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CERATOZETOIDEA (ACARI: ORIBATIDA)
OF LOWLAND TROPICAL RAINFOREST, LA SELVA, COSTA RICA

by Valerie M. BEHAN-PELLETIER*

SUMMARY: The oribatid mite superfamily Ceratozetoidea is poorly represented in the Neotropics of Central America. Nine species in seven genera, representing four families, were recorded from a variety of habitats in primary and secondary lowland tropical rainforest at Estación Biológica La Selva, Heredia, Costa Rica. Seven of these species are new to science and are described on the basis of adult specimens: Selvazetes sylvanus n. gen., n.sp., Allozetes alas n.sp., (Mycobatidae); Lamellobates reticulatus n.sp., Paralamellobates striatus n.sp. (Austrachipteriidae); Heterozetes heleios n.sp., Zetominus naias n.sp., (Zetomimidae) and Ceratozetes ambigus n.sp. (Ceratozetidae). A table presents the key differences between these nine ceratozetoid species. Heterozetes heleios and Zetominus naias are sexually dimorphic with most of the anal plates and ventral plate porose in males, but not in females. Similar sexual dimorphism exists in Z. cristatus (Hammer), known from Argentina. I discuss the synonymy of Hamobates with Zetomimus, and the placement of Allozetes in Mycobatidae.

RESUMÉ : La superfamille Ceratozetoidea est mal représentée en Amérique Centrale. Neuf espèces appartenant à sept genres répartis en quatre familles ont été recensées dans une variété de forêts pluvieuse tropicale primaire et secondaire à Estación Biológica La Selva, Heredia, Costa Rica. Sept de ces espèces sont nouvelles pour la Science et leurs descriptions sont basées sur les adultes : Selvazetes sylvanus n. gen., n.sp., Allozetes alas n.sp., (Mycobatidae); Lamellobates reticulatus n.sp., Paralamellobates striatus n.sp. (Austrachipteriidae); Heterozetes heleios n.sp., Zetominus naias n.sp., (Zetomimidae) et Ceratozetes ambigus n.sp. (Ceratozetidae). Les différences majeures entre les neuf espèces de Ceratozetoidea sont illustrées à l’aide d’un tableau. Heterozetes heleios et Zetominus naias montrent un dimorphisme sexuel avec les régions poreuses sur les plaques anales et ventrales des mâles. Z. cristatus (Hammer), d’Argentine, montre le dimorphisme sexuel de la même manière. La synonymie de Hamobates avec Zetomimus, et le placement de Allozetes en Mycobatidae sont discutés.

INTRODUCTION

Systematics, ecology and population dynamics of the oribatid mite fauna of primary and secondary lowland tropical rainforest are the subject of ongoing research as part of the Arthropods of La Selva (ALAS) Project (COLWELL, 1996). Estación Biológica La Selva at 10°26'N 84°1'W and 50–150m elevation, is the biotically rich field station of the Organization for Tropical Studies in the Atlantic lowland, evergreen tropical rainforest of Costa Rica (McDADE et al., 1993).

The superfamily Ceratozetoidea has been the focus of extensive sampling during this project, and specimens have been collected by both qualitative and
quantitative techniques, throughout the year. There were no published records of Ceratozetoidea from Costa Rica prior to this study, and only one species was known from Central America: *Guatemala-zetes aelleni* Mahunka (Ceratozetidae), from Guatemala (Mahunka, 1979; Balogh & Balogh, 1990).

The purpose of this paper is to describe adults of new species of Ceratozetoidea, in the families Mycobatidae, Austrachipteriidae, Zetomimidae and Ceratozetidae, from lowland tropical rainforest in Costa Rica, and to provide a table presenting the key differences between adults of the nine species represented. A subsequent paper, following completion of the ALAS Project, will present a key to all ceratozetoid species at La Selva.

**Material and methods**

Morphological terminology used in this study follows that developed by F. Grandjean (see Trave & Vachon, 1975 for references). The following conventions of measurement and description are used: pro-dorsal structures, setae: measured on dissected, slide mounted specimens; ro: rostral seta; le: lamellar seta; in: interlamellar seta; ex: exobothridial seta; ss: sensillus; total length: measured from tip of rostrum to posterior edge of notogaster, on specimens in cavity slides; notogastral length to width ratio: measured when viewed perpendicular to circumgastric scissure, on specimens in cavity slides; leg setal formula: famulus is included in tarsal setal count on leg I and solenidial counts are in parentheses; psdm: free-standing lamina of the dorsomedial scale of the bothridial wall which inserts on the ventromedial scale.

The unideficient nomenclature for notogastral setae is used herein, with the holotrichous nomenclature in parentheses. Synonymies of these two notations are based on probable homologies among Grandjean’s notogastral setal nomenclatures, as outlined by Norton in Balogh & Balogh (1988).

Abbreviations for Acari collections are: INBio: Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica; CNC: Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa, Canada; FMNH: Field Museum of Natural History, Chicago, USA; RAN: collection of Roy A. Norton, Syracuse, USA.

Abbreviations for collectors are: VBP: Valerie Behan-Pelletier; EEL: Evert E. Lindquist; RAN: R. A. Norton; ALAS team: E. E. Lindquist, V. Behan-Pelletier and ALAS parataxonomists D. Brenes, R. Vargas, M. Panigaua and N. Oconotrillo.

Specimens for scanning electron microscopy were critical point dried, mounted on Al stubs with double sided sticky tape, and gold-coated in a Hummer sputter apparatus. Specimens for figures 28 and 29 were macerated with lactic acid and the notogaster was dissected before preparation for scanning electron microscopy.

**Mycobatidae**

I include the genera *Allozetes* and *Selvazetes* (described below) in Mycobatidae, recognizing that this placement may change subject to a phylogenetic analysis of the superfamily. For example, Pavlitshenko (1994) proposed the family Cereselli-dae with the following characteristics: posterior notogastral tectum present, divided or not, and tarsi and tibiae without dorsal ridges. He included in this family the type genus *Ceresella* Pavlitshenko and *Cyrtozetes* Behan-Pelletier. On the basis of this definition other genera should be included in this family, including *Allozetes* and *Selvazetes*, e.g., the genera *Guatemala-zetes*, *Lamellobates* and *Paralamellobates*, and the mycobatid genus *Zachvatkinibates*.

The systematic relationships between genera and families in the Ceratozetoidea have not been studied, and the polarities of character states used in the current classification are undefined. It is clear that a thorough phylogenetic analysis of members of the superfamily, based on both adults and immatures, is needed to resolve relationships and establish a well-supported classification.
Selvazetes n. gen.

Type species: Selvazetes sylvanus n. sp.; monotypic.

Diagnosis: Adults have the following unique combination of character states: lamellae strongly converging, almost fused at base of lamellar cusps; sensillus bilaterally barbed; tutorial cusp absent; notogaster with 10 pairs of setae; without lenticulus; octotaxic system developed as four pairs of porose areas; posterior notogastral tectum developed laterally, absent medially; tarsus heterotridactylous.

Description: Adult. Poronotic, brachypyline oribatid mites, placed in the Mycobatidae (Grandjean, 1954). Lamellae narrow, strongly converging, almost fused at base of lamellar cusps; cusps of medium length, tapered, bearing lamellar setae (Fig. 10). Bothridium with scales svm, sdm and svi well developed. Sensillus bilaterally barbed (Figs. 11, 12). Humerosejugal porose organs Aj, Am, Ah expressed; sublamellar porose area, Al, present (Fig. 4). Genal tooth long, subtriangular, with carina extending along length (Fig. 4). Tutorium without cusp (Figs. 4, 10, 12). Pedotectum I large, convex dorsally, covering acetabulum I (Fig. 3). Custodium pointed distally (Figs. 2, 12). Circumpedal carina present (Fig. 3). Epimeral setal formula 3-1-3-3. Notogaster slightly longer than wide, with 10 pairs of setae and 4 pairs of porose areas (Fig. 1). Posterior notogastral tectum developed laterally, absent medially (Figs. 3, 13). Pteromorphs curved ventrally, immovable, without line of desclerotization (hinge). Six pairs of genital, 1 pair of aggenital, 3 pairs of analan, and 2 pairs of anal setae. Postanal porose area present. Axillary saccule of subcapitulum present (Fig. 9). Solenidion q2 on tibia I inserted on anterodorsal apophysis (Fig. 5). Famulus positioned between solenidia w17 and w27 on tarsus I. Tarsi heterotridactylous, without enlarged tarsal pulvillus.

