Dorsal Chaetotaxy of Neotropical Species Supports a Basal Position for the Genus Lepidonella Among Scaled Paronellidae (Collembola, Entomobryoidea)

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Dorsal chaetotaxy of neotropical species supports a basal position for the genus *Lepidonella* among scaled Paronellidae (Collembola, Entomobryoidea)

Felipe N. Soto-Adames[1,*] *and Bruno C. Bellini*[2]

Abstract

Lepidonella is a small genus of scaled Paronellidae comprising 12 species distributed mainly across the Ethiopian, Oriental and Australian biogeographic regions. Most species are poorly described by current standards and little is known about their dorsal chaetotaxy. Previous observations of the chaetotaxy of the second and third abdominal segments led to suggestions that *Lepidonella* may be more closely related to *Lepidocyrtus* than to other paronellids, thus rendering Paronellidae polyphyletic. Here we describe the complete dorsal chaetotaxy of the Neotropical species, *Lepidonella incerta* (Mari Mutt, nec Handschin), and *Lepidonella zeppelinii* **sp. nov.**, to evaluate the position of *Lepidonella* among genera of scaled Paronellidae. The abundant, largely undifferentiated chaetotaxy of *L. incerta* and *L. zeppelinii* **sp. nov.** suggests a basal position for *Lepidonella* among scaled Paronellidae. Putative synapomorphies of the chaetotaxy of the head and metathorax supporting the monophyly of *Lepidonella* lead us to conclude that most similarities in chaetotaxy between New World *Lepidonella* and *Lepidocyrtus* represent symplesiomorphies. We also conclude that Paronellidae s. lat. (i.e., including Cyphoderinae) is derived from an Orchesellinae or Heteromurini-like species and is sister to Entomobryinae. In addition, we describe *L. zeppelinii* **sp. nov.** from Brazil, the first member of the genus described for South America, we propose a new name, *L. marimuti* **n. name**, for *L. incerta* (Mari Mutt), which is a junior homonym of *L. incerta* (Handschin), transfer to the genus *Trogolaphysa* two species previously assigned to *Lepidonella*, and provide an identification key to the species of *Lepidonella* of the world.

Key Words: Bromacanthini, Brazil, Puerto Rico, Hispaniola, Caatinga Biome, edaphic fauna, new species

Resumen

Lepidonella es un género de la familia Paronellidae que incluye 12 especies distribuidas principalmente en las zonas biogeográficas de Africa, el sur y este asiático y Oceanía. Las descripciones de la mayoría de las especies son breves y excluyen detalles de la quetotaxia. Las pocas observaciones disponibles sobre la quetotaxia de *Lepidonella* han sugerido a varios autores que este género está más cercanamente relacionado a la tribu Lepidocyrtini de Entomobryidae que a otros miembros de la familia Paronellidae. En esta contribución describimos la quetotaxia dorsal de dos especies neotropicales, *L. incerta* (Mari Mutt, nec Handschin) y *L. zeppelinii* **sp. nov**., para evaluar la posición de *Lepidonella* en la familia Paronellidae. La abundante y poco diferenciada quetotaxia de las species americanas sugieren una posición basal para *Lepidonella* entre los paronélidos con escamas. Posibles sinapomorfias en la quetotaxia de la cabeza y el metatórax, que apoyan la monofilia de *Lepidonella*, nos llevan a concluir que la similitudes entre *Lepidonella* and Lepidocirtini son atribuibles a simplesiomorfias. Basándonos en esta conclusión y en evidencia obtenida de la bibliografía, proponemos la hipótesis de que la familia Paronellidae s. lat. (incluyendo Cyphoderinae) es hermana de la subfamilia Entomobryinae y se originó a partir de ancestros semejantes a miembros de la tribu Heteromurini (Entomobryidae). Además, describimos *L. zeppelinii* **sp. nov.**. de Brasil, el primer miembro Sudamericano de este género, proponemos un nombre nuevo, *L. marimuti*, nombre nuevo, para *L. incerta* (Mari Mutt), que es homónimo de *L. incerta* (Handschin), transferimos al género *Trogolaphysa* dos especies previamente incluidas en *Lepidonella*, y ofrecemos una clave dicotómica para identificar las especies de *Lepidonella* del mundo.

