setation of protonymphal leg IV normal (0-0-0-0-7). Seta *d* absent on tibiae I to IV and genua I to III.

Remarks:

Octotaxic System — Openings of notogastral saccules are minute and the filiform tubules are difficult to see, hence their presence may have been overlooked in previous descriptions and re-descriptions of species of *Paralamellobates*, e.g., *P. ceylanicus* (Engelbrecht 1986). The dimorphic morphology of the octotaxic system in *Paralamellobates* and *Lamellobates*, with *Sa*, *S2* and *S3* long, filiform tubules, and *S1* an elongated saccule is unique among Brachypylina.

Classification — *Lamellobates* and *Paralamellobates* are very similar genera, differing primarily in the shape of the median dens of the lamella. Bhaduri and Raychaudhuri (1968) defined *Paralamellobates* (as subgenus of *Lamellobates*) as having

"lamellae with free tips" in contrast to the rounded medial dens found in species of *Lamellobates*. A further difference between the genera found in some keys is the number of pairs of anal and adanal setae, but this seems variable. The illustration of the type species, *P. bengalensis* (Bhaduri and Raychaudhuri 1968, their fig. 6) shows 2 pairs of anal and 2 pairs of adanal setae, the complement in *Lamellobates*. Balogh (1972) and Balogh & Balogh (1992), although recognizing *P. bengalensis* as type species, defined *Paralamellobates* by the presence of only one pair of adanal setae and a large interlamellar area, in contrast with two pairs of adanal setae as well as a small interlamellar area for *Lamellobates*. Tseng (1984), who recorded *P. bengalensis* from Taiwan, illustrated (his fig. 157) 2 pairs of anal and 1 pair of adanal setae. Similarly, Ramani & Haq (1984) who reared *P. bengalensis* from India, show 2 pairs of anal and 1 pair adanal setae in their unpublished illustrations (N. Ramani pers. comm.). Subsequently, Engelbrecht (1986) and Behan-Pelletier (1998) discussed this discrepancy between the original diagnosis of *Paralamellobates* and that of Balogh (1972) and Balogh and Balogh (1992). Anal and adanal setation was not described for *Paralamellobates misella* (Berlese, 1910), but a single pair of anal and adanal setae was illustrated for its synonyms, *P. ceylanicus* and *P. striatus* (Engelbrecht 1986, Behan-Pelletier 1998).

Redescription of *Paralamellobates misella* (Berlese, 1910) (Figs. 1-7)

Oribatella misella Berlese, 1910

Paralamellobates misella (Berlese, 1910); Subías (2004)
Oribatella ceylanicus Oudemans, 1915; Mahunka (1977)

Paralamellobates ceylanicus (Oudemans, 1915); Mahunka (1977)

Oribatella schoutedeni Balogh, 1959

Paralamellobates schoutedeni (Balogh, 1959); Mahunka (1977)

Paralamellobates striatus Behan-Pelletier, 1998; **new synonymy**

Material Examined — Specimens of *Paralamellobates misella* (details below) were reared from four adults intercepted in New Zealand from banana im-

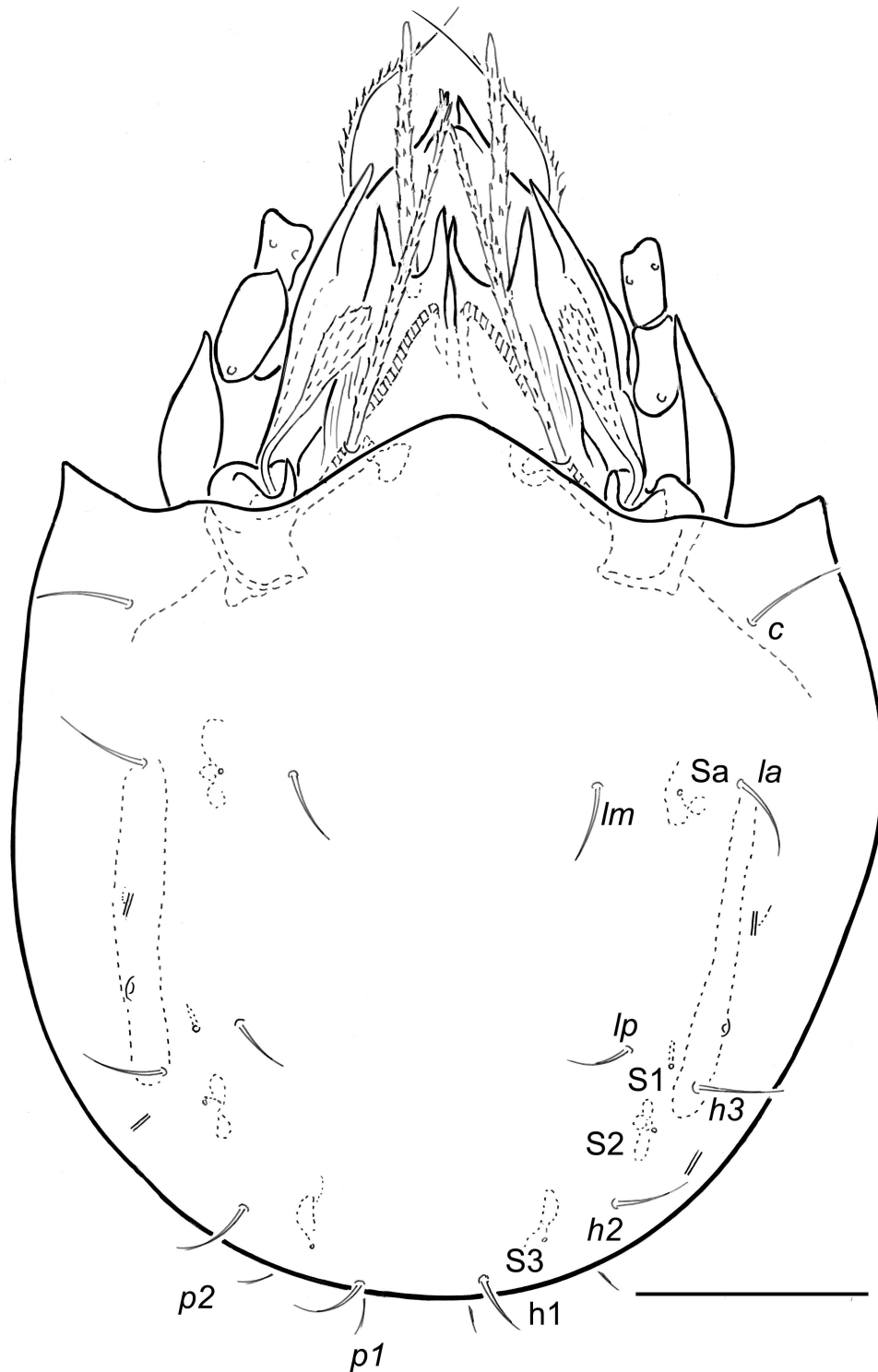


FIGURE 1: *Paralamellobates misella* (Berlese), adult female, dorsal aspect, legs not illustrated, except for proximal segments of leg I. Scale bar = 50.