Etymology. The generic prefix 'selva' is the Spanish for 'forest', referring to the habitat of the type species; -zetes is a common generic suffix in the Ceratozetoidae.

Remarks. This genus can be distinguished from other genera of Mycobatidae by the posterior tectum of the notogaster which is developed laterally and absent medially, and the strongly converging lamellae.

Selvazetes sylvanus n. sp.

Figs. 1–13

Diagnosis: Total length 388–446 µm; rostrum rounded medially with pair of acuminate lateral teeth; lamella 100–108 µm long; setae le and in about 18 and 66 µm long, respectively; free margin of bothridial scale psdm flat to slightly convex; tutorium about 60 µm long, with small tooth proximally and large tooth distally; custodium about 30 µm long.

Adult Measurements. Mean total length: female (n = 9) 426 µm (range 389–446 µm); male (n = 10) 403 µm (range 388–413 µm). Mean maximum notogastral width: female (n = 9) 268 µm (range 259–284); male (n = 6) 254 µm (range 250–259).

Integument. Integument microtuberculate over entire body and leg segments. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall; extending medially on prodorsum to interlamellar region.

Prodorsum. Rostrum rounded medially with pair of strongly developed, acuminate lateral teeth (Fig. 2). Setae ro directed anteriorly, strongly barbed, about 40 µm, mutual distance at their base about 42 µm. Lamellae strongly converging, fused at base of lamellar cusps, 100–108 µm long. Lamellar cusp 34–46 µm long, tapering to width of lamellar seta; bearing thick, sparsely barbed seta le, about 18 µm long, arising anteriorly on cusp (Fig. 10). Seta in barbed, 64–68 µm long, extending anteriorly of base of lamellar cusps. Mutual distance of setal pairs le and in approximately 10–18 and 44–48 µm, respectively. Sensillus bilaterally barbed, clavate, rounded distally, 70–86 µm long from base of bend in bothridium to tip, directed anteromedially (Fig. 11). Seta ex barbed, about 20 µm long. Bothridium with scales svm and svi well developed, rounded, sdm small, rounded; free margin of psdm flat to slightly convex. Humerosejugal porose area Aj long, oval.

Lateral Aspect of Podosoma. Genal tooth long, subtriangular, with carina extending along length (Fig. 4). Tutorium about 60 µm long, without striae, with two teeth dorsally, small tooth proximally and
Figs. 1–4: *Selvazetes sylvanus* n. gen., n. sp., adult ♀.

1. — Dorsal aspect. 2. — Dorsal detail of rostrum. 3. — Ventral aspect. 4. — Lateral aspect of prodorsum and podosoma after removal of legs, subcapitulum and notogaster (sacculus Ah indicated by arrow). Scale bars represent 50 μm.
Figs. 5-9: Selvazeta sylvanus n. gen, n. sp., adult ♀.
Figs. 10-13. Selvazetes sylvanus n. gen., n. sp., adult ♀.
large tooth distally (Figs. 4, 12). Custodium long, narrow, triangular, about 30 μm long. Discidium triangular between acetabula III and IV. Humerosjejugal porose organ Ah expressed as large sacculus with broad aperture.

Notogaster. Slightly longer than wide, ratio of 1:2:1. Notogastral setae smooth, thin, acuminate, c about 28 μm long, other notogastral setae 6–10 μm. Four pairs of porose areas positioned as in Fig. 1, with seta β₂ arising closely adjacent to porose area A2 (arising in middle of A2 unilaterally on one specimen). Posterior notogastral tectum absent medially for width of 20–30 μm.

Ventral Region. Epimeral setae lc, 3b and 3c thick, barbed, about 26, 20 and 30 μm long, respectively, other epimeral setae about 10 μm long, with few barbs. Anterior three pairs of genital setae barbed, 15–20 μm long, posterior three pairs of genital setae, and aggenital, anal and adanal setae smooth, about 10 μm. Adanal seta ad₂ positioned closer to margin of anal plate than lyrifissure lad (Fig. 3). Postanal porose area oval, about 110 μm long.

Gnathosoma. Axillary saccule of subcapitulum about 20 μm long, narrow (Fig. 9). Cheliceral digits toothed.

Legs (Figs. 5–8). Setation (I to IV): trochanters 1-1-2-1; femora 5-5-5-3-2; genua 3(1)-3(1)-1(1)-2; tibiae 4(2)-4(1)-3(1)-3(1); tarsi 20(2)-15(2)-15-12. Solenidion ω₁ on tarsus I tapered, curving dorsally over segment, slightly thicker than acuminate ω₂ (Fig. 5). Genu IV with ventral spur. Seta s of tarsus I eupatidial.

Material examined. Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, 8 March 1993 (D. BRENES and R. VARGAS), from primary forest soil; deposited in the Acari Collections of INBio. Paratypes: 15 adults with same data as holotype; 120 adults with same data as holotype except on the following dates: 4, 6, 7, 8, 10, 11, 13, 15 January 1993, 1, 2, 4, 5, 8 February 1993, 4, 5, 9, 10, 11, 13 March 1993, 30 April, 1, 30 May, 22 June, 3, 30 August, 29 September, 30 October 1993, 29 November 1993; 36 with same data as holotype except from soil of successional plots on: 4, 7, 9 January 1993, 1, 28 February, 8 March 1993, 30 May 1993, 12, 29 June, 3 August, 1 September, 29 November 1993, 2, 3 January 1994, 2 adults with same data as holotype, except in soil at edge of experimental swamp. Paratypes deposited in the Acari collections of INBio, the CNC, FMNH and RAN.

Etymology: The specific epithet sylvanus is from the Latin for “forest”, and refers to the habitat of this species in litter and soil of primary and secondary tropical rainforest.

Remarks: 1. The type series consisted of both male and female specimens; females have 0–2 eggs per specimen.

2. This is the most commonly found ceratozetoid mite in lowland tropical forest at La Selva. It is mainly an inhabitant of soil in primary forest, and adults were collected from this habitat in all months of the year, other than July and December. It was also collected from soils of secondary forest.

Allozetes Berlese

Allozetes was first proposed by Berlese (1913) as a subgenus of Ceratozetes, with Ceratozetes (Alloze­tes) pusillus Berlese as type species. He distinguished it by the following combination of character states: dorsesejugal scissure absent, absence of interlamellar setae, and tarsi monodactylous. Berlese described the type species A. pusillus as lacking notogastral setae, and did not comment on the octotaxic system. Subsequently described species have minute interlamellar setae and an inconspicuous octotaxic system, and this may also pertain to the type species.

The octotaxic system is incomplete in all known species of Allozetes other than A. dispar Hammer (1973), which has four pairs of normally positioned porose areas, and A. lacandonicus Mahunka & Palacios-Vargas (1996), which is described as having four pairs of saccules and a median porose area. Ohkubo (1981) described a reduced state of this system, with sacculi-like structures anterolateral to seta km (e₂), in A. levis Ohkubo; these structures were illustrated as pores. Allozetes africamus Balogh, 1958 and A. translamellatus Hammer, 1973 have a centro-
dorsal pore on the notogaster, but lack any expression of the normal octotaxic system. The species described below shows development of pairs of porose areas in addition to the centrodorsal porose area. The centrodorsal pore or porose area may represent the example, in which Al apparently is absent. However, the normal octotaxic system. The species described below shows development of pairs of porose areas in addition to the centrodorsal porose area. Thus, it is also possible that the centrodorsal porose area is a de novo structure, similar to the acronotic pore in Galumnidae, as noted by NORTON et al. (1997).

Species of Allozetes have a posterior notogastral tectum and thus the genus is tentatively moved from Ceratozetidae to Mycobatidae, although this placement may change following phylogenetic analysis of these families.