Palabras Clave: Bromacanthini, Brasil, Puerto Rico, Española, Caatinga, fauna edáfica, especie nueva

Resumo

Lepidonella compreende um pequeno gênero de Paronellidae com escamas, com 12 espécies reconhecidas, distribuídas principalmente entre as Regiões Biogeográficas Etiopiana, Oriental e Australiana. A maioria das espécies do gênero foi pobremente descrita tendo em vista os parâmetros atuais, e pouco é conhecido sobre sua quetotaxia dorsal. Observações prévias da quetotaxia do segundo e terceiro segmentos abdominais sugerem que *Lepidonella* pode ser mais proximamente relacionado a *Lepidocyrtus* que a outros paronelídeos, o que tornaria Paronellidae um grupo polifilético. Aqui descrevemos a quetotaxia dorsal completa de duas espécies neotropicais do gênero, *L. incerta* (Mari Mutt, nec Handschin) e *L. zeppelinii* **sp. nov.**, para avaliar a posição de *Lepidonella*

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entre os gêneros de Paronellidae com escamas. A quetotaxia abundante e amplamente indiferenciada de *L. incerta* e *L. zeppelinii* **sp. nov.** sugere posição basal para *Lepidonella* entre os Paronellidae com escamas. As sinapomorfias potenciais na quetotaxia cefálica e do metatórax que suportam o monofiletismo de *Lepidonella* nos levam a concluir que a maioria das similaridades na quetotaxia das espécies do Novo Mundo de *Lepidonella* e *Lepidocyrtus* representam simplesiomorfias. Também concluímos que os Paronellidae são derivados de um ancestral dentre os Orchesellinae ou Heteromurini (ou táxon similar) e juntos formam o grupo irmão de Entomobryinae. Descrevemos também *L. zeppelinii* **sp. nov.** oriunda do Brasil, o primeiro membro do gênero descrito para a América do Sul; propusemos um novo nome, *L. marimuti*, para *L. incerta* (Mari Mutt), que é um homonimo de menor para *L. incerta* (Handschin); transferimos duas espécies de *Lepidonella* para *Trogolaphysa*; e providenciamos uma chave de identificação para as espécies de *Lepidonella* em todo globo.

Palavras Chave: Bromacanthini, Brasil, Porto Rico, República Dominicana, Caatinga, fauna edáfica, nova espécie

