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

Valerie M. Behan-Pelletier¹, Dongmei Li² and Qing Hai Fan²

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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 from Costa Rica, 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 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 Niedbała (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 Niedbała 2013), Saudia 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 Tegoribatidae, 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 Corpuz-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 brachypyrine genus by Norton and Ermilov (2014). Recently, the genus has been placed in Punctoribatidae (=Mycobatidae) by Ermilov and Anichkin (2013) and Ermilov and Niedbała (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 Travé 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.

<table>
<thead>
<tr>
<th>Gene</th>
<th>Primer name</th>
<th>Sequence (5'-3')</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>18S rRNA</td>
<td>1096F</td>
<td>GGTAATTCTGGAGCTAATAC</td>
<td>Holterman et al. 2006</td>
</tr>
<tr>
<td></td>
<td>1912R</td>
<td>TTTACGGTCAGAACKACTAGG</td>
<td>Holterman et al. 2006</td>
</tr>
<tr>
<td></td>
<td>1813F</td>
<td>TGCGGAGAGGTGAATAT</td>
<td>Holterman et al. 2006</td>
</tr>
<tr>
<td></td>
<td>2646R</td>
<td>GCTACCTTTGTTACGGACTTTT</td>
<td>Holterman et al. 2006</td>
</tr>
<tr>
<td>D2/D3 of 28S rRNA</td>
<td>D2A</td>
<td>ACAAGTACCGTGAGGAAAGT</td>
<td>Nunn 1992</td>
</tr>
<tr>
<td></td>
<td>D3B</td>
<td>TGGGAAGGAAACCGCTACTA</td>
<td>Nunn 1992</td>
</tr>
<tr>
<td>COI</td>
<td>CI-J-1718F</td>
<td>GGAGGATTTGGAAAATGATTAGTCCC</td>
<td>Simon et al. 1994</td>
</tr>
<tr>
<td></td>
<td>COI-REVA</td>
<td>GATAAAACGTAAATGAAAATGAGCTAC</td>
<td>Gotoh et al. 2009</td>
</tr>
</tbody>
</table>

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 unideficience nomenclature for notogastral setae is used herein; probable synonyms 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-zyme® 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, Ceratozetoeida, Cymbaeremaeoidea, Eutegaeoidea, Hydrozetoeida, Liceremaeoidea, Oribatelloidea, Oripodoidea, Phenopelopoidea, Tectocepheoidea and Eremaezetoeida) were downloaded from GenBank.

All DNA sequences were aligned with Geneious alignment and then re-aligned with MUSLE in Geneious Pro 7.1.5 under the 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 ± 1°C, 42 ± 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. Humerosejugal 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, SI 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 ω2 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 — Apheredermous. Body colorless, cuticle without sclerites or plicae, bearing granular cerotegument. All or most gastronomic setae long, setiform; larval setation unideficient, 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. Aggenital setal formula (larva to tritonymph): 0-1-3-5. Oribatella misella (Berlese, 1910) (Figs. 1-7)

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 redescriptions 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: Paralannellobates 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 saccule; 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: Paralamellobites 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 A1 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 sacculus, 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 sacculus 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 ω 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 (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.

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 about 28 – 32. Bothridial seta clavate, heavily barbed, 80 – 85 µm long, tapered distally (Fig. 5).


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. 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 saccule 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 φ1 on tibia I very long and tapered positioned on anterodorsal tubercle, about 64 – 72 in nymphs. Solenidion φ2 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)
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 saccules. 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

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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* (Ceratozetotoidea) in BOLD and *Scutovertex pictus* (Linceremaeidea) (GU208586 and GU208587) in GenBank. Phylogenetic analysis of COI sequences from the cohort brachypylina 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 Sarcoptiformes 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 brachypylina 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 Linceremaeidea) and *Eremaeozetes* sp. (Eremaeozetidae of superfamily Eremaeozetoidea), with 100 percent pp support. *P. misella* is not closely related to Punctoribatitidae 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 premoult 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 brachypyline mites using 18S sequences; *Paralamellobates misella* (Berlese) is indicated by dot.
TABLE 3: Summary of analysis of character state polarities in Paralamellobates and selected higher taxa. Characters in boldface are considered apomorphic. Abbreviations: NgNBP, notogaster without posterior tectum; NgTLP, notogaster with posterior tectum; NgTLPO, notogaster with overlapping posterior tectum; A, porose areas; S, saccules; DDC, companion seta.