Allozetes alas n. sp.
Figs. 14-17

Diagnosis. Total length 284 μm; rostrum with strong lateral teeth and strong medial tooth; notogaster and ventral plate microtuberculate, without sculpturing; porose area Aa not evident, A2 small, positioned closely adjacent to seta lp (f2); A3 medium in size, anterior to seta h1; centrodorsal porose area present, subequal in size to A2; custodium absent.

Adult Measurements. Total length: female (n = 1) 284 μm; notogastral width 188 μm.

Integument. Integument microtuberculate over entire body and leg segments. Longitudinal striae on pteromorphs anteromedially; striae on ventral plate laterally. Longitudinal striae 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 with pair of strongly developed lateral teeth, bordering strong medial tooth (Fig. 14). Seta ro directed anteriorly, barbed, acuminate, about 50 μm long. Lamellae positioned laterally, about 50 μm long, of which cusps about 14 μm long; bearing thick, heavily barbed lamellar seta, about 32 μm long, arising slightly anteroventrally on lamellar cusp. Translamella present, about 45 μm wide, about 2 μm deep medially, expanding to about 10 μm deep laterally; laterally translamellar margin bent posteriorly, lying under lamellar cusp (Fig. 14). Seta in small, thin, about 3 μm long. Mutual distance of setal pairs is in approximately 45 and 49 μm, respectively. Sensillus barbed, fusiform, about 74 μm long from base of bend in bothridium to tip, directed anterolaterally. Alveolus of seta express, seta not evident. Bothridium cup-shaped. Humerosejugal porose area A not evident.


Notogaster. Slightly longer than wide; ratio 1.03:1. Ten pairs of smooth, acuminate notogastral setae, c and p series about 14 μm, la (cp), ln (e2), lp (f2) and h series about 14-20 μm. Dorsosejugal scissure absent (Fig. 14). Lenticulus absent. Porose area Aa not evident, A2 small, closely adjacent to seta lp (f2); A3 medium in size, anterior to seta h1; centrodorsal porose area present, subequal in size to A2 (Fig. 14). Posterior notogastral tectum complete, without overlapping lobes. Immovable pteromorphs curved ventrally, without line of desclerotization.

Ventral Region. Epimeral setal formula 2/3-1-2-1, setae thin, smooth; 1a expressed only as alveolus on one side of holotype; 2a and 3a expressed as alveoli; 1b and 3b about 6 μm, seta on epimere IV about 3 μm long. Six pairs of genital, 1 pair aggenital, 3 pairs of adanal, and 2 pairs of anal setae; setae smooth, thin, about 6 μm long. Postanal porose area not evident.


Legs. Setation (I to IV): trochanter I 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(1); tarsi 17(2)-15(2)-15-12. Tarsi monodactyous, without enlarged tarsal pulvillus. Famulus on tarsus I long, positioned distally to solenidia (Fig. 16). Solenidion p, of tibia I not inserted on
Figs. 14–17: Allocetes alas n. sp., adult ♀.

anterodorsal apophysis (Fig. 16). Genu I with ventral spur (Fig. 16). Seta \( r^* \) on genua and tibiae I and II short, spinous, and distinctly thicker than other setae on segment (Figs. 16, 17). Seta \( s \) of tarsus I eupathidial.

**Material examined.** Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, 21 February 1995 (D. BRENES and R. VARGAS) from fungi; deposited in the Acari collections of INBio. Paratype: 1 with same data as holotype except Annexo Flaminia, by Rio Puerto Viejo, 5 June 1997 (ALAS Team), from litter of cana brava (Gyneterum sagittatum (Gramineae)); deposited in the CNC.

**Etymology:** This species is named for the ALAS Project (Arthropods of La Selva) and the collaborating parataxonomists. This project provided the opportunity to collect oribatid mites in the lowland tropical rainforest ecosystem of Costa Rica.

Allozetes lacandonicus  
Mahunka and Palacios-Vargas, 1996

**Material examined.** COSTA RICA: Heredia, La Selva, Annexo Flaminia, by Rio Puerto Viejo, 5 June 1997: ALAS Team, 3 from Retana & Gramalote (Paspalum fasciculatum (Gramineae)) in old field which is sometimes flooded.  

**Remarks:** MAHUNKA & PALACIOS-VARGAS (1996) described *A. lacandonicus* with four pairs of saccules and the centrodorsal porose area present, whereas specimens from La Selva lack saccules and express only the centrodorsal porose area. I have examined a paratype specimen of *A. lacandonicus* which shows the centrodorsal porose area and pores, without associated saccules in the position of Sa. There are other pores on the notogaster, but these are not associated with saccules, and their position is not that of the octotaxic system.

**AUSTRACHIPTERIIDAE**

**Balogh & Balogh (1992)** place *Lamellobates* and related genera, *Paralamellobates*, *Sacculozetes* and *Hypozetes*, in the Austrachipteridae, a family proposed by LUXTON (1985) within the superfamily Ceratozetoidea. NÜBEL-REIDELBACH & WOAS (1992) suggested that placement of *Austrachiapteria* in the Ceratozetoidea is questionable. These latter authors also suggested a possible relationship between *Lamellobates* and Mycobatidae, based on the shared presence of a posterior notogastral tectum with overlapping lobes (BEHAN-PELLETIER, 1988). This character state is found also in the poronotic Adhaesozeti- dae (WALTER & BEHAN-PELLETIER, 1993), but this probably represents convergence. I retain *Lamellobates* and *Paralamellobates* in Austrachipteridae, although this placement may change following phylogenetic analysis of ceratozoid families.

**Lamellobates Hammer**

**Lamellobates intermedius**  
Nübel-Reidelbach and Woas, 1992

**Material examined:** COSTA RICA: Heredia, La Selva, Annexo Flaminia, by Rio Puerto Viejo, 5 June 1997, ALAS Team, 21 females from Retana & Gramalote (Paspalum fasciculatum (Gramineae)) in old field which is sometimes flooded; 17 females from Begoniacea along old farm road; 27 February 1994 (D. BRENES and R. VARGAS), 4 females from soil in secondary forest; 5, 12 January 1994 (D. BRENES and R. VARGAS), 2 females from soil in primary forest; 21 January 1994 (D. BRENES and R. VARGAS), 2 females from litter in axil of *Palmas* sp.; 1 May 1995 (D. BRENES and R. VARGAS), 1 female from Rigidoporus biokoensis fungus.  

**Remarks:** NÜBEL-REIDELBACH & WOAS (1992) noted variability in shape of the abaxial lamellar teeth; those on the specimens from La Selva are longer and broader than the adaxial teeth, as were those of some specimens illustrated by these authors. Also, see remarks on octotaxic system following description of *L. reticulatus* n. sp. (below).

**Lamellobates reticulatus** n. sp.  
Figs. 18–29

**Diagnosis.** Total length 280–308 \( \mu \)m; medial margins of lamellar cusps rounded and touching antero-
Figs. 18-20: *Lamellobates reticulatus* n. sp., adult ♀.

Figs. 21–26: *Lamellobates reticulatus* n. sp., adult ♀.

Figs. 27–29: *Lamellobates reticulatus* n. sp., adult ♀.

medially, lateral margin straight, bearing small lateral tooth; with anteriorly directed, tongue-shaped translaminar thickening; distinct reticulate pattern in middle of pteromorph; pedotectum I with 7 to 9 short, strong ridges on dorsal margin; nine pairs of notogastral setae; solenidion \( w_2 \) absent from tarsus II; seta \( s \) of tarsus I setiform.

**Adult Measurements.** Mean total length: female \((n = 8)\) 297 \(\mu\)m (range 280–308 \(\mu\)m). Mean notogastral width: female 201 \(\mu\)m (range 196–212).

**Integument.** Integument microtuberculate over entire body and leg segments. Distinct reticulate pattern in middle of pteromorph (Figs. 19), on lateral region of epimere I (Fig. 20), and on paraxial surface of femur IV. Curved striae on lamellae (Fig. 22). Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region.