The family Paronellidae includes Entomobryoidae with elongated fourth abdominal segment, dens smooth and cylindrical that taper gradually towards the distal end, and mucro of varied morphology, rarely bidentate or falcate. The family has been divided into 4 tribes (Paronellini, Bromacanthini, Callyntrurini and Cremastocephalini) based on chaetotaxy (Mitra 1993; Soto-Adames et al. 2014) and most species display a distinctive habitus that distinguishes them from members of the family Entomobryidae. The exceptions are members of tribe Bromacanthini (genera *Lepidonella* Yosii, 1960 and *Bromacanthus* Schött, 1925), which have been described as having a Lepidocyrtini-like habitus (e.g., Yosii 1960). Tribes Callyntrurini, Paronellini and Bromocanthini are characterized by the presence of scales, and whereas the idiochaetotaxy of Callyntrurini (Mitra 1974; Yoshi 1982) and Paronellini (Soto-Adames & Taylor 2013; Jantarit et al. 2013; Soto-Adames et al. 2014) has been well documented, the chaetotaxy of Bromacanthini remains largely undescribed. The few details known about the idiochaetotaxy of Bromacanthini are limited to drawings of the second and third abdominal segments, and bothriotrichal complex of the fourth abdominal segments of a few species (e.g., Yoshii 1981; Mari Mutt 1987; Yoshii & Suhardjono 1992a). Published accounts of the chaetotaxy of *Lepidonella* and *Bromacanthus* show more similarity with the chaetotaxy of Lepidocyrtus than with other scaled Paronellidae. Mari Mutt (1987), upon describing *Lepidonella incerta*, suggested that body shape, organization of eyes in the eye patch, the presence of an apical bulb on the fourth antennal segment and dorsal chaetotaxy of the trunk pointed at a closer relationship of *Lepidonella* to *Lepidocyrtus* than to other Paronellidae, thus rendering the family polyphyletic. Mitra (1993) echoed Mari Mutt's (1987) hypothesis, but did not provide additional information about chaetotaxy in support of the hypothesis. Information on the chaetotaxy of other segments is necessary to validate Mari Mutt's hypothesis because, as it was made clear in the analysis of Paronellini (Soto-Adames et al. 2014), the organization of the second and third segments may be conserved and synapomorphies relating *Lepidonella* to other Paronellidae may be found elsewhere on the head and body. In order to evaluate the hypothesis that similarities in the chaetotaxy of the second and third abdominal segments place *Lepidonella* closer to *Lepidocyrtus* that to other scaled Paronellidae, we present a complete description of the dorsal chaetotaxy of the head and body of 2 species of Neotropical *Lepidonella*.

Most species of *Lepidonella* are restricted to Africa, India, Southeast Asia and Australia (Bellinger et al. 2014). Only *L. incerta*, has been previously reported from the Americas (Puerto Rico and the US Virgin Islands, Mari Mutt 1988; Soto-Adames 2002). Two additional species of Neotropical *Lepidonella* were reported from the Atlantic Rainforest of northeastern Brazil (Bellini & Zeppelini 2009; Santos-Rocha et al. 2011), but those determinations are unconfirmed and the species remain undescribed. Here we describe a new species form Brazil, and compare the complete dorsal chaetotaxy of the new species with that of *L. incerta*, provide a new name for *L. incerta* (Mari Mutt 1988) and present an identification key to all named species of *Lepidonella*.

Materials and Methods

Specimens were cleared in liquid of Nesbitt's solution or hydrochloric acid and mounted in Hoyer's mounting medium. Drawings were first made using a drawing tube; final drawings were assembled into plates using CorelDRAW X6 software. Abbreviations used in the descriptions are: Ant., Abd. and Th. for antennae, abdomen and thorax, respectively. Types of *Lepidonella zeppelinii* **sp. nov**. are deposited in the Collembola Collection of Departamento de Botânica, and in the Collembola Collection of Museu Nacional/UFRJ, Rio de Janeiro, Brazil, under acronym CM/MNRJ; slides of *L. incerta* (Mari Mutt) are deposited in the collection of the Illinois Natural History Survey at the University of Illinois, Champaign, USA (INHS) and the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA (CMNH).

The dorsal chaetotaxy of the head is described following the AMS system of Jordana & Baquero (2005) and Soto-Adames (2008), whereas body chaetotaxy follows Szeptycki (1979). The macroseta formula follows Soto-Adames & Taylor (2013) and represents all macrosetae on anterior part of head, posterior part of head/Th. 2 (posterior to the collar), Th. 3/ Abd. 1, Abd. 2, Abd. 3, Abd. 4 columns A and B + Column C + Column T and all macrosetae external to T. The labial formula follows Christiansen & Bellinger (1998) in that upper case represent macrosetae, lower case microsetae, underline represents ciliate setae and not underlined smooth setae. Among scaled Entomobryoidea, adult Lepidocyrtini show the simplest and least differentiated idiochaetotaxy with respect to first instar (Szeptycki 1979; Mari Mutt 1988; Soto-Adames 2010). *Lepidonella* spp. have a largely unmodified idiochaetotaxy when compared with other Paronellidae with scales and the homologies of setae suggested here are based on comparisons with the chaetotaxy of Lepidocyrtini. In the section on dorsal chaetotaxy, we first describe the general chaetotaxy of *Lepidonella,* emphasizing elements common to the 2 species examined, followed by a discussion of homology determinations in cases where they conflict with previous homology hypotheses in Lepidocyrtini (Szeptycki 1979; Soto-Adames 2010). In the figures accompanying the descriptions, setae of uncertain homology are followed by a question mark (?).