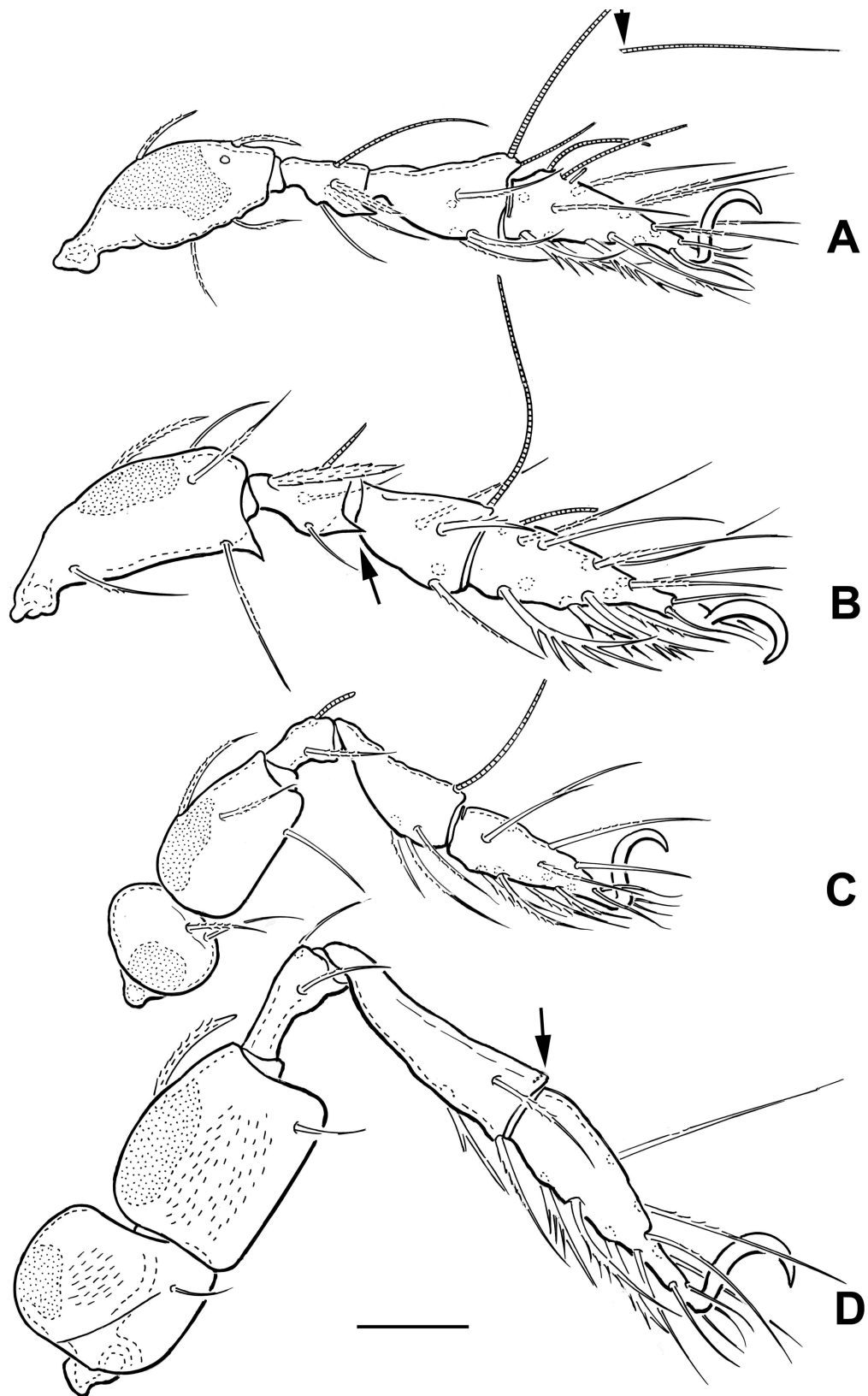


FIGURE 2: *Paralamellobates misella* (Berlese), adult female, legs I-IV, all antiaxial aspect: A – leg I, trochanter not illustrated; B – leg II, trochanter not illustrated, with arrow to ventral tooth on genu; C – leg III; D – leg IV, with arrow to small ridge on tibia. Scale bar 20.

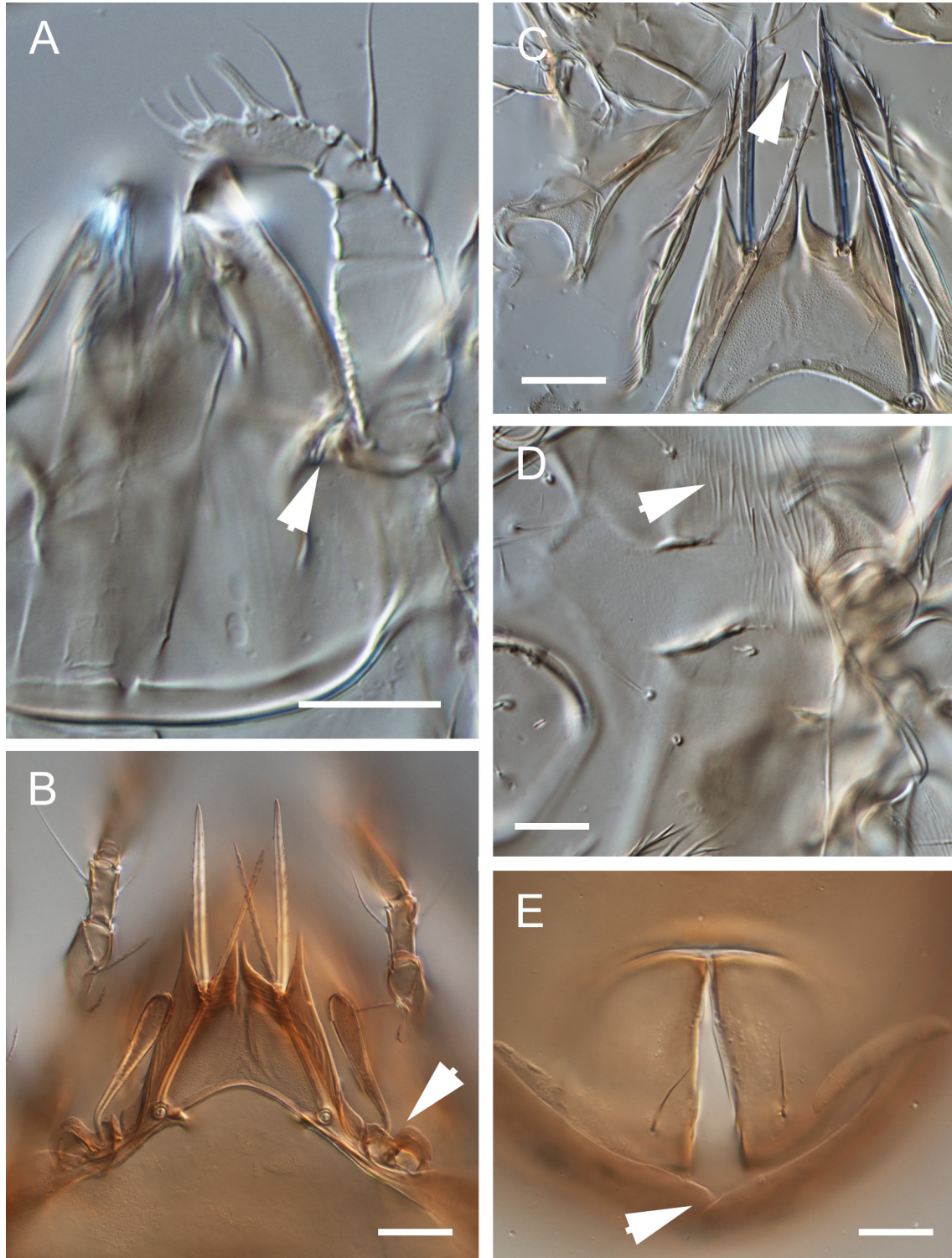


FIGURE 3: *Paralamellobates misella* (Berlese). Differential interference contrast microscope images of adults: A – gnathosoma ventral view, with arrow to axillary sacculus; B – prodorsum (4 layers combined), with arrow to bothridium; C – detail of prodorsum, with arrow to rostrum; D – lateral region of coxisternum with arrow to lateral ridges; E – posterior region showing single pair of anal setae and overlapping lobes of posterior notogastral tectum (indicated by arrow). Scale bars: A-D = 20.

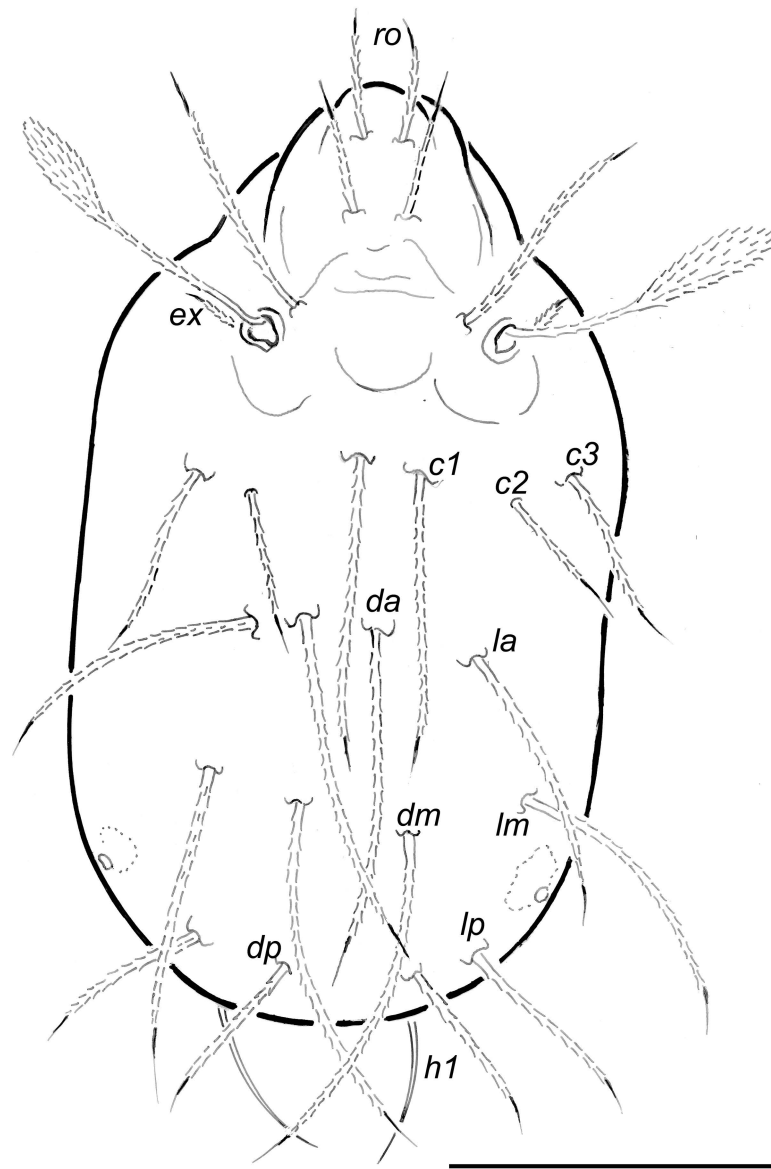


FIGURE 4: *Paralamellobates misella* (Berlese), larva, dorsal aspect, legs not illustrated. Scale bar = 50.