**Prodorsum.** Rostrum with pair of lateral teeth flanking less sclerotized medial dens (Fig. 24). Seta \( r_0 \) directed anteriorly, strongly barbed, 50–54 \(\mu\)m, mutual distance at their base about 55 \(\mu\)m. Lamellae broad, converging, 66–70 \(\mu\)m long, with anteriorly directed, tongue-shaped translaminar thickening (Fig. 18). Lamellar cusps broad, 18–24 \(\mu\)m long, medial margin convex, lateral margin straight, bearing small lateral tooth, about 8 \(\mu\)m long, anterior margin straight or concave. Seta \( l_0 \) thick, spinous, 66–70 \(\mu\)m long, arising anteroventrally on lamellar cusp (Fig. 22). Seta \( l_1 \) thick, barred, about 101 \(\mu\)m long, extending beyond tip of rostrum; borne on small tubercles. Mutual distance of setal pairs \( l_0 \) and \( l_1 \) approximately 20 and 48 \(\mu\)m, respectively. Sensillus barred, clavate, 54–60 \(\mu\)m long from base of bend in bothridium to tip, directed anteromedially (Figs. 18, 22). Seta \( e_x \) about 20 \(\mu\)m long (Fig. 27). Bothridium cup-shaped, with well-developed ventrolateral scale. Humerosejugal porose area \( A_j \) long, oval.

**Lateral Aspect of Podosoma.** Genal tooth long, subtriangular, with carina extending along length (Fig. 27). Tutorium 80–84 \(\mu\)m long, with striae along length and two teeth proximally on dorsal margin; with pointed tutorial cusp about 24 \(\mu\)m long. Pedotectum I convex dorsally, with 7 to 9 short, strong ridges on dorsal margin (Fig. 27). Dorsal margin of pedotectum I ventral to insertion of seta \( e_x \). Custodium short, triangular, about 10 \(\mu\)m long. Discidium triangular between acetabula III and IV. Humerosejugal porose area \( A_h \) present, sublamellar porose area \( A_l \) absent (Fig. 27).

**Notogaster.** Slightly longer than wide, ratio of 1.15:1 (Figs. 18, 21). Nine pairs of smooth, acuminate notogastral setae, \( c \) and \( l_2 \) (cp), \( l_m \) (\( e_3 \)), \( l_p \) (\( f_3 \)) 28–30 \(\mu\)m, \( h \) series 22 \(\mu\)m and \( p_1 \), \( p_2 \) 14–18 \(\mu\)m long. Anterior tectum strongly convex medially between bothridia. Lentilicus absent. Octotaxic organs developed as sacculi; \( S_2 \), \( S_2 \) and \( S_3 \) long, filiform tubules (Figs. 18, 26), \( S_1 \) elongated sacculus (Figs. 18, 25). Posterior notogastral tectum developed, divided medially, with overlapping lobes (Fig. 20). Pteromorphs curved ventrally, immovable, without line of sclerotization.

**Ventral Region.** Epimeral setal formula 3–1–3–3; \( I_c \) barbed, longest and thickest epimeral seta, about 26 \(\mu\)m, other epimeral seta about 10 \(\mu\)m long, with few barbs (Fig. 20). Genital and aggenital setae barbed, anterior three pairs of genital setae positioned along anterior margin of genital plate. Three pairs of anal setae and two pairs of anal setae. Anal and anal setae smooth, about 16 \(\mu\)m and 10 \(\mu\)m long, respectively. Postanal porose area oval, about 10 \(\mu\)m long.

**Gnathosoma.** Axillary saccula of subcapitulum present. Cheliceral digits toothed, chelicera with porose region abaxially.

**Legs.** 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)–1(3)–3; tarsi 17(2)–15(1)–15–12. Tarsi monodactylos. Solenidia absent from tibiae IV. Solenidia and famulus on tarsus I inserted proximally, famulus positioned distally to solenidia (Fig. 28). Solenidion \( w_2 \) absent from tarsus II (Fig. 29). Genua I and II with distinct ventral spur, genu IV with minute ventral spur. Seta \( r_0 \) on tibia II and genua I and II long, spinous, distinctly thicker than other setae on segment; seta \( r_0 \) on genu II longer than other setae on segment (Figs. 28, 29). Seta \( s \) of tarsus I setiform (Fig. 28).

**Material examined.** Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, Sendero Occidental, 13 November 1992 (D. Brenes), from litter and soil 0–7.5cm depth in open grassy area; deposited in the Acari collections of...
INBio. Paratypes: 7 adults with same data as holotype; 12 adults with same data as holotype except Annexo Flaminia, by Rio Puerto Viejo, 5 June 1997; ALAS Team, 12 from Retana & Gramalote (Paspalum fasciculatum (Gramineae)) in old field which is sometimes flooded; 1 from Pachira fruit along path; 3 females with same data as holotype except no date and habitat (P. QUÉSADA). Paratypes deposited in the Acari collections of INBio, the CNC, FMNH and RAN.

Etymology. The specific epithet refers to the reticulate pattern on the pteromorph of this species.

Remarks: Similarities between Lamellobates, Paralamellobates, Sacculozetes and Hypozetes were discussed in BEHAN-PELLETIER & RYABININ (1991). The following remarks deal with specific characters of Lamellobates not discussed previously.

1. Octotaxic system: This system is composed of filiform tubule Sa, S2, S3 and elongated saccule S1 (terminology follows that of NORTON et al., 1997). The openings of these are minute and the filiform tubules are difficult to see, hence their presence may have been overlooked in descriptions of L. quadricornis Pérez-Iñigo and Baglio, 1985, L. angolensis BALOGH, 1958, L. orientalis Csizár, 1961, L. botari BALOGH and MAHUNKA, 1977, L. gyöergyi BALOGH and MAHUNKA, 1977, and L. hausseri MAHUNKA, 1977. HAMMER (1958) noted the presence of pores in L. palustris Hammer, positioned as for the openings of tubules in L. reticulatus n.sp. Although MAHUNKA (1977) did not comment on the octotaxic system, he did illustrate a small saccule in L. hausseri in the same position as S1 in L. reticulatus. NÜBEL-REIDELBACH & WOAS (1992) noted the presence of filiform tubules on the notogaster of L. intermedius NÜBEL-REIDELBACH and WOAS, but did not give the number present or illustrate these clearly. They indicated and illustrated a pair of very short notogastral setae close to the position of lp (f2). These setae on their fig. 23a are in the same position as the elongated saccules S1 of L. reticulatus n.sp. I have also examined specimens of L. intermedius from La Selva (see above) and specimens of Lamellobates from Florida, USA, Mexico and India housed in the CNC, and all have 9 pairs of notogastral setae, S1 expressed as an elongated saccule, and Sa, S2 and S3 long and filiform.

2. Notogastral setae: L. reticulatus has 9 pairs of notogastral setae, with c1, c3, da (d1), dm (d2), dp (e1) f1 and p3 absent, a number also found in L. intermedius, L. palustris, L. quadricornis and illustrated for L. gyöergyi. BALOGH & MAHUNKA (1977) noted 10 pairs of setae in L. botari, but illustrated only 9 pairs. Similarly, ENGELBRECHT (1986) noted 10 pairs of setae for L. angolensis, but only illustrated 9 pairs. In all illustrations of Lamellobates species the positions of notogastral setae are similar.

3. Absence of solenidion o2 from tarsus II. This solenidion is absent from L. reticulatus, L. angolensis (ENGELBRECHT, 1986), L. intermedius, and specimens of undescribed species of Lamellobates from Florida, USA, Mexico and India housed in the CNC. None of the other descriptions of Lamellobates species give the chaetotaxy for tarsus II. Solenidion o2 also is absent from tarsus II in Mycobates Parmeliae (Michael) and M. beringianus BEHAN-PELLETIER of the family Mycobatidae (BEHAN-PELLETIER, 1994).

4. Abaxial porous area on chelicera. NÜBEL-REIDELBACH & WOAS (1992) noted the absence of this porous area in L. intermedius; it is present, though difficult to detect, in L. reticulatus n.sp.

5. Possible thelytoky. I have not seen male specimens of any Lamellobates species, nor have they been noted in the literature; it is possible that thelytoky is the mode of reproduction.

6. Eggs. The egg surface has irregular, longitudinal rows of round, oval or oblong tubercles, 1–2 μm in width, extending along its length. I have observed a similar pattern on the eggs of species of Paralamellobates and Zachvatkinibates and this character state may prove to be useful in analyzing relationships in Ceratozetidea.