Lepidonella Yosii, 1960

Paronellinae with 8+8 eye; antennae shorter than the body; first antennal segment shorter than head; Ant. 4 not subdivided or annulated; apically rounded or truncate scales present on head, body and ventral face of furcula; Abd. 2-4 with 2, 3, 2 bothriotricha; dorsal chaetotaxy complete or almost complete, with few dorsal macrosetae; metafemoral organ absent; manubrial spines absent; dens with 1-2 rows of spines; distal lobe of dens absent; mucro variable, with 3-5 teeth.

REMARKS

As defined above, *Lepidonella* differs from *Bromacanthus* only in the absence of the femoral organ. Mucro morphology in *Lepidonella* is unusually variable, even for a paronellid, and several *Lepidonella* species share the compact mucro present in *Bromacanthus*. The combination of mucro shape and geographic distribution suggest *Lepidonella* may not be monophyletic. The analysis presented below identifies several putative chaetotaxy apomorphies (e.g., presence of head seta Pm2, metathoracic seta a6 inserted posterior to seta m5, etc.) supporting the monophyly of *Lepidonella*. However, most named species are poorly described and head and metathorax chaetotaxy is known only for the species described here.

***Lepidonella zeppelinii* sp. nov. Soto-Adames & Bellini (Figs. 1-14)**

DESCRIPTION

Size. Total length of holotype 1,8 mm. Habitus typical entomobryoid (Fig. 1).

Color. Specimens in alcohol pale yellow with dark blue pigment covering eyepatches, and light blue pigment over antennae, lateral margins of meso- and metathorax, and terminal region of Abd. 4 and 5.

Scales. Brownish, apically rounded or truncate, and striated. Scales covering Ant. I-II, both faces of head, thorax, abdomen, all leg segments, and ventral face of manubrium and dentes. Ventral tube without scales.

Head. Antennae shorter than body (Fig. 1). Ant. 4 not subdivided or annulated, apical bulb absent. Ant. 3 sense organ as in Fig. 2, with 2 rods and 3 lateral guard sensilla; additional blunt sensilla are scattered through the distal end of the segment. Eyes 8+8, lenses A to F well developed, subequal, lenses G and H smaller, barely visible in cleared specimens (Fig. 4). Eyepatch valley with 4-5 mesosetae; q, t, r, p always present; s sometimes absent (Figs. 3-4). Head dorsal chaetotaxy (Fig. 3) with 14 pre-antennal macrosetae (An series); 6 anterior setae (macrosetae A0 and A2; microsetae, A1a, A1, A3 and A5); 4 medio-ocellar setae (microsetae M1, M2 and M3 and macroseta M4); 3 sutural microsetae (S2, S4 and S6); 3 post-sutural microsetae (Ps2, Ps3 and Ps5); and 13 posterior setae (microsetae Pa1, Pa2, Pa5, Pm1, Pm2, Pp1, Pp2, Pp3, Pp4 and Pp5; macroseta Pa5 and Pm3; and bothriotrix Pa6). Prelabral setae ciliate, labral setae smooth. Distal margin of labrum smooth, without spine-like structures. Pleural setae differing: basal seta smooth, as long as other surrounding setae; distal seta smooth and short. Maxillary palp with apical and basal setae smooth, apical setae longer than basal; sublobal plate with 2 appendages (Fig. 7). Labial palp papilla E with 4 setae, lateral appendage acuminate, seta-like, surpassing tip of papilla (Fig. 8). Proximal setae of labial palp smooth (Fig. 6). Labial triangle formula as M1M2M3rEL1L2A1-5; r smooth and reduced (Fig. 6). All post labial setae ciliate; setae along ventral groove 4+4, cervical setae 7+7; other postlabial setae as in Fig. 5.