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DISCUSSION

Relationships of Paralamellobates

Characters of Paralamellobates were compared with those of Lamellobates, and other poronotic Brachypylina including members of the Eremeroidea, Licneremaidea, Phenopelopoeida (Phenopelopidae), Achippterioidea (Achippteridae, Tegoribatidae), Oribatelloidea (Oribatellidae) Ceratozoidea (Chamobatidae, Punctoribatidae), 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 Ceratozoidea, Phenopelopoidea, Oribatellidae, Achippteridae, and most Tegoribatidae (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 Zelazna 1994, Seniczak et al. 2014). In contrast, plicate nymphs are found in Eremeroidea, Licneremaidea (Adhaesozetidae, Dendroeroetidae Licneremaidea, Micreremidae, Passalozetiidae, Scutoverticidae); Achippterioidea (Achippteridae, Tegoribatidae) and the Phenopelopoidea (Phenopelopidae, Undoloribatidae). Immatures of Oribatellidae are apopheredermous. Macrosclerites are found in nymphs of all Ceratozoidea, 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) (Gustavioidae) 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 (Tegoribatidae) and members of the Licneremaeoidea, Phenopelopoidea and Achippterioidea (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 Mycobates acuspidatus Spain, 1968, some genera of Oripodoidea (Balogh & Balogh 1992), the licneremaeoid Lamellareidae (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 punc toribatid Mycobates acuspidatus 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 Eremaeozetoidea, Licneremaeoidea, Phenopelopoidea, 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 Phenopelopoidea, 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), Zeptomotrichidae (Oripodoidea), and Punctoribatitidae (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 Eremaeozetoidea, Licneremaeoidea, Phenopelopoidea, and Achipteriiidae. The postanal porose area is also found in Ceratozetoidea, Galumnoidea, Oribatellidae, and Tegoribatidae and its presence is considered apomorphic.

Octotaxic System — The octotaxic system in adult *Paralamellobates* and *Lamellobates* is composed of 4 pairs of saccules, 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, Phenopelopoidea, Galumnoidea, Oribatellidae, Tegoribatidae and is considered apomorphic; it is absent from Eremaeozetoidea, 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 phenopelopod subfamily Phenopelopinae (*Eupelops* and *Peloptylus*) (Grandjean 1964), and in *Neoliodes theleproctus* (Hermann, 1804) (Neoliodidae) (Grandjean 1964). Solenidion ϕ is present in all species of *Tectoribates* (Tegoribatidae) (Behan-Pelletier and Walter 2013), and in species of *Tegoribates* (new obsv. VBP), but is absent in *Hypozetes* (Tegoribatidae), 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 filosus* 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* *filosus*. 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 Eremaeozoetoidea and Licneremaeoidea (Behan-Pelletier 2001, Norton and Behan-
Pelletier 2009). In contrast, seta $d$ is retained to the tritonymph in Tegoribatidae, 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 $\omega_2$ is absent from 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 Brachypyllina, this solenidial absence is rare, but also is found in *Mycobates parmeliace* (Michael, 1884) and *M. beringianus* Behan-Pelletier, 1994 of the ceratozetoid family Puncctoribatidae (Behan-Pelletier 1994), and also in *Micreremus brevipes* (Michael, 1888) of the licneremaeid 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 Puncctoribatidae or as unplaced brachypyline genera. Among early derivative poronotic Brachypyllina, no exclusive synapomorphies relate Paralamellobates to Eremaeozetoidea, Licneremaoida, Achipteriidae or Oribatellidae. Similarities in 2 character states support, or are consistent with, a relationship between Paralamellobates and Tegoribatidae: (i) absence of the axillary saccule 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 Tegoribatidae (Behan-Pelletier and Walter 2013), although some gastronotal setae of Paralamellobates are carried on large tubercles as in Tegoribatidae (Behan-Pelletier 2001).

Of the characters discussed above, similarity in 5 character states supports or is consistent with a relationship between Paralamellobates and Puncctoribatidae (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 $p_3$ in nymphs and adults with the puncctoribatid 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 saccule in immatures and adults; and (v) a postanal porose area in the adult. Although Paralamellobates lacks macro sclerites in immatures, the apomorphy for the Ceratozetoidea and Galumnoidea, macro sclerites 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 Puncctoribatidae. The phylogenetic tree based on 18S shows families well separated from each other and forming sep-
parate 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 brachypyline taxa. Presently, we concur with Ermilov & Anichkin (2013) and Ermilov & Niedbała (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 analal setae............

.............. *P. bengalensis* Bhaduri and Raychaudhuri — Notogaster with 1 pair analal setae............

............................. *P. misella* (Berlese) (= *Paralamellobates schoutedeni* (Balogh), *P. ceylanicus* (Oudemans) and *P. striatus* Behan-Pelletier)

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