Paralamellobates Bhaduri and Raychaudhuri

Paralamellobates striatus n. sp.

Figs. 30–33

Diagnosis. Total length 244–266 μm; longitudinal striae on lateral region of epimere I, present or not on
Figs. 30-33: Paralamellobates striatus n. sp., adult ♂.

other epimeres; medial margin of lamellar cusps parallel and contiguous, with medial and lateral teeth about 14 µm long; tutorium about 60 µm long; pedotectum I with about 4 short, strong ridges on dorsal margin; single pair of anal and adanal setae.

**Adult Measurements.** Mean total length: female \( n = 10 \) 253 µm (range 243–266 µm). Mean notogastral width: female 177 µm (range 159–191).

**Integument.** Integument microtuberculate over entire body and leg segments. Longitudinal striae on lateral region of epimere I (Fig. 31), and on paraxial surface of femora III and IV. In two specimens longitudinal striae present throughout epimeral region, extending onto ventral plate laterally. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region.

**Prodorsum.** Rostrum with pair of strongly developed lateral teeth; no medial tooth (Fig. 30). Seta ro directed anteriorly, barbed, acuminate, about 54 µm long, mutual distance at their base about 42 µm. Lamellae broad, converging, about 58 µm long, of which cusps 20 µm long and 20 µm wide, with medial and lateral teeth subequal in length, about 14 µm. Medial margins of cusps parallel and contiguous. Seta le thick, with few barbs, 46–50 µm long, arising anterolaterally on lamellar cusp, medial to lateral tooth (Fig. 30). Seta in thick, barbed, about 78 µm long, extending beyond tip of tutorium; borne on small tubercles. Mutual distance of setal pairs le and in approximately 24 and 48 µm, respectively. Sensillus barbed, clavate, about 56 µm long from base of bend in bothridium to tip; directed anteriorly. Alveolus of seta ex present, seta not evident. Bothridium cup-shaped, with well-developed ventrolateral scale. Humerosegulal porose area Aj long, oval.

**Lateral Aspect of Podosoma.** Genal tooth long, subtriangular, with carina extending along length. Tutorium about 60 µm long, with striae along length and tooth proximally on dorsal margin; with pointed tutorial cusp about 16 µm long. Pedotectum I convex dorsally, with about 4 short, strong ridges on dorsal margin. Dorsal margin of pedotectum I ventral to insertion of seta ex. Custodium triangular, about 16 µm long (Fig. 31). Discidium triangular between acetabula III and IV. Humerosegulal porose area Ah present, sublamellar porose area Al present.

**Notogaster.** Slightly longer than wide, ratio of 1.13:1. Nine pairs of smooth, acuminate notogastral setae, e about 22–24 µm, la (cp), lm (e2), lp (f2) and h series about 14 µm, and p1, p2 about 8 µm long. Anterior tectum strongly convex medially between bothidia. Lenticulus absent. Octotaxic organs developed as sacculi; Sa, S2 and S3 long, filiform tubules, S1 elongated saccules. Posterior tectum developed, divided medially, with overlapping lobes. Pteromorphs curved ventrally, immovable, without line of desclerotization.

**Ventral Region.** Epimeral setal formula 3-1-3-3; 1c barbed, longest and thickest epimeral seta, about 20–24 µm, other epimeral seta about 14 µm long, thin, smooth. Genital setae with few barbs, anterior three pairs of genital setae positioned along anterior margin of genital plate. Aggenital pair and single pair each of anal and adanal setae smooth, about 14 µm (aggenital setae absent in one specimen) (Fig. 31). Postanal porose area oval, about 6 µm long.

**Gnathosoma.** Axillary saccule of subcapitulum present. Cheliceral digits toothed, chelicera with porose region abaxially.

**Legs.** 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. Tarsi monodactylous, without enlarged tarsal pulvillus. Solenidion absent from tibia IV. Solenidia and famulus on tarsus I inserted proximally, famulus distal to solenidia (Fig. 32). Solenidion \( \omega_2 \) absent from tarsus II (Fig. 33). Genua I, II and IV with ventral spur. Seta \( f' \) on genu II spinous, and distinctly thicker than other setae on segment (Fig. 33); seta \( f' \) on genu I spinous and thicker than other setae on segment (Fig. 32).

**Material examined.** Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, Annexo Flaminia, by Río Puerto Viejo, 5 June 1997: ALAS Team, from Gramalote (Paspalum fasciculatum (Gramineae)) leaves in old field which is sometimes flooded; deposited in the Acari collections of INBio. Paratypes: 15 adults with same data as holotype; 9 with same data as holotype except from Retana & Gramalote (Paspalum fasciculatum (Gramineae)) litter; 6 with same data as holotype except from dead leaves of Gynerium sagittatum (Gramineae); with same data as holotype except Sendero
Occidentale, 13 November 1992 (D. BRENES), from litter and soil 0–7.5 cm depth in open grassy area; 1 female with same data as holotype, except 10 February 1994 (V. BEHAN-PELLETIER); 3 females with same data as holotype except 5 January 1994 (D. BRENES and R. VARGAS), from soil at close to experimental swamp in primary forest; 2 females with same data as holotype except 21 January 1994 (D. BRENES and R. VARGAS), from litter in axil of Palmas sp. Paratypes deposited in INBio, CNC, FMNH and RAN.

Etymology: The specific epithet “striatus” refers to the striae on the lateral epimeral region.

Remarks: See remarks following the description of Lamellobates reticulatus n. sp. The following remarks deal with specific characters of Paralamellobates not discussed previously.

1. Octotaxic System: The openings of notogastral sacculi are minute and the filiform tubules are difficult to see, hence their presence may have been overlooked in previous descriptions of species of Paralamellobates, e.g., P. ceylanicus (Oudemans) (ENGELBRECHT, 1986).

Classification: ENGELBRECHT (1986) discussed the discrepancy between the original diagnosis of Paralamellobates, with the character state of “lamellae with free tips” used to separate the subgenus from Lamellobates (BHADURI & RAYCHAUDHURI, 1968), and the character state used by BALOGH (1972) and BALOGH & BALOGH (1992), namely presence of only one pair of adanal setae. Both character states are expressed in P. striatus n. sp. However, this genus needs revision and a clarification of the generic diagnosis.

ZETOMIMIDAE

SHALDYBINA (1966) established the family Zetomimidae based on the absence of macro sclerites on the hysterosoma of immatures, absence of a humeral organ, and the absence of a setal pair of the h series in the larva (11 pairs of gastronotal setae). Later (SHALDYBINA, 1974), she recognized the absence of macro sclerites as representing a secondary loss, and presented a more complete diagnosis of the family. Characters of adults included in her diagnosis were: (a) different number of claws on tarsi I and tarsi IV; (b) arrangement of genital setae in an almost regular longitudinal row; (c) displacement of the genital opening anteriorly, so that epimeral setae 2a and 3a are in transverse alignment; (d) seta r on genua I and II short and spiniform; and (e) genua I and II with ventral cusps. All of these character states are subject to homoplasies within the Ceratozetoidea, other than the different number of claws on tarsi I and IV. As with other families in the Ceratozetoidea a phylogenetic analysis is needed to establish how diagnostic these character states are for the family. For example, all tarsi of Naiazetes reevesi Behan-Pelletier, which I consider a member of the Zetomimidae, are tridactylous (BEHAN-PELLETIER, 1996). See Remarks following description of Ceratozetes intermedius n. sp. (below).

A synapomorphy of described species of the three zetomimid genera, Heterozetes, Naiazetes and Zetomimus is the size of the male genital sclerite; it is large and subequal in length to the genital plate. In representatives of Chamobatidae, Ceratozetidae, Euzetidae and Mycobatidae the male genital sclerite is at most half the length of the genital plate (BEHAN-PELLETIER, 1996).

Heterozetes Willmann

Heterozetes heleios n. sp.