Body. Complete macroseta formula 32/30/0244+0+9 (Figs. 3, 9-10). Chaetotaxy of Th. 2 as in Fig. 9: with 1 anterior (a5) and 3 posterior macrosetae (p3 complex, possibly comprising p4 and a duplication of p3); medial row with 4 microsetae (m2, m4, m5, m6?); posterior row with 4 microsetae (p1, p2, p5, p6, m6). Th. 3 with 15 setae: 5 anterior microsetae (a1, a2, a4, a6, a7); 5 medial microsetae (m4, m5, m6, m6a?, m7); and 5 posterior microsetae (p1, p3, p4, p5, p6). Abd. 1 with 1 accessory sensilla (as) and 8-9 microsetae: setae m2, m3, m4, a5, p5, p6, m6 and a6 always present; seta m5 present or absent. Abd. 2 with 2 bothriotricha (m2, a5), 2 macrosetae (m3, m5) and 1 sensilla (as): m2 surrounded by 3 fan-shaped setae (mi, a2, m3e), sensilla as and macroseta m3; microseta a3 inserted external to m2; a5 surrounded by 4 fan-shaped setae (Li, Lm, a6 and m4?) and macroseta m5; microsetae a3, p5, p5a, a6, p6, m6 and el? present. Abd. 3 with 3 bothriotricha (m2, a5, m5), 4 macrosetae (m3, am6, pm6, p6) and 2 sensilla (as, d2); m2 surrounded by 2 fan-shaped setae and microseta a2; a5 and m5 surrounded by 8 fan-shaped setae; 6 other microsetae present (p5 m7, p7, m7e, p7p, el?). Abd. 4 with 4 inner and 9 outer macrosetae (Fig. 10) with 8+8 posterior setae

Legs. Trochanteral organ shaped as in Fig. 11, with approximately 21 small spine-like setae. Hind empodial complex as in Fig. 12, tenent-hair weakly spatulate, clearly shorter than unguis. Unguis with 4 inner teeth, basal paired teeth larger than distal unpaired teeth; external teeth inserted near middle of outer edge of unguis. Unguiculus (Fig. 12) lanceolate to acuminate, with outer margin finely serrated.

Ventral Tube. Anterior face with many ciliate setae. Latero-distal flaps with 6+6 smooth mesosetae. Posterior face with 11+11 ciliate setae.

Furcula. Dens bearing 2 dorsal rows of weakly ciliate spines, with up to 23 spines in each row (Fig. 13). Mucro longer than wider, with 4 blunt teeth (Fig. 13-14).

TYPE MATERIAL

Holotype: Brazil, Rio Grande do Norte, Macaíba municipality, 12.X.2011, coll. B. C. Bellini, female, in preparation, deposited at Collembola Collection of DBEZ/UFRN. Paratypes: Same locality as holotype, 1 male and 2 females in preparation deposited at Collembola Collection of DBEZ/UFRN; 1 male and 1 female in preparation deposited at the CM/MNRJ.

DISTRIBUTION AND HABITAT

Lepidonella zeppelinii **sp. nov.** was found in different locations of Macaíba and Natal municipalities, Rio Grande do Norte State, northeastern Brazil. The new species was found in urban remnants of Atlantic Rain Forest, over sand dune soil and dead foliage. This distribution suggests the species has some resilience to anthropic impacts. The climate of the region is 'As' following Koeppen system, with a long dry summer and short wet winter (Kottek et al. 2006).