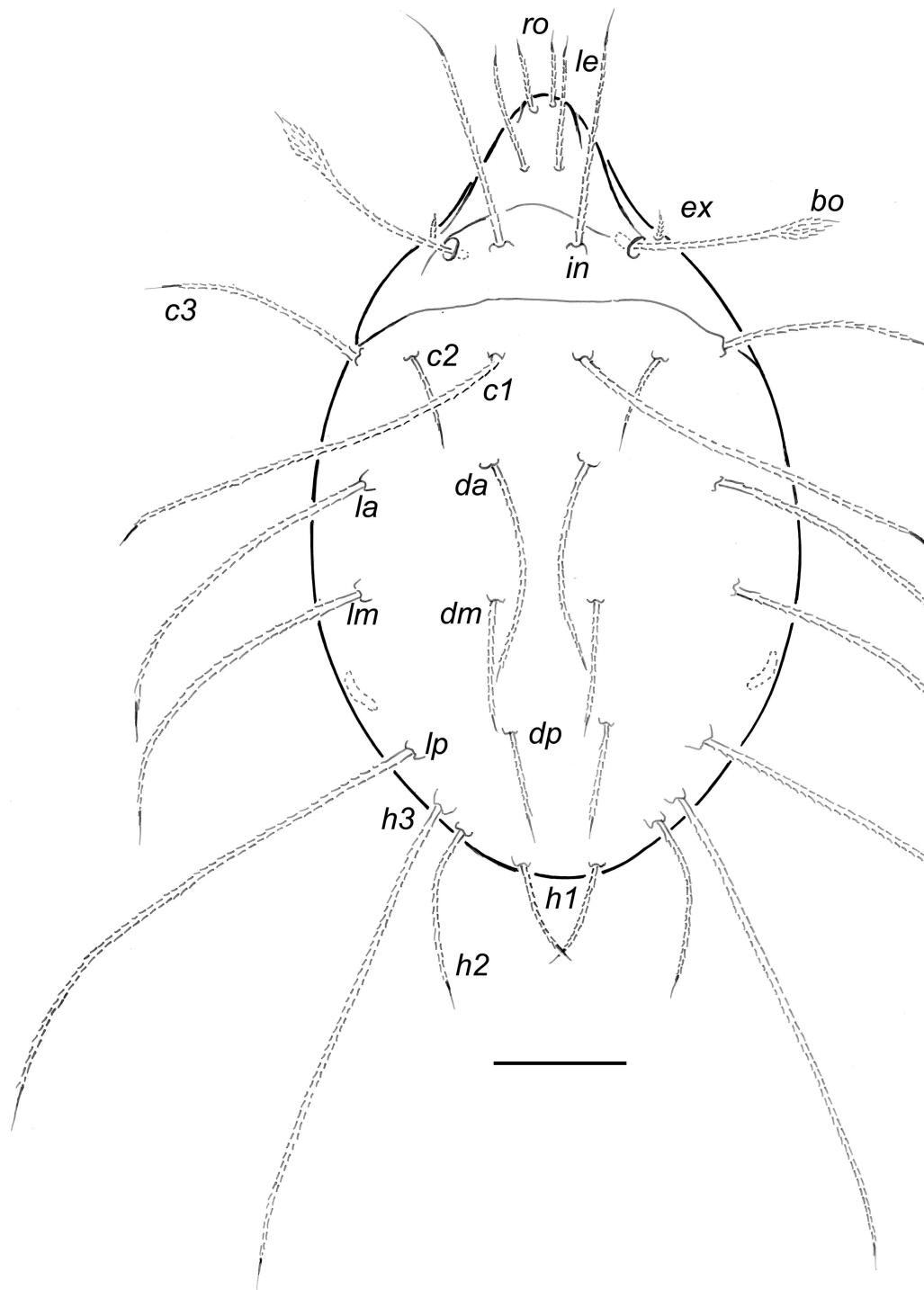


FIGURE 5: *Paralamellobates misella* (Berlese), tritonymph, dorsal aspect, legs not illustrated. Scale bar = 50.

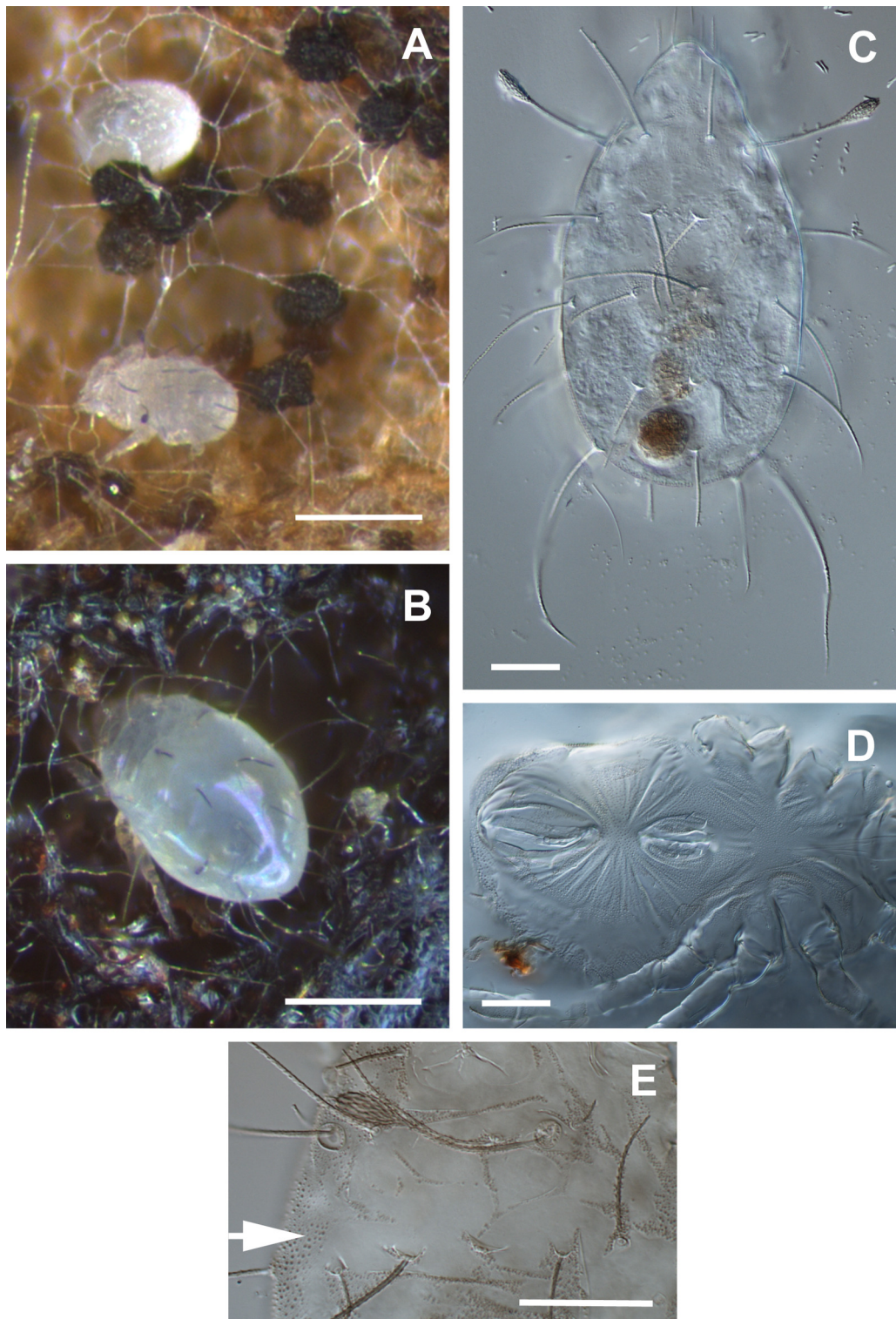


FIGURE 6: *Paralamellobates misella* (Berlese): A – Egg and larva photographed live among fungal hyphae in growth medium, surrounded by faecal pellets of adults; B – deutonymph photographed live, showing length of interlamellar seta, usually broken in preserved specimens; C – tritonymph, dorsal showing absence of sclerotization; D,E, Differential interference contrast microscope images of immatures: D – tritonymph, ventral, showing absence of sclerotization; E – larva, part of prodorsum, showing tubercle nature of cerotegument (arrow). Scale bars: A, B = 100, C, D = 20, E = 30.