Figs. 34–41, 44–47

Diagnosis: Total length 544–596 μm; rostrum with medial crest and pair of weakly developed lateral teeth; lamellae about 160 μm long; seta in about 150 μm long, extending anterior to tip of lamellar cusps; tutorium about 160–180 μm long; with long, triangular cusp, 66–72 μm long; octotaxic system absent; only alveolus of notogastral setae expressed; ventral plate of male porose, other than band of cuticle extending between genital and anal plates; anal plate of male with subcircular porose area; axillary sacculus of subcapitulum absent.
Figs. 34-37: *Heterozetes helios* n. sp., adult ♂.

34. — Dorsal aspect. 35. — Ventral aspect. 36. — Subcapitulum. 37. — Lateral aspect of prodorsum and podosoma after removal of legs, subcapitulum and notogaster. Scale bars represent 50 μm.
Adult Measurements. Mean total length: female \((n = 11)\) 576 \(\mu m\) (range 564–596 \(\mu m\)); male \((n = 7)\) 551 \(\mu m\) (range 544–564 \(\mu m\)). Mean notogastral width: female \((n = 9)\) 470 \(\mu m\) (range 432–499); male \((n = 6)\) 442 \(\mu m\) (range 428–454).

Integument. Integument microtuberculate over entire body and leg segments. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region. Longitudinal striae on tutorium (Fig. 40).

Prodorsum. Rostrum with medial crest, with pair of weakly developed lateral teeth (Figs. 40, 41). Setae ro directed anteriorly, barbed, 86–94 \(\mu m\), mutual distance at their base about 96 \(\mu m\). Lamellae converging, about 160 \(\mu m\) long. Lamellar cusp tapered, about 60 \(\mu m\) long, with or without small lateral dens; bearing thick, sparsely barbed lamellar setae, 64–74 \(\mu m\) long, arising anteriorly on cusp. Mutual distance of lamellar cusps at their base about 46 \(\mu m\).

Seta in barbed, about 150 \(\mu m\) long, extending anterior to tip of lamellar cusps (Fig. 34). Mutual distance of setal pairs le and in approximately 32 and 80 \(\mu m\), respectively. Sensillus minutely barbed, fusiform, about 96 \(\mu m\) long from base of bend in bothridium to tip, directed anteriorly to anteromedially (Figs. 34, 38). Seta ex expressed only as alveolus (Fig. 37). Bothridium with scales svm and svl well developed, svm pointed; free margin of psdm flat to slightly convex. Humerocephalal porose area Aj long, oval.

Lateral Aspect of Podosoma. Genal tooth subtriangular, with carina extending along length (Figs. 37, 40). Tutorium about 160–180 \(\mu m\) long, with well-developed, longitudinal striae; with triangular cusp, 66–72 \(\mu m\) long (Fig. 40). Pedotectum I convex dorsally, with dorsal margin just ventral to alveolus of seta ex. Custodium short, broadly triangular, about 16 \(\mu m\) long. Discidium triangular between acetabula III and IV. Humerocephalal porose area Ah present. Sublamellar porose area Al absent.

Notogaster. Length subequal to width, ratio 1:1. Lenticulus present. Ten pairs of setal alveoli arranged as in Fig. 34 (additional setal alveolus c unilaterally on one specimen). No evidence of octotaxic system. Pteromorphs curved ventrally, immovable, without line of desclerotization (Fig. 38).

Ventral Region. Epimeral apodeme II and sejugal apodeme fused medially, such that epimeres II lack distinct medial sejugal apodeme. Epimeral setae barbed, formula 3-1-3-3; seta la about 38 \(\mu m\), Ib, 2a, 3a, 4a, 4b about 30–36 \(\mu m\); 3b about 60 \(\mu m\), 3c about 24 \(\mu m\), 4c about 14 \(\mu m\), 4e thickest seta, about 62 \(\mu m\) long (Fig. 35). Genital setae positioned in longitudinal row on plates; genital and aggenital setae barbed, 30–34 \(\mu m\) long. Ratio of length of genital sclerite to genital plate about 0.9: 1.0. Anal and adanal setae smooth or with few barbs, about 24 \(\mu m\) long. Postanal porose area not evident. Ventral and anal plates of female without porose regions. Ventral plate of male porose, other than band of integument between genital and anal plates. Male with subcircular porose area on anl plates (Fig. 35).

Gnathosoma. Axillary saccule of subcapitulum absent. Mentum with lateral apophyses, in longitudinal line with and opposing ridge on each gena (Figs. 36, 39). Chelicera with porose region abaxially; cheliceral digits toothed (Fig. 39).

Legs. 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(1); tarsi 18(2)-15(2)-15-12. Tarsus I monodactylous, tarsi II–IV tridactylous, all tarsi without enlarged tarsal pulvillus (Figs. 44–47). Solenomion of tibia I inserted proximally on segment. Famulus positioned between solenidia on tarsus I. Genua I and II with small tooth ventrodistally. Adaxial porose area on femora I and II extending onto abaxial face dorsally. Seta F of genua I and II short, spinous, positioned almost dorsally on segment (Figs. 44, 45). Seta s of tarsus I eupathidial (Fig. 44).

Material examined. Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, Experimental swamp, 22 May 1995 (V. BEHAN-PELLETIER and R. A. NORTON) from vegetation on surface of water; deposited in the Acari collections of INBio. Paratypes: 20 adults with same data as holotype; deposited in the Acari collections of INBio, the CNC, the FMNH, and RAN.

Etymology: The specific epithet “helleios” is Greek for “dwelling in a marsh” and refers to the habitat of this species.

Remarks: 1. A pair of porose organs are found on the ventral plate of males of the amerobelbid Hellen-
Figs. 38–41: *Heterozetes helios* n. sp., adult ♂
Figs. 42–43, *Ceratozetes ambiguus* n. sp., adult ♀.
42. — Anterolateral aspect of prodorsum. 43. — Rostrum and chelicera (Trågårdh’s organ indicated by arrow).
FIGS. 44–47: *Heterocetes helios* n. sp., adult ♂.

44. — Leg I. 45. — Leg II. 46. — Leg III. 47. — Leg IV. Trochanter removed from legs I and II; all legs in abaxial view. Scale bar represents 50 μm.
amerus ionicus (Mahunka) (Bernini & Arcidiacono, 1985), but these are distinct porose organs positioned laterally on the ventral plate, in contrast to the almost complete porosity of the ventral plate in male H. heleios. The distinct sexual dimorphism in porose organs shown by adults of this species possibly plays a role in intraspecific communication (Norton & Alberti, 1997). These authors postulate that males may produce semiochemicals (sex-attractants or general aggregation pheromones) that are involved in reproductive biology.

2. The absence of the axillary saccule of the subcapitulum is considered a secondary loss. The axillary saccule of the subcapitulum has been found in all other ceratozetoid species examined, including species of Heterozetes and Zetomimus (Norton & Behan-Pelletier, 1986), except for Guatemalozetes (Behan-Pelletier & Ryabinin, 1991) and an undescribed species of Heterozetes in the CNC.

Zetomimus Hull

Zetomimus naias Hull

Figs. 48-60

Diagnosis. Total length 300–332 μm; rostrum with medial crest, with lateral teeth; lamellae about 76 μm long; seta in 64–68 μm long, not reaching tip of lamellar cusps; tutorium about 96 μm long; notogastral setae 2–6 μm long; four pairs of porose areas, A1 positioned anterior to seta lp (f2); two pairs of adanal setae; ventral and anal plates of female without porose regions other than postanal porose area, ventral and anal plates of male porose, other than area of integument around aggenital setae and medial band of integument on anal plates; movable digit of chelicerata without teeth; fixed digit with two small teeth; tarsi I and II monodactylous, tarsi III and IV tridactylous; claw on tarsus I with two proximoventral spurs, medial claw of tarsi II to IV with single proximoventral spur, lateral claws of tarsi III and IV sharply bent medially.

Adult Measurements. Mean total length: female (n = 9) 320 μm (range 312–332 μm); male (n = 10) 315 μm (range 300–330 μm). Mean notogastral width: female (n = 9) 243 μm (range 232–248); male (n = 10) 233 μm (range 224–248).

Integument. Integument microtuberculate over entire body and leg segments; striae laterally on epimere I. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region.