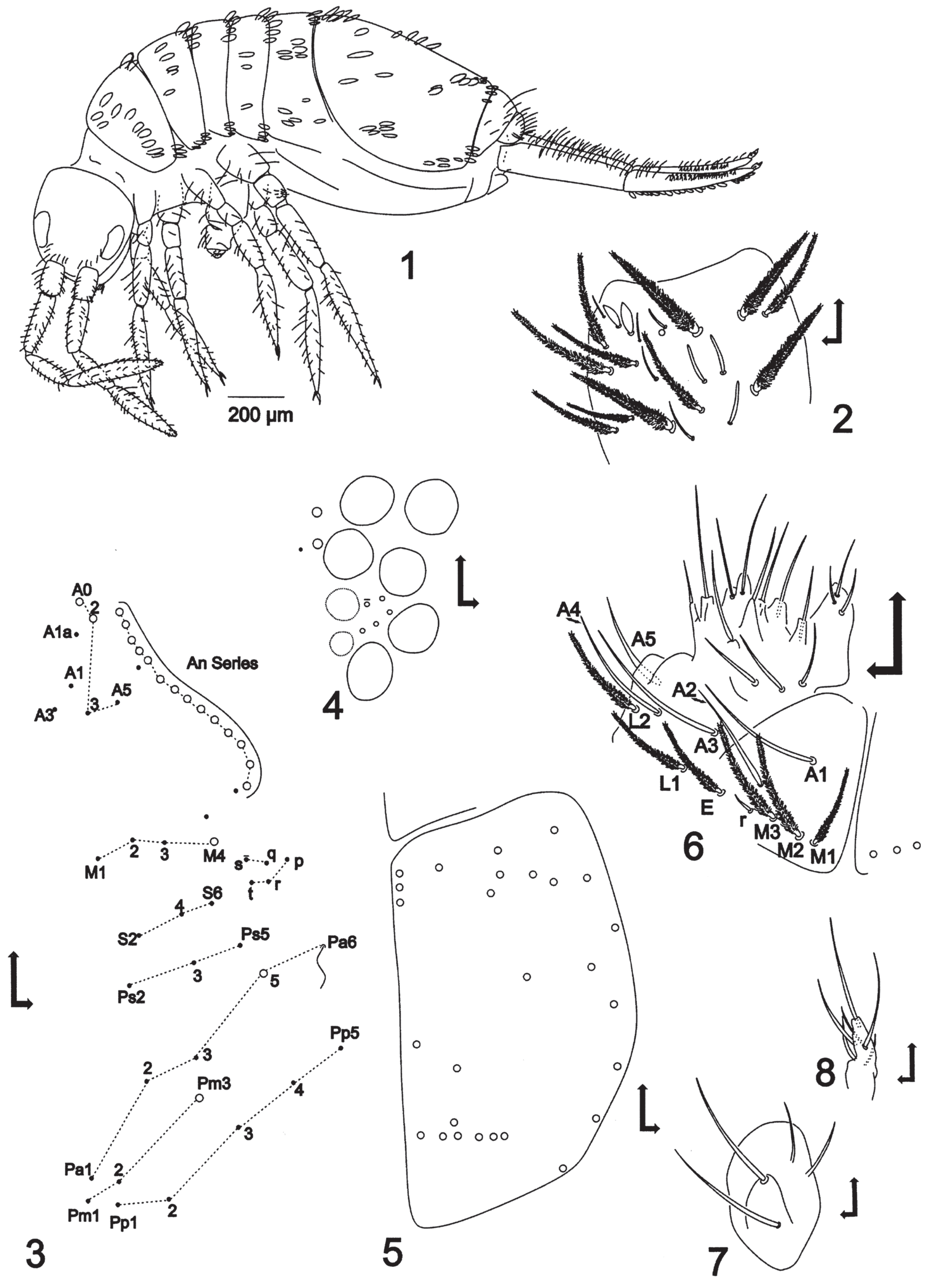
REMARKS

Lepidonella zeppelinii **sp. nov**. is the only member of the genus with lanceolate unguiculus, four inner macrosetae on Abd. 4, scales covering Ant. 1-2 and all leg segments, and labial triangle setae M2 and E ciliate. The new species is most similar to L. *lecongkieti*, but the characters listed above distinguish the two species. Among the incompletely described species, *L. zeppelinii* **sp. nov.** is most similar to *L. flava* (Carpenter, 1916), but the new species carries four inner ungual teeth and four mucronal teeth whereas *L. flava* has three ungual teeth and five mucronal teeth.