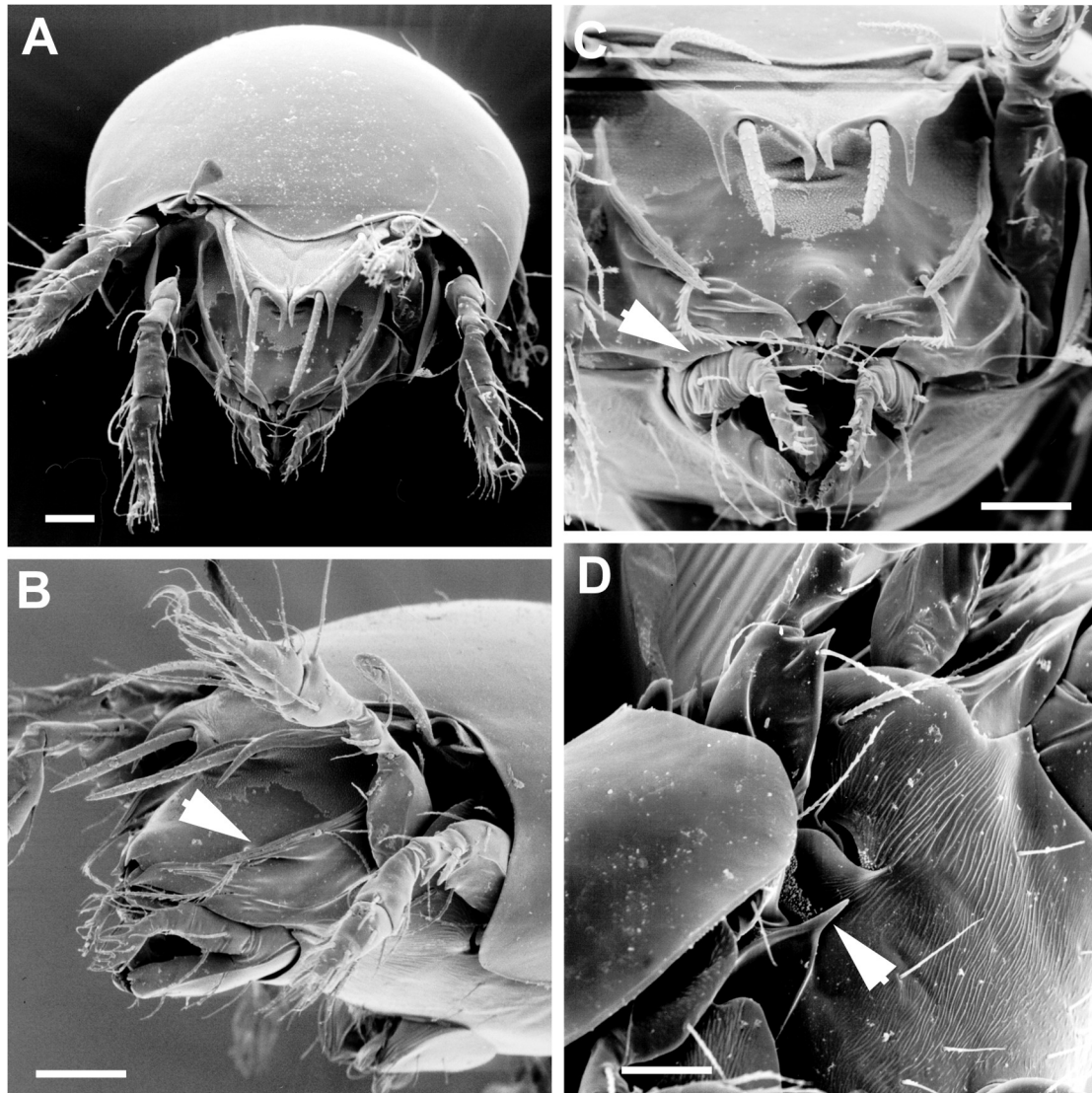


FIGURE 7: *Paralamellobates misella* (Berlese). Scanning electron micrographs of specimens from Costa Rica: A – Frontal aspect; B – Anterolateral aspect, with arrow to tutorium; C – detail of frontal aspect, with arrow to genal tooth; D – coxisternal region showing ridges on epimeres, with arrow to Custodium. Scale bars: A-D = 20.

ported from the Philippines on 26 July 2014. These are housed in the Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada.

Diagnosis — Adult. Total length 254–278; longitudinal striae on lateral region of epimeres I, present or not on epimeres II; medial margin of lamellar cusps parallel and contiguous, with medial and lateral teeth about 21 long; tutorium 64–71 long, of which cusp about 19; pedotectum I with 4 short, strong ridges on dorsal margin; notogastral setae thin, smooth 13–23 long, with *c2* longest.

Adult Measurements — Males unknown. Mean total length: female ($n = 10$) 266 (range 254–278). Mean notogastral width ($n = 8$): female 185 (range 168–192).

Integument — Microtuberculate over entire body and leg segments. Longitudinal striae, about 20, on lateral region of epimere I (Figs 3D, 7D), on dorsal surface of pedotectum I, on tutorium and on paraxial surface of femora III and IV. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region.

Prodorsum — Rostrum flattened to rounded medially, with pair of strongly developed teeth (Figs 1, 3C, 7C). Seta *ro* directed anteriorly, barbed, acuminate, 52–56 long, mutual distance at their base about 44. Lamellae broad, converging, about 59, of which cusps 21 long and 20 wide, with medial and lateral teeth subequal in length, about 16. Medial margins of cusps parallel and contiguous. Seta *le* thick, with few barbs, 53–58 long, arising anterolaterally on lamellar cusp, medial to lateral tooth (Figs 1, 3C). Seta *in* thick, barbed, 79–85 long, extending beyond tip of tutorium; borne on small tubercles. Mutual distance of setal pairs *le* and *in* approximately 21–23 and 46, respectively. Bothridial seta barbed, clavate, 56–59 long from base of bend in bothridium to tip, directed anteriorly. Seta *ex* about 3 long, easily overlooked. Bothridium with well-developed medial and lateral scales (Figs 1, 3B).

Lateral Aspect of Podosoma — Genal tooth long, subtriangular, with carina extending along length (Fig. 7C). Tutorium 64–71 long, of which pointed cusp about 19; tutorium with striae along length

(Figs 3C, 7C). Pedotectum I convex dorsally, with 4 short, strong ridges on dorsal margin. Dorsal margin of pedotectum I ventral to insertion of seta *ex*. Custodium triangular, 16–19 long (Figs 3D, 7D). Discidium triangular between acetabula III and IV. Sublamellar porose area Al not evident.

Notogaster — Slightly longer than wide, ratio of 1.15:1. Nine pairs of smooth, acuminate notogastral setae, *c2* 20–24, *l* series 13–19, *h* series about 17, and *p1*, *p2* about 14 long (Fig. 1). Anterior tectum strongly convex medially between bothridia. Length of filiform tubules Sa, S2 and S3 not determined, S1 elongated saccule, about 6.

Ventral Region — Epimeral seta *1c* barbed, longest and thickest epimeral seta, about 29, other epimeral seta 14–17 long, thin, smooth. Genital setae with few barbs, about 13 long. Aggenital pair and single pair each of anal and adanal setae smooth, about 9 long. Postanal porose area oval, about 8 wide.

Gnathosoma — Axillary saccule of subcapitulum about 3 (Fig. 3A).

Legs (Figs 2A–D) — Setation (I to IV): trochanters 1-1-2-1; femora 5-5-3-2; genua 3(1)-3(1)-1(1)-2; tibiae 4(2)-4(1)-3(1)-3; tarsi 18(2)-15(1)-15-12. Solenidia and famulus on tarsus I inserted proximally, famulus distal to solenidia (Fig. 2A). Solenidion $\omega 2$ absent from tarsus II (Fig. 2B). Genua I, II and IV and femur II with ventral spur. Seta *l''* on genua I and II spinous, and distinctly thicker than other setae on segment, about 17 and 23 long, respectively (Figs 2A, B). Short, transverse ridge, about 6 long, present distally on tibia IV (Fig. 2D, arrow).

Description: Immatures: Dimensions — Total length: larva ($n = 3$) 153 (range 151–156); protonymph ($n = 3$) 204 (range 192–216); deutonymph ($n = 2$) 220 (200, 240); tritonymph ($n = 3$) 253 (range 232–288).