Prodorsum. Rostrum with strong medial crest, with pair of well-developed lateral teeth (Figs. 52, 53, 55). Seta ro directed anteriorly, barbed, 46–50 μm, mutual distance of pair at their base about 56 μm. Lamellae converging, about 76 μm long. Lamellar cusp tapering nearly to width of lamellar seta, about 18 μm long, without lateral dens; bearing thick, sparsely barbed seta le, 40–46 μm long, anteriorly on cusp. Mutual distance of lamellar cusps at their base, about 32 μm. Seta in barbed, 64–68 μm long, nearly reaching tip of lamellar cusps. Mutual distance of setal pairs le and in approximately 26 and 46 μm, respectively. Sensillus minutely barbed, fusiform, about 70 μm long from base of bend in bothridium to tip, directed anteriorly to anteromedially (Figs. 48, 54). Seta ex barbed, about 37 μm long. Bothridium cup-like with pointed medial scale. Humerosjejugal porose area Aj long, oval.

Lateral Aspect of Podosoma. Genal tooth subtriangular, with carina extending along length (Fig. 50). Tutorium about 96 μm long, with well-developed, longitudinal striae dorsally (Fig. 54); with long, triangular cusp, about 38 μm long. Pedotectum I convex dorsally, with dorsal margin just ventral to insertion of seta ex. Custodium narrowly triangular, about 34 μm long (Fig. 50). Discidium triangular between acetabula III and IV. Humerosjejugal porose area Ah present. Sublamellar porose area A1 not evident. Ridge present dorsoposteriorly to acetabulum IV (Fig. 50).

Notogaster. Slightly longer than wide, ratio 1.06:1. Lenticulus present. Ten pairs of smooth setae, about 2–6 μm long arranged as in Fig. 48. Four pairs of porose areas; A1 positioned medially, anteriorly to seta lp (f2). Posterior notogastral tectum absent. Pteromorphs curved ventrally, immovable, without line of desclerotization, pointed or not anteroventrally.
Figs. 48-51: Zetonomus naias n. sp., adult ♂.
48. — Dorsal aspect. 49. — Ventral aspect, showing porose ventral and anal plates. 50. — Lateral aspect of prodorsum and podosoma after removal of legs, subcapitulum and notogaster. 51. — Chelicera, abaxial aspect. Scale bars represent 25 μm.
Figs. 52-57: Zetamimus nahas n. sp., adult ♂.
52. — Prodorsum. 53. — Rostrum. 54. — Lateral aspect of prodorsum. 55. — Lateral aspect of rostrum and subcapitulum. 56. — Tarsus I, showing claw. 57. — Partial leg III.
Figs. 58–60: Zetomimus naias n. sp., adult ♂.

58. — Leg I. 59. — Leg II. 60. — Leg III. Trochanter removed from legs I and II; all legs in abaxial view. Scale bars represent 25 μm.
Ventral Region. Epimeral setae with few barbs, formula 3-1-2-3; seta lb about 26 μm, le about 20 μm; other epimeral setae 10–16 μm. Genital and aggenital setae with few barbs, about 12 μm long. Two pairs of adanal setae. Anal and adanal plates of female without additional porose regions. Ventral and anal plates of male porose, other than area of cuticle anterior to aggenital setae and medial band of integument on anal plates (Fig. 49). Ratio of length of genital sclerite to genital plate about 0.94:1.

Gnathosoma. Axillary saccule of subcapitulum absent. Mentum with pair of lateral apophyses (Fig. 55). Movable digit of chelicera without teeth; fixed digit with two small teeth (Fig. 51). Chelicera with porose region abaxially.

Legs. Setation (I to IV): trochanters 1-1-2-1; femora 5-5-3-2; genua 2(1)-2(1)-1(1)-2; tibiae 4(2)-4(1)-3(1)-3(1); tarsi 20(2)-15(2)-15-12. Tarsi I and II monodactylous, tarsi III and IV tridactylous; claw on tarsus I with two proximoventral spurs (Figs. 56, 58), medial claw of tarsi II to IV with single proximoventral spur; lateral claws on tarsi III and IV strongly bent, with middorsal spur (Figs. 57, 60). All tarsi without enlarged tarsal pulvillus. Solenidion p1 on tibia I not on anterodorsal tubercle. Adaxial porose area on femora I and II extending onto abaxial face dorsally. Seta f' of genu I short, spinous, positioned almost dorsally on segment. Seta s of tarsus I eupatholic. Small spine anterodorsally on tibia II.

Material examined. Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, Experimental Swamp, 22 May 1995 (V. BEHAN-PELLETIER and R. A. NORTON) from vegetation on surface of water; deposited in the Acari collections of INBio. Paratypes: 20 adults with same data as holotype; deposited in the Acari collections of INBio, the CNC, FMNH, and RAN.

Etymology: The specific epithet “naias” is the Greek for “water-nymph”, and refers to the aquatic habits of this species.

Remarks: I include this species in the genus Zetomimus on the basis of the following shared characters: adult tarsi I and II with one claw; tarsi III and IV with three claws. SHALDYBINA (1969) considered the genus Hamobates (with two species: H. cristatus and H. spinosus (HAMMER, 1962), a junior synonym of Zetomimus, based on the dactyly of tarsi I to IV, a synonymy with which I agree (see also OHKUBO (1987)). Unfortunately this synonymy has been ignored in most keys and classifications, with Hamobates being considered a member of the Ceratozetidae (e.g., BALOGH, 1972; BALOGH & BALOGH, 1990, 1992). Species of Zetomimus known from north temperate regions have 3 pairs of adanal setae; Z. naias shares the loss of a pair of adanal setae with Z. cristatus and Z. spinosus, the two Chilean species recombined from Hamobates.

I examined the holotypes of Z. cristatus (Hammer, 1962) and Z. spinosus (Hammer, 1962), housed in the Zoologisk Museum, Copenhagen, Denmark. The male holotype of Z. cristatus has both ventral and anal plates porose, as in Z. naias. The species are easily distinguished on the basis of size: Z. naias is 300–332 μm in length whereas Z. cristatus is about 580 μm. The female holotype of Z. spinosus is almost identical to females of Z. naias, but is slightly larger (360 μm), has a longer dorsodistal spine on tibia II, and has a trilobed rostrum.

Zetomimus cristatus, Z. naias, Heterozetes heleios and the mycobatid Zachvatkinibates martimimus (BEHAN-PELLETIER, 1988) are the only ceratozetoid species known with sexually dimorphic porose organs; however only the former three species have a porose ventral plate and porose regions on the anal plates in the male. As already noted under H. heleios, these possibly play a role in intraspecific communication (NORTON & ALBERTI, 1997).

CERATOZETIDAE

CERATOZETES Berlese

Ceratozetes ambiguus n. sp. Figs. 42, 43, 61–66

Diagnosis. Total length 376–447 μm; rostrum without medial crest, with lateral teeth; striae late-
rally on epimere I; lamellae about 116 μm long; seta in about 125 μm long, extending anterior to tip of lamellar cusps; tutorium about 134 μm long; notogastral seta e about 16 μm, l and h series about 10 μm long, p series about 24 μm long; four pairs of porose areas, with A1 positioned anterior to seta lp (j2); ventral and anal plates of males and females without porose areas other than postanal porose area; all tarsi heterotridactylous.

**Adult Measurements.** Mean total length: female ($n = 7$) 428 μm (range 416–447 μm); male ($n = 7$) 389 μm (range 376–402 μm). Mean notogastral width: female ($n = 6$) 319 μm (range 311–328); male ($n = 6$) 297 μm (range 288–305).

**Integument.** Integument microtuberculate over entire body and leg segments; striae laterally on epimere I. Cerotegument granular, present between pteromorph, pedotectum I, tutorium, and lateral body wall, extending medially on prodorsum to interlamellar region.

**Prodorsum.** Rostrum rounded medially without crest, with several small ridges converging on pair of
Figs. 63–66: Ceratozetes ambiguus n.sp., adult ♀.