This species shows a combination of characters suggesting a transitional stage between *Lepidonella* and *Trogolaphysa*. The distribution of postlabial setae in columns C, presence of cervical setae, differentiation of distal pleural seta, duplication of seta p3 on the mesothorax and reduction in number of microsetae on the first abdominal segment point to affinities with *Trogolaphysa* (Soto-Adames & Taylor 2013). However, the presence of head seta Ps3, relative position of eyes G and H and the absence of fourth abdominal bothriotricha D4 place *L. zeppelinii* **sp. nov.** outside of *Trogolaphysa*.

ETYMOLOGY

The new species honors Douglas Zeppelini, for his incessant mentoring and years of support to the junior author.



Figs. 1-8. *Lepidonella zeppelinii* **sp. nov.**, arrows point anteriorly and outer sides, setae that may be present or absent are marked with a line; (1) Habitus; (2) Sense organ antennal segment 3 and associated setae and sensilla; (3) Dorsal chaetotaxy of head, open and closed circles are macro- and microsetae, respectively; (4) Eyepatch; (5) Chaetotaxy of postlabium, all setae are ciliate; (6) Labial palp and labial triangle; (7) Maxillary palp and sublobal plate; (8) Labial papilla E.

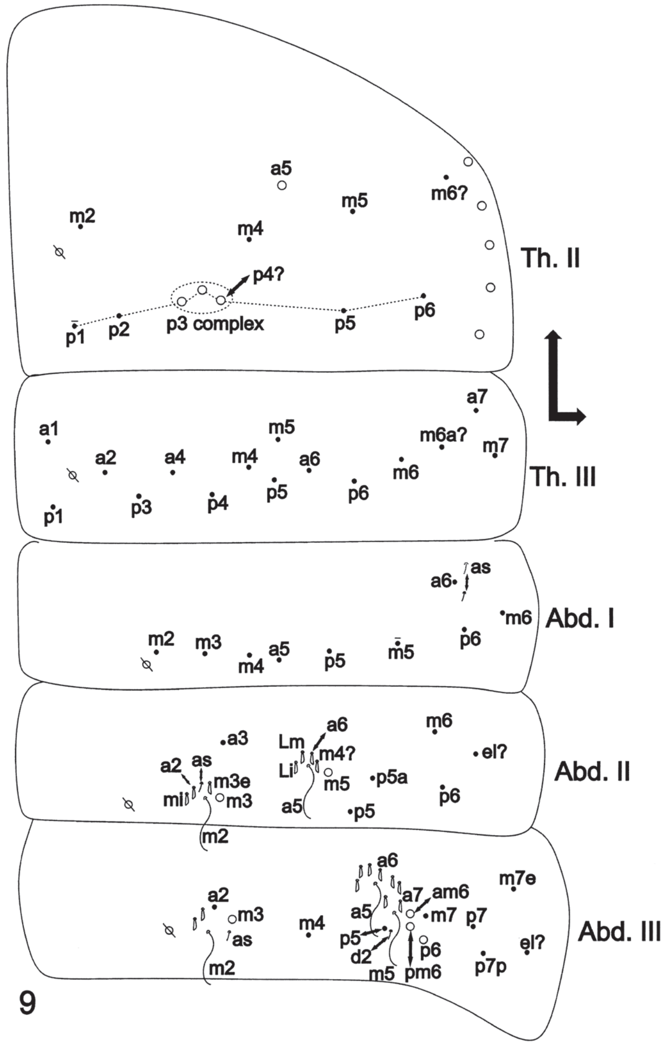


Fig. 9. *Lepidonella zeppelinii* **sp. nov**., dorsal chaetotaxy of thorax 2 to abdomen 3.