Integument — Integument weakly microtuberculate, without evidence of sclerotization or porose regions. Globular cerotegument well-developed (Fig. 6E).

Larva (Figs 4, 6A) Prodorsum — Setae *ro*, *le*, *in* long, barbed, tapered, about 17, 20, and 37 long, respectively. Seta *ex* short, barbed, isodiametric along

length, about 6 long. Mutual distance of pair *ro* about 7, of pair *le* about 9 and of pair *in* about 28. Bothridial seta clavate, heavily barbed, about 49 long, tapered distally (Fig. 4).

Gastronotic region — Margin rounded, shape oval, weak swelling around setal insertions. Eleven pairs of setae, long, barbed, setiform, subequal in shape, borne on short tubercles. Setal lengths approximate (due to some terminal breakage and difficulty in measurement): *c1* (47), *c2* (23 – 26), *c3* (31 – 35), *da* (60), *dm* (54), *dp* (31 – 33), *la* (48), *lm* (54), *lp* (29 – 36), *h1* (15), *h2* (29); setae *c3* and *l* series flagellate. Mutual distance of pair *da* about 21, pair *dm* about 26 and pair *dp* about 27.

Protonymph Prodorsum — Setae *ro*, *le*, *in* long, barbed, tapered, about 18, 28, 48 long, respectively. Seta *ex* short, barbed, isodiametric along length, about 7 long. Mutual distance of pair *ro* about 7, of pair *le* about 16 and of pair *in* about 25. Bothridial seta clavate, heavily barbed, about 60 long, tapered distally.

Gastronotic region — Margin rounded, shape oval, weak swelling around setal insertions. Fourteen pairs of setae, long, barbed, setiform, subequal in shape. Setal lengths approximate (due to some terminal breakage and difficulty in measurement): *c1* (70), *c2* (27), *c3* (49), *da* (53), *dm* (45), *dp* (32), *la* (60), *lm* (61), *lp* (105), *h1* (10), *h2* (23), *h3* (58), *p1* (7), *p2* (8); setae *c1* and *l* series and *h3* flagellate. Mutual distance of pair *da* about 25, pair *dm* about 21 and pair *dp* about 19.

Deutonymph (Fig. 6B) Prodorsum — Setae *ro*, *le*, *in* long, barbed, tapered, except *in* flagellate distally, about 21, 37, and 75 long, respectively. Seta *ex* short, barbed, isodiametric along length, about 7 long. Mutual distance of pair *ro* about 9, of pair *le* about 12 and of pair *in* about 27. Bothridial seta clavate, heavily barbed, about 82 long, tapered distally.

Gastronotic region — Margin rounded, shape oval, weak swelling around setal insertions. Fourteen pairs of setae, long, barbed, setiform, subequal in shape, except setae *c1* and *l* series and *h3* flagellate distally. Setal lengths approximate (due to some terminal breakage and difficulty in measurement): *c1* (136), *c2* (26), *c3* (60), *da* (71), *dm* (56), *dp* (39), *la*

(123), *lm* (107), *lp* (184), *h1* (39), *h2* (29), *h3* (139), *p1* (17), *p2* (18). Mutual distance of pair *da* about 29, pair *dm* about 31 and pair *dp* about 25.

Tritonymph (Fig. 5) Prodorsum — Setae *ro*, *le*, *in* long, barbed, tapered, except *in* flagellate, 23 – 36, 46 – 54, 92 – 102 long, respectively. Seta *ex* short, barbed, isodiametric along length, 7 – 11 long. Mutual distance of pair *ro* about 9, of pair *le* about 14 and of pair *in* 28 – 32. Bothridial seta clavate, heavily barbed, 80 – 85 μ m long, tapered distally (Fig. 5).

Gastronotic region — Margin rounded, shape oval, weak swelling around setal insertions. Fourteen pairs of setae, long, barbed, setiform, subequal in shape, except setae *c1* and *l* series and *h3*, *h2* flagellate distally. Setal lengths approximate (due to some terminal breakage and difficulty in measurement): *c1* (159 – 180), *c2* (27 – 53), *c3* (51 – 88), *da* (86 – 112), *dm* (56 – 74), *dp* (48), *la* (171 – 178), *lm* (134 – 154), *lp* (215 – 255), *h1* (54 – 74), *h2* (71 – 82), *h3* (186 – 230), *p1* (24 – 26), *p2* (26 – 33). Mutual distance of pair *da* about 42, pair *dm* about 43 and pair *dp* about 39.

Ventral Region — Epimeral plates not defined by either sclerotization or porose integument. Development of epimeral setae (larva to adult): 3-1-2, 3-1-2-1, 3-1-2-2, 3-1-2-2, 3-1-2-2. Development of genital, aggenital, anal and adanal setae (larva to adult): 0-1-3-5-6, 0-0-1-1-1, 0-0-0-1-1, 0-0-1-1-1, respectively. Epimeral, genital, aggenital, anal and adanal setae smooth, acuminate, about 5 – 10 long in tritonymph. Integument surrounding opening of opisthonotal gland not sclerotized or porose.

Gnathosoma — Axillary sacculae present from protonymph (possibly too small to see in larva). Palpal eupathidium *acm* attached to solenidion along distal three-quarters of solenidial length in all immatures.

Legs — Development of setae and solenidia given in Table 2. Solenidion ϕ_1 on tibia I very long and tapered positioned on anterodorsal tubercle, about 64 – 72 in nymphs. Solenidion ϕ_2 of tibia I short and weakly tapered, about 4 long in deutonymph, about 6 long in tritonymph, about 20 long in adult. Porose areas present on femora I to IV and trochanters III and IV (easily visible in adult)

TABLE 2: Ontogeny of setiform organs in *Paralamellobates misella* (Berlese). Setae (Roman) and solenidia (Greek) are indicated; parentheses indicate pseudosymmetrical pairs of setae.

	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
Larva	–	$d\ bv''$	$\sigma\ (l)$	$\varphi_1\ (l)\ v'$	$(ft)\ (tc)\ (p)\ (u)\ s\ (a)\ (pv)\ (pl)\ e\ \omega_1$
Protonymph	–	–	–	–	ω_2
Deutonymph	v'	(l)	–	φ_2	
Tritonymph	–	–	v'	v''	(it)
Adult	–	v'	–	–	–
Leg II					
Larva	–	$d\ bv''$	$\sigma\ (l)$	$\varphi\ (l)$	$(p)\ (tc)\ (ft)\ (u)\ s\ (a)\ (pv)\ \omega_1$
Protonymph	–	–	–	v'	–
Deutonymph	v'	(l)	–	–	–
Tritonymph	–	–	v'	v''	(it)
Adult	–	v'	–	–	–
Leg III					
Larva	–	$d\ ev'$	$\sigma\ l'$	$\varphi\ v'$	$(p)\ (tc)\ (ft)\ (u)\ s\ (a)\ (pv)$
Protonymph	–	–	–	–	–
Deutonymph	v'	–	–	–	–
Tritonymph	l'	l'	–	(l)	(it)
Adult	–	–	–	–	–
Leg IV					
Protonymph	–	–	–	–	$(p)\ ft''\ (u)\ (pv)$
Deutonymph	–	$d\ ev'$	$d'\ l'$	v'	$(tc)\ (a)\ s$
Tritonymph	v'	–	–	(l)	–
Adult	–	–	–	–	–

present but difficult to see in tritonymph because of unsclerotized integument and layer of granular cerotegument; not evident in larva, protonymph or deutonymph.

Remarks on *Paralamellobates misella*

Morphology — We compared specimens used in this redescription with type material of *Paralamellobates striatus* and consider them conspecific, thus, *P. striatus* is a junior synonym of *P. misella*, **new syn.** There are 2 corrections to make to the description of *P. striatus* (Behan-Pelletier 1998). The bothridium of *P. striatus* is described as "cup-shaped, with well-developed ventrolateral scale", whereas both ventrolateral, ventromedial and dorsomedial scales are well-developed (Fig. 3B) as is common in Ceratozetidae and Punctoribatidae (Behan-Pelletier

1994). Also, the epimeral setal formula is incorrectly given as 3-1-3-3, rather than 3-1-2-2.

In his redescription of adult *Paralamellobates ceylanicus*, Engelbrecht (1986) did not notice the octotaxic system, probably because of the unusual expression of the sacculi. He also gave an epimeral setation of 2-1-2-2, overlooking setae *1c*.

We have not seen male specimens of *Paralamellobates misella* and no males were recorded among the material of *P. striatus* from Costa Rica. It is possible that thelytoky is the mode of reproduction. This undoubtedly contributes to the wide distribution of *P. misella* which shows an almost pantropical distribution. In contrast, Haq and Ramani (1984) who studied development of *P. bengalensis* on leaves of *Dioscorea alata* L., the water yam, in the laboratory noted the deposition of spermatophores in this

species.