63. — Subcapitulum. 64. — Lateral aspect of prodorsum and podosoma after removal of legs, subcapitulum and notogaster. 65. — Leg I. 66. — Leg II. Trochanter removed from legs I and II; legs in abaxial view. Scale bars represent 50 μm.
small lateral teeth (Fig. 43). Seta ro directed anterio-
medially, barbed, about 78 μm long, mutual distance at their base about 78 μm. Lamellae slightly conver-
ging, about 116 μm long. Lamellar cusp tapering nearly to width of lamellar seta, 30–40 μm long, without lateral dens; bearing thick, sparsely barbed seta le, 46–68 μm long, arising anteriorly on cusp. Mutual distance of lamellar cusps at their base about 42 μm. Seta in barbed, about 125 μm long, extending anteriorly to tip of lamellar cusps. Mutual distance of setal pairs le and in approximately 34 and 54 μm, respectively. Sensillus minutely barbed, narrowly fusiform, 110–118 μm long from base of bend in bothridium to tip, directed anteriorly to laterally (Fig. 61). Seta ex barbed, about 20 μm long (Fig. 64). Bothridium with scales svm and svl well developed, svm tapered; free margin of psdm convex. Humero-
jugal porose area Aj long, oval.

Lateral Aspect of Podosoma. Genital tooth subtriangular, with carina extending along length. Tutorium about 134 μm long, with well-developed, longitudinal striae dorsally (Fig. 42); with triangular cusp, about 45 μm long. Pedotectum I convex dor-
sally, with dorsal margin just ventral to insertion of seta ex. Custodium short, narrow, about 20 μm long (Fig. 64). Discidium triangular between acetabula III and IV. Humerojugal porose areas Am and Ah present. Sublamellar porose area Al not evi-
dent.

Notogaster. Slightly longer than wide, ratio 1.08:1. Lenticulus present. Ten pairs of smooth setae, c, la (cp), lm (e2), lp (f2) and h series about 10–16 μm long, p series about 24 μm long, arranged as in Fig. 61. Four pairs of porose areas; A1 positioned anterior to seta lp (f2). Posterior notogastral tectum absent. Pter-
romorphs curved ventrally, immovable, without line of desclerotization.

Ventral Region. Epimeral setal with few barbs, formula 3-1-3-3; setae 1a, 2a, 3a, 4a, 4c about 16 μm long, 1c about 34 μm long, 1b, 3c, 4b 24–30 μm long. Genital and agenital regions with few barbs, about 26 μm long. Ratio of length of genital sclerite to genital plate about 0.7:1. Three pairs of adanal setae. Anal and adanal setae smooth, about 11 μm long. Postanal porose area oval, about 36 μm long. Ventral and anal plates of males and females without porose areas other than postanal porose area.

Gnathosoma. Axillary saccule of subcapitulum absent. Mentum with subtriangular, lateral apophy-
eses, covering base of gena laterally (Fig. 63). Chelicere-
dal digits toothed. Chelicera with porose region abaxially.

Legs. 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(1); tarsi 20(2)-15(2)-15-12. Tarsi hetero-
tridactylous. All tarsi without enlarged tarsal pulsilus. Solenidion q1 on tibia I not on anterodorsal tubercle (Fig. 65). Adaxial porose area on femora I and II extending onto abaxial face dorsally. Seta s of tarsus I eupathidial.

Material examined. Holotype: adult female. COSTA RICA: Heredia, Estación Biológica La Selva, Experimental swamp, 22 May 1995 (V. BEHAN-PELLETIER and R. A. NORTON) from vegetation on surface of water; deposited in the Acari collections of INBio. Paratypes: 20 adults with same data as holotype; deposited in the Acari collections of INBio, the CNC, the FMNH and the RAN.

Etymology: The specific epithet “ambiguus” is from the Latin meaning “doubtful” and refers to similarity this species shows to members of the genus Heterozetes.

Remarks. This species bears much similarity to members of the genus Heterozetes, namely: the short genal tooth, the overall shape of lamellae and sensilla, and the presence of a lateral apophysis on the mentum. However, unlike species of Heterozetes, all tarsi are tridactylous, and the genital sclerite of males is about two-thirds the length of the genital plates, instead of subequal in length to genital plates.

DISCUSSION

The ceratozetoid fauna of lowland tropical rainfo-
rest in Costa Rica though diverse at the generic level is less species rich than I expected on the basis of M. HAMMER’s research in the Andes Mountains of South America (HAMMER, 1958, 1961, 1962). Monthly quantitative collecting using Berlese extractors in primary and secondary forest yielded six species; the three species which are semi-aquatic were only collected when the swamp at La Selva contained standing water. Undoubtedly, collecting in additional habitats
### Table 1. — Key differences between ceratozetoid species in lowland tropical rainforest, Costa Rica (+, present; −, absent; ?, unknown).

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>MYCOBATIDAE</th>
<th>AUSTRACHIPTERIIDAE</th>
<th>ZETOMIMIDAE</th>
<th>CERATOZETIDAE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Selvazetes sylvanus n.sp.</td>
<td>Allozetes alas n.sp.</td>
<td>Lamellobates intermedius</td>
<td>Heterozetes helios n.sp.</td>
</tr>
<tr>
<td></td>
<td>Allozetes lacandonicus Maitunks &amp; Painoso-Vargas</td>
<td>Lamellobates reticulatus n.sp.</td>
<td>Paralamellobates striatus n.sp.</td>
<td>Zetominus naias n.sp.</td>
</tr>
<tr>
<td></td>
<td>Ceratozetes sylvarum n.sp.</td>
<td>Allozetes alas n.sp.</td>
<td>Lamellobates reticulatus n.sp.</td>
<td>Ceratozetes ambiguus n.sp.</td>
</tr>
<tr>
<td>Total length (µm)</td>
<td>380-446</td>
<td>284</td>
<td>246-272</td>
<td>270-280</td>
</tr>
<tr>
<td>Lateral teeth (rostrum)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Medial tooth (rostrum)</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Medial crest (rostrum)</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Lamella</td>
<td>strongly converging</td>
<td>laterally positioned</td>
<td>laterally positioned</td>
<td>cusps tooth-like medially, contiguous</td>
</tr>
<tr>
<td>Translamella</td>
<td>minute</td>
<td>+</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Sensillae; length µm</td>
<td>bilaterally barbed, 70-86</td>
<td>barbed, fusi-form, 74</td>
<td>barbed, cla-vate, 66</td>
<td>barbed, cla-vate, 68</td>
</tr>
<tr>
<td>Tutorial cusp; length µm</td>
<td>−</td>
<td>18</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Humero-sejugal A</td>
<td>sacculus</td>
<td>porose area</td>
<td>porose area</td>
<td>porose area</td>
</tr>
<tr>
<td>Dorso-sejugal scissure</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Notogastral scissure</td>
<td>Notogastral scissure; length (µm)</td>
<td>10 pairs; 6-28</td>
<td>10 pairs; 2-20</td>
<td>10 pairs; 14</td>
</tr>
<tr>
<td>Octotaxic system</td>
<td>4 pairs</td>
<td>sacculi and median porose area</td>
<td>4 pairs</td>
<td>sacculi</td>
</tr>
<tr>
<td>Posterior tectum of notogaster</td>
<td>developed laterally</td>
<td>+</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Epimeral setation</td>
<td>3-1-3-3</td>
<td>2/3-1-2-1</td>
<td>1-1-2-1</td>
<td>2-1-3-3</td>
</tr>
<tr>
<td>Ventral plate scutellation</td>
<td>−</td>
<td>−</td>
<td>reticulate</td>
<td>−</td>
</tr>
<tr>
<td>Postanal porose area (µm)</td>
<td>110</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Porose ventral plate</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Porose anal plates</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Pairs of adanal setae</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Axillary subcapitular scutule</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Teeth on movable digit of chelicera</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Dactyly</td>
<td>3-3-3-3</td>
<td>1-1-1</td>
<td>1-1-1</td>
<td>1-1-1</td>
</tr>
<tr>
<td>Gemma I and II seta</td>
<td>setiform</td>
<td>short, spinous</td>
<td>short, spinous</td>
<td>long, spinous</td>
</tr>
</tbody>
</table>

*Table 1.*
and microhabitats at La Selva, such as in open pasture, and in the canopy, will yield more species, and collecting of this kind is one of the objectives of the ongoing phase of the Arthropods of La Selva Project. A subsequent paper will describe additional ceratozetoid species from lowland tropical rainforest and microhabitats at La Selva in this region and include a key to species.

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