MATERIAL EXAMINED

Brazil, Rio Grande do Norte, Macaíba municipality, 12.X.2011, coll. B. C. Bellini, 4 females and 2 males. Macaíba municipality, 10.VII.2013, coll. R. V. C. Lima, 3 males. Natal municipality Parque da Cidade, B. C. Bellini, 1 male and 1 female. All specimens deposited in the Collembola Collection at DBEZ/UFRN.

Lepidonella marimuti Soto-Adames and Bellini, **new name** for *Lepidonella incerta* (Mari Mutt, 1988), nec Handschin, 1925 (Figs. 15-23)

Microparonella incerta Mari Mutt, 1988: 404 (original description); Mari Mutt & Bellinger 1996: 171 (Catalog of Neotropical Collembola)

Lepidonella incerta (Mari Mutt, 1988) Deharveng & Bedos 1995: 22 (new combination); Soto-Adames 2002: 99 (new record, US Virgin Islands).

ADDITIONS TO ORIGINAL DESCRIPTION

Head. Subapical sense organ of Ant. 4 capitate, minute (Fig. 17). Main sensilla on Ant. 3 sense organ short, barely projecting beyond cuticular fold, in some individuals appearing as pegs wider near the middle than at the tip (Fig. 18), whereas in other individuals they are capitate (Fig. 19). Head dorsally (Figs. 15-16) with 6-7+6-7 setae on antennal (An) row and 5 macrosetae (A0, A2, A3, M2, S3, Pa5). Pleural setae coarsely ciliate, subequal, as long as surrounding ciliate setae. Sublobal plate of outer maxillary palp with 3 appendages (Fig. 20). Labial papilla E with 4 basal setae, lateral appendage acuminate, seta-like, curved anteriorly. Labial palp with 5 serrate proximal setae. Postlabial region with few scales ('v'-shaped symbols in Fig. 21) and setae; 1-2 short smooth setae present, all other setae ciliate; setae along cephalic groove 3+3, posterior seta considerably larger than anterior setae; cervical setae absent.

Body. Complete macrosetae formula 51/10/0242+1+7 (Figs. 15, 22-23). Mesothorax with macroseta p3 (Fig. 22). Abd. 1 seta a6 present. Abd. 2 with a2, m3e, a6 and all supplementary setae ciliate; a3 anterior and internal to a2; macrosetae m3 and m5 present. Abd. 3 with a2, a3, a6, a7 and all supplementary setae ciliate; p3 inserted close to bothriotrix m2; d2 present; a7 inserted internal to am6, and posterior to bothriotrix a5; macrosetae am6, pm6, p6 and m7e present. Abd. 4 (Fig. 23) with inner macrosetae B5, B6 and C1, inserted in zones 9, 10 and 7, respectively; supplementary setae anterior to bothriotrix T2 ciliate, all other setae in bothriotrichal complex smooth; T6, D3, E2, E3 and F1 large macrosetae; D2 and F3 small macrosetae; E1 a smooth microseta, F2 absent; posterior setae 7+7.

Legs. Trochanteral organ 'V'-shaped, with 14-16 setae.

REMARKS

This is the only member of the genus with an apical bulb on Ant. 4 and an elongate mucro with 3 teeth. This is the most morphologically distinct and isolated member of the genus so far described. There is extensive variation in color pattern, ranging from the distinctive pattern accompanying the originally description of the species (Fig. 30 in Mari Mutt, 1987) to individuals without pigment except for antennae, eye patch and coxae. The individuals from the Dominican Republic are identical to the material from Puerto Rico and the US Virgin Islands in all morphological details.

ETYMOLOGY