Genetics — DNA sequences of COI (1054 bp), D2/D3 region of 28S (807 bp) and 18S (1593 bp) genes were obtained with identical sequences for each individual mite. Although COI is good marker for inter- and intra-species analysis, there are no closely related COI sequences for *P. misella* in BOLD and GenBank databases, the closest matches are 80 % identities with *Scutozetes lanceolatus* (Ceratozetidae) in BOLD and *Scutovertex pictus* (Licnere-maeoidea) (GU208586 and GU208587) in GenBank. Phylogenetic analysis of COI sequences from the cohort brachypyline revealed that *P. misella* did not cluster with any known species using Bayesian and PHYML analyses.

DNA sequences of D2/D3 region for *P. misella* showed 82% identities with *Anachipteria acuta* (Achipterioidea) (JQ000356), and a Sarcotiformes sp. (JN0083151) in BLAST search. The available 28S DNA sequences of brachypyline mites are mainly for the D3 region with 300 bp length in GenBank. Phylogenetic analysis of D3 sequences of cohort brachypyline did not provide clear resolution for *P. misella*.

The 18S gene has proven useful for resolving relationships of distantly related lineages of Acari (Cruickshank, 2002; Murrell *et al.*, 2005). Phylogenetic analysis of 18S sequences for *P. misella* and the available sequences of brachypyline mites showed a similar tree topology for PHYML and MrBayes analyses, thus only the Bayesian tree of the 18S sequences is given in Fig. 8. The phylogenetic tree showed that *P. misella* formed a clade with *Scutovertex sculptus* (Scutoverticidae of superfamily Licnere-maeoidea) and *Eremaozetes* sp. (Eremaozetidae of superfamily Eremaozetoidea), with 100 percent *pp* support. *P. misella* is not closely related to Punctori-batidae based on current molecular information.

Biology — Examination of gut contents of these specimens indicated that *P. misella* is fungivorous, with conidia and conidiophores of a species of *Cladosporium* (Capnodiales: Davidiellaceae) found in its digestion system. Adult females deposited their eggs singly in cracks or cavities in the fruit end. Usually a female laid 1 to 3 eggs per day. Twenty seven eggs developed to adults. The mites went

through larval and three nymphal stages with four quiescent phases at the end of each active stage. All active stages moved around and scraped the surface substance, presumably fungi, from time to time. Development from egg to adult varied from 26 to 37 days (average 34). Mites took 7 to 10 days (average 8.3) to complete the egg development. The larval stage (including the quiescence) lasted 3 to 5 days (average 4.2). The duration of nymphal development (including the quiescence) lasted 11 to 18 days (average 14.2) including protonymph 4 to 5 days (average 4.4), deutonymph 4 to 6 days (average 4.8) and tritonymph 3 to 7 days (average 4.9). The total duration for postembryonic pre-adult development was 21 to 33 days (average 27.0).

Other habitats — Engelbrecht (1986) based his redescription of *Paralamellobates ceylanicus* on specimens collected from soil, a cultivated field planted with sugar cane and from bitter orange fruit and from leaves of pumpkin (*Faria occidentalis*). *Paralamellobates misella* (as *P. shoutedeni*) was collected from a nest of a warbler, *Prinia inornata* Sykes, in West Bengal (Gupta 1989).

Paralamellobates bengalensis — Ramani and Haq (1984) studied the biology of *Paralamellobates bengalensis* associated with the weed species *Eupatorium odoratum* (= *Chromolaena odorata* (L.) R.M. King & H. Rob.), and found both adults and immatures feeding on the ventral surface of older leaves of this plant. Haq and Ramani (1984) studied development of this species on leaves of *Dioscorea alata* L., the water yam, in the laboratory at a temperature of 29 C° and 80 % humidity. They recorded development from egg to adult of 27 days, with a consistent pre-moult period of 2 days. All active stages feed on the undersurface of leaves, and the authors considered that they possibly disseminated fungal spores. As indicated above, they noted the deposition of spermatophores. Unpublished illustrations of the larval and nymphal stages (N. Ramani pers. comm.) show morphology very similar to that in *P. misella*.

Neena and Haq (1991) recorded gregarine protozoans in the guts of 25 of the 200 adult *Paralamellobates bengalensis* they examined.

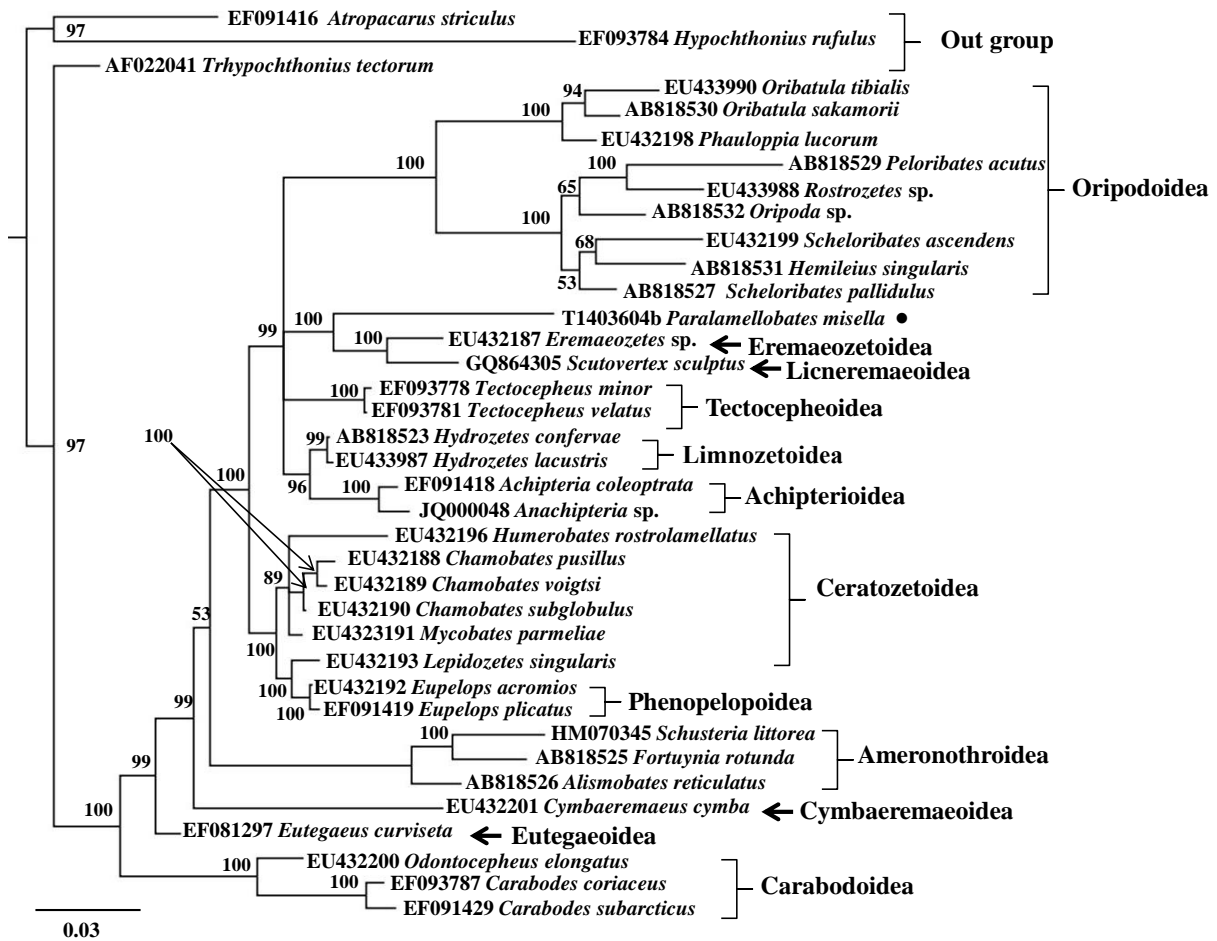


FIGURE 8: Bayesian tree of brachypylinae mites using 18S sequences; *Paralamellobates misella* (Berlese) is indicated by dot.

TABLE 3: Summary of analysis of character state polarities in *Parlamellobates* and selected higher taxa. Characters in boldface are considered apomorphic. Abbreviations: Ng NBP, notogaster without posterior tectum; NgTLP, notogaster with posterior tectum; NgTLPO, notogaster with overlapping posterior tectum; A, porose areas; S, sacculi; DDC, companion seta *d* of genua I-III and tibiae I-IV absent throughout ontogeny (el); present to the tritonymph (n3); present to the adult (Ad). (Data from: Behan-Pelletier (2001), Behan-Pelletier and Walter (2013), Behan-Pelletier *et al.* (2005), Coetzee (1987), Norton and Behan-Pelletier (2009), Senczak and Senczak (2014).

Character/state	Eremaozetioidea	Licremnaeioidea	Phenopelopidae	Achipteridae	Tegoribatidae	Orbatellidae	Punctoribatidae	Chamobatidae	Oripodoidea	<i>Parlamellobates</i>
Adult										
Notogaster	Ng TLP	Ng NBP, Ng TLP, Ng TLPO	Ng NBP, Ng TLP	Ng NBP, Ng TLP	Ng TLP, Ng TLPO	Ng TLP	Ng TLP, Ng TLPO	Ng TLP	Ng NBP, Ng TLPO	Ng TLPO
Bifurcating erotegument	No	No	Yes	No	No	No	No	No	No	No
Ocotaxic system dimorphic	No	No	Present/absent	Present	Present	Present	Present/absent	Present	Present/absent	Absent
Seta <i>P</i> ₃	Present	No	Present/absent	No	Yes	Yes	Yes	Yes	No	Yes
Postanal porose area	No	No	Yes	No	Yes	Yes	Yes	Yes	No	Yes
Axillary sacculi	No	No/Yes	No/Yes	No	No/Yes	Yes	Yes	Yes	No	Yes
Genal incision	No	Yes	Yes/No	Yes	Yes/No	Yes	Yes	Yes	Yes	No
Solenidion on tibia IV	Yes	Present/Absent	Present	Present	Present	Present	Present/Absent	Present	Present/Absent	Absent
Solenidion on tarsus II	Present	Yes	Yes/No	Yes	Yes/No	Yes	Yes	Yes	Yes	1 or 2 pairs
Anal setation	2 pairs	1 or 2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	2 pairs	1 or 2 pairs	1 or 2 pairs
Adanal setation	3 pairs	2 or 3 pairs	3 pairs	3 pairs	3 pairs	3 pairs	3 pairs	3 pairs	1-3 pairs	1 or 2 pairs
Immatures										
Integument	Plicate	Plicate	Plicate/tuberculate	Plicate	Plicate/tuberculate	Apopheredermous	Macroscerites	Macroscerites, smooth	Porose microscerites	Smooth
Humeral organ	no	No	No	No	No	Yes	Yes	Yes	No	No
Companion seta <i>d</i> (tibia I-III)	DDC el, DDC n3	DDC el, DDC n3	DDC el	DDC el	DDC n3	DDC el	DDC el	DDC el	DDC el	DDC el
Companion seta <i>d</i> (tibia IV)	DDC el, DDC n3	DDC el, DDC n3	DDCAd	DDC n3	DDC n3	DDC el	DDC el	DDC el	DDC el	DDC el
Larval seta <i>h</i> ₃	Present	Present/absent	Present/absent	Present/absent	Present/absent	Present	Present	Present	Present	Absent

DISCUSSION

Relationships of *Paralamellobates*

Characters of *Paralamellobates* were compared with those of *Lamellobates*, and other poronotic Brachypylina including members of the Eremaozetoidea, Licneremaeoidea, Phenopelopoidea (Phenopelopidae), Achipterioidea (Achipteriidae, Tegeribatidae), Oribatelloidea (Oribatellidae) Ceratozetoidea (Chamobatidae, Puncatoribatidae), Oripodoidea, within a cladistic framework as much as possible. The table of relationships given in Behan-Pelletier (2001) is updated as Table 3, herein.

Prodorsum — Adult *Paralamellobates* share the apomorphic presence of a well-developed genal tooth with members of the Ceratozetoidea, Phenopelopoidea, Oribatellidae, Achipteriidae, and most Tegeribatidae (absent in *Hypozetes*).

Opisthosoma — The opisthosomal integument of immature *Paralamellobates misella* is smooth, lacking plicae, porose regions and any indication of sclerites, including around the opening of the opisthonotal gland, found in many groups (Figs 6A-E). Among poronotic Brachypylina this type of opisthosoma is known only for some species of Chamobatidae (Seniczak and Solhøy 1988, Seniczak and Żelazna 1994, Seniczak *et al.* 2014). In contrast, plicate nymphs are found in Eremaozetoidea, Licneremaeoidea (Adhaesozetidae, Dendroeremaeidae, Licneremaeidae, Micreremidae, Passalozetidae, Scutoverticidae); Achipterioidea (Achipteriidae, Tegeribatidae) and the Phenopelopoidea (Phenopelopidae, Unduloribatidae). Immatures of Oribatellidae are apopheredermous. Macrosclerites are found in nymphs of all Ceratozetoidea, other than some species of Chamobatidae, as noted above, and all Galumnoidea for which immatures are known (Norton and Ermilov 2014). Porose microsclerites are an apomorphy of Oripodoidea (Grandjean 1953). We interpret the absence of sclerotization in *Paralamellobates* as a loss, one that converges with the smooth opisthosomal integument in immatures of some non-poronotic taxa, e.g., larval *Dorycranosus* (Seniczak and Seniczak 2010) (Gustavioidea) and *Oppia* (Seniczak 1975) (Oppioidea).

Setae *h3* appears in the protonymph, rather than in the larva; the larva thus has 11 pairs of gastronotal setae. This delay in appearance of *h3* is widespread in poronotic Brachypylina, including *Hypozetes* (Tegeribatidae) and members of the Licneremaeoidea, Phenopelopoidea and Achipterioidea (Behan-Pelletier 2001).

Nymphs of *Paralamellobates* have a bideficient setation, with absence of seta *p3* in addition to the usual seta *f1*. Adults of *Paralamellobates* have 9 pairs of notogastral setae, with *c1*, *c3*, *d* series, *f1* and *p3* absent, a number that probably also characterizes *Lamellobates*. Although Balogh and Mahunka (1977) noted 10 pairs of setae in *L. molecula* (Berlese, 1916) (as *L. botari*), they illustrated only 9 pairs. Similarly, Engelbrecht (1986) noted 10 pairs of setae for *L. molecula* (as *L. angolensis* Balogh, 1958), but only illustrated 9 pairs. In all illustrations of *Paralamellobates* and *Lamellobates* species the positions of the 9 pairs of notogastral setae are similar. Absence of seta *p3* is rare among poronotic Brachypylina (Balogh & Balogh 1992), but has also been recorded for the punctoribatid *Mycozetes oleariae* Spain, 1968, some genera of Oripodoidea (Balogh & Balogh 1992), the licneremaeoid *Lamelareidae* (Coetzee 1987) and, along with loss of *p2*, for the phenopelopid *Peloptulus* (Weigmann 2010).

The length of some gastronotal setae in immature *P. misella* is striking (Figs 4, 5, 6B) and is equally striking in unpublished illustrations of immatures of *P. bengalensis* (N. Ramani, pers. comm.). Difference in length between lateral setae (*la*, *lm*, *lp*, *h3*, *h2*) and medial setae (*da*, *dm*, *dp* and *c1* and *c2*) is much greater in the deutonymph and tritonymph (lateral setae ca. 2X length medial setae) than in the larva (length subequal) and protonymph (lateral setae ca. 1.3X length medial setae). Such difference in length (but not morphology) between lateral and medial gastronotal setae in immatures is rare, but is known in all immatures of the punctoribatid *Mycobates acuspoidatus* Behan-Pelletier *et al.*, 2001. There also can be differences in gastronotal setal length among immatures of some of apopheredermous *Oribatella* species (Behan-Pelletier 2011, Seniczak and Seniczak 2013). The relevance of this character state for relationships is unclear.

Immatures of *Paralamellobates* lack the humeral organ, which is almost universally present in immatures of Ceratozetoidea, Galumnoidea and Oribatellidae (Norton *et al.* 1997, Norton and Alberti 1997). It is absent in Eremaozetoidea, Licneremaeoidea, Phenopeloidea, Achipterioidea, and non-poronotic taxa.

Notogaster — Adult *Paralamellobates* have a posterior notogastral tectum which is medially divided with overlapping lobes. A posterior notogastral tectum is present in at least some members of all poronotic, brachypyline superfamilies, other than Phenopeloidea, and the polarity of this character state is unresolved (Norton & Behan-Pelletier 2009). However, the expression of this tectum, with unfused, medial lobes (overlapping or not) is rare, and is a character state which *Paralamellobates* shares with *Lamellobates*, the unplaced genus *Sacculozetes*, Adhaesozetidae (Licneremaeoidea), Zetomotrichidae (Oripodoidea), and Punctoribatidae (Ceratozetoidea) among poronotic Brachypylina (Behan-Pelletier 2001; Behan-Pelletier and Eamer 2008, Grandjean 1953; Walter and Behan-Pelletier 1993). The rarity of a divided notogastral tectum in Brachypylina and its possible origin was addressed by Grandjean (1955) and Behan-Pelletier (1988), but the adaptive value of a divided tectum is unclear.

Venter — A most distinctive character of adult *Paralamellobates* and *Lamellobates* is the reduction of adanal setation to 1 or 2 pairs. This reduced number is rare in poronotic Brachypylina (Balogh & Balogh 1992), though it is also found in *Sacculozetes*. Adult *Paralamellobates* have the postanal porose area on the ventral plate, a structure absent from the Eremaozetoidea, Licneremaeoidea, Phenopeloidea, and Achipteriiidae. The postanal porose area is also found in Ceratozetoidea, Galumnoidea, Oribatellidae, and Tegeribatidae and its presence is considered apomorphic.

Octotaxic System — The octotaxic system in adult *Paralamellobates* and *Lamellobates* is composed of 4 pairs of sacculs, but the structure of these is unique. They are dimorphic with Sa, S2 and S3 filiform, and S1 short and tubular (Behan-Pelletier 1998). This dimorphism is a synapomorphy of these genera.

Gnathosoma — The mouthparts of *Paralamellobates* are similar to those of most members of Ceratozetoidea: a mental tectum is lacking, chelicerae are developed normally, eupathidium *acm* is fused along much of its length to the solenidion on the palp tarsus, and the axillary saccul of the infracapitulum is present. The latter character state is found in adults of some Licneremaeoidea, and all Ceratozetoidea, Phenopeloidea, Galumnoidea, Oribatellidae, Tegeribatidae and is considered apomorphic; it is absent from Eremaozetoidea, Oripodoidea and Achipteriiidae.

Legs — *Paralamellobates* lack solenidion φ on tibia IV of the nymphs and adult. While its loss from the regressive protonymphal leg is general in oribatid mites, its loss from later instars is a rare apomorphy in the Brachypylina. For those with known ontogeny, it is expressed only in the phenopelopoid subfamily Phenopelopinae (*Eupelops* and *Peloptulus*) (Grandjean 1964), and in *Neoliodes theleproctus* (Hermann, 1804) (Neoliodidae) (Grandjean 1964). Solenidion φ is present in all species of *Tectoribates* (Tegeribatidae) (Behan-Pelletier and Walter 2013), and in species of *Tegoribates* (new obsv. VBP), but is absent in *Hypozaetes* (Tegeribatidae), a possible loss.

Among Brachypylina where only the adult is known, solenidion φ is absent from tibia IV of adult *Lamellobates*, where leg setation is known, e.g., *L. intermedius* Nübel-Reidelbach & Woas 1992, *L. reticulatus* Behan-Pelletier, 1998, and from tibia IV of adult *Sacculozetes filiosus* Behan-Pelletier and Ryabinin 1991. Engelbrecht (1986) did not describe the leg setation for *P. ceylanicus*, but he illustrated an alveolus with no visible solenidion on tarsus IV in *Lamellobates molecula* (as *L. angolensis*), and indicated its presence in the leg solenidial formula. Similarly, Behan-Pelletier and Ryabinin (1991) noted the alveolus for solenidion on tibia IV in *Sacculozetes filiosus*. In *P. misella* there is neither solenidion nor alveolus.

Immatures and adults of *Paralamellobates* lack seta *d* on genua I-III and all tibiae (DDC el, *sensu* Grandjean 1953). They share this apomorphic character state with all members of the Ceratozetoidea and some Eremaozetoidea and Licneremaeoidea (Behan-Pelletier 2001, Norton and Behan-

Pelletier 2009). In contrast, seta *d* is retained to the tritonymph in Tegeribatidae, to the tritonymph on tibia IV of Achipteriidae, and to the adult on tibia IV of Phenopelopinae. In Phenopelopinae seta *d* on tibia IV has no companion solenidion, whereas *d* is associated with the solenidion in Achipteriidae. Norton and Behan-Pelletier (1986) proposed that the unusual retention of *d* on tibia IV of the adult of Phenopelopinae may involve an atavistic reversal associated with the need for at least some sensory capacity in the dorsal area of tibia IV, but this argument is not supported by the absence of both seta and solenidion from tibia IV of adult *Paralamellobates*, *Sacculozetes* and *Lamellobates*, and the tegoribatid *Hypozetes*.

Solenidion ω_2 is absent from tarsus II from all species of *Paralamellobates* and *Lamellobates* where leg setation has been described, e.g., *P. striatus*, *Lamellobates molecula* (as *L. angolensis*) (Engelbrecht 1986), *L. reticulatus* Behan-Pelletier, 1998. Among poronotic Brachypylina, this solenidial absence is rare, but also is found in *Mycobates parmelliae* (Michael, 1884) and *M. beringianus* Behan-Pelletier, 1994 of the ceratozetoid family Punctoribatidae (Behan-Pelletier 1994), and also in *Micreremus brevipes* (Michael, 1888) of the licneremaeoid family Micreremidae (Pfingstl and Krisper 2011).

Family placement of *Paralamellobates*:

We noted in the Introduction that most authors had placed *Paralamellobates*, and *Lamellobates* in Oribatellidae or Achipteriidae. More recently, they have been included in Punctoribatidae or as unplaced brachypylina genera. Among early derivative poronotic Brachypylina, no exclusive synapomorphies relate *Paralamellobates* to Eremaozetoidea, Licneremaeoidea, Achipteriidae or Oribatellidae. Similarities in 2 character states support, or are consistent with, a relationship between *Paralamellobates* and the Phenopeloidea: (i) absence of solenidion from tibia IV in post-protonymphal immatures and adult; and (ii) presence of the axillary sacculus of the subcapitulum. Absence of solenidion φ from tibia IV is unique to Phenopelopinae and *Lamellobates*, *Paralamellobates*, *Sacculozetes*, and *Hypozetes* (Tegeribatidae) among poronotic Brachypylina. But this

solenidial loss is also expressed in the brachypylina *Neoliodes theleproctus*, in the Enarthronota (Grandjean 1946, Norton & Fuangarworn 2015), and in *Malaconothrus* (Grandjean 1964). However, *Paralamellobates* lacks the apomorphy unique to the Phenopeloidea, namely the blocky cerotegument of adults, which is birefringent in polarised light.

Similarity in 4 character states supports or is consistent with a relationship between *Paralamellobates* and Tegeribatidae: (i) presence of the axillary sacculus of the subcapitulum; (ii) presence of postanal porose area (iii) integument surrounding opening of opisthonotal gland non-porose in immatures; (iv) humeral organ absent from immatures. However, *Paralamellobates* lack the plicate and tuberculate integument of immature Tegeribatidae (Behan-Pelletier and Walter 2013), although some gastronal setae of *Paralamellobates* are carried on large tubercles as in Tegeribatidae (Behan-Pelletier 2001).

Of the characters discussed above, similarity in 5 character states supports or is consistent with a relationship between *Paralamellobates* and Punctoribatidae (Ceratozetoidea), yet none is unique, all show convergence. (i) They share the presence of a divided posterior notogastral tectum; although this character state is convergently expressed also in the poronotic Adhaesozetidae and Zetomotrichidae. (ii) They share absence of setae *p3* in nymphs and adults with the punctoribatid *Mycozetes oleariae*, though we recognise that such a reduced setation also occurs in some Oripodoidea (Balogh and Balogh 1992). They also share (iii) the absence of seta *d* on genua I–III and all tibiae (DDC el, *sensu* Grandjean 1954) with all Ceratozetoidea; (iv) the presence of the axillary sacculus in immatures and adults; and (v) a postanal porose area in the adult. Although *Paralamellobates* lacks macrosclerites in immatures, the apomorphy for the Ceratozetoidea and Galumnoidea, macrosclerites are also absent in some immature Chamobatidae and may be convergently lost in *Paralamellobates*.

At present, molecular data does not support placement of *Paralamellobates* in Punctoribatidae. The phylogenetic tree based on 18S shows families well separated from each other and forming sep-

arate clades. *P. misella* is in a clade with the scutoverticid *Scutovertex sculptus* Michael, 1879 (Licneremaeoidea) and the eremaeozetid, *Eremaeozetes* sp. (Eremaeozetoidea), a placement unsupported by morphology.

The molecular data is convincing, but we hesitate to agree until data on the 18S gene is available for more brachypylina taxa. Presently, we concur with Ermilov & Anichkin (2013) and Ermilov & Niedbala (2013) and include *Paralamellobates* and its sister taxon, *Lamellobates* in the ceratozetoid family Punctoribatidae, recognizing that we need further information on immatures of poronotic Brachypylina and more complete molecular analysis to support this relationship.

Key to adults of *Paralamellobates*

- 1(2) Notogaster with 2 pairs adanal setae.
 *P. bengalensis* Bhaduri and Raychaudhuri
 — Notogaster with 1 pair adanal setae.
 *P. misella* (Berlese)
 (= *Paralamellobates schoutedeni* (Balogh), *P. ceylanicus* (Oudemans) and *P. striatus* Behan-Pelletier)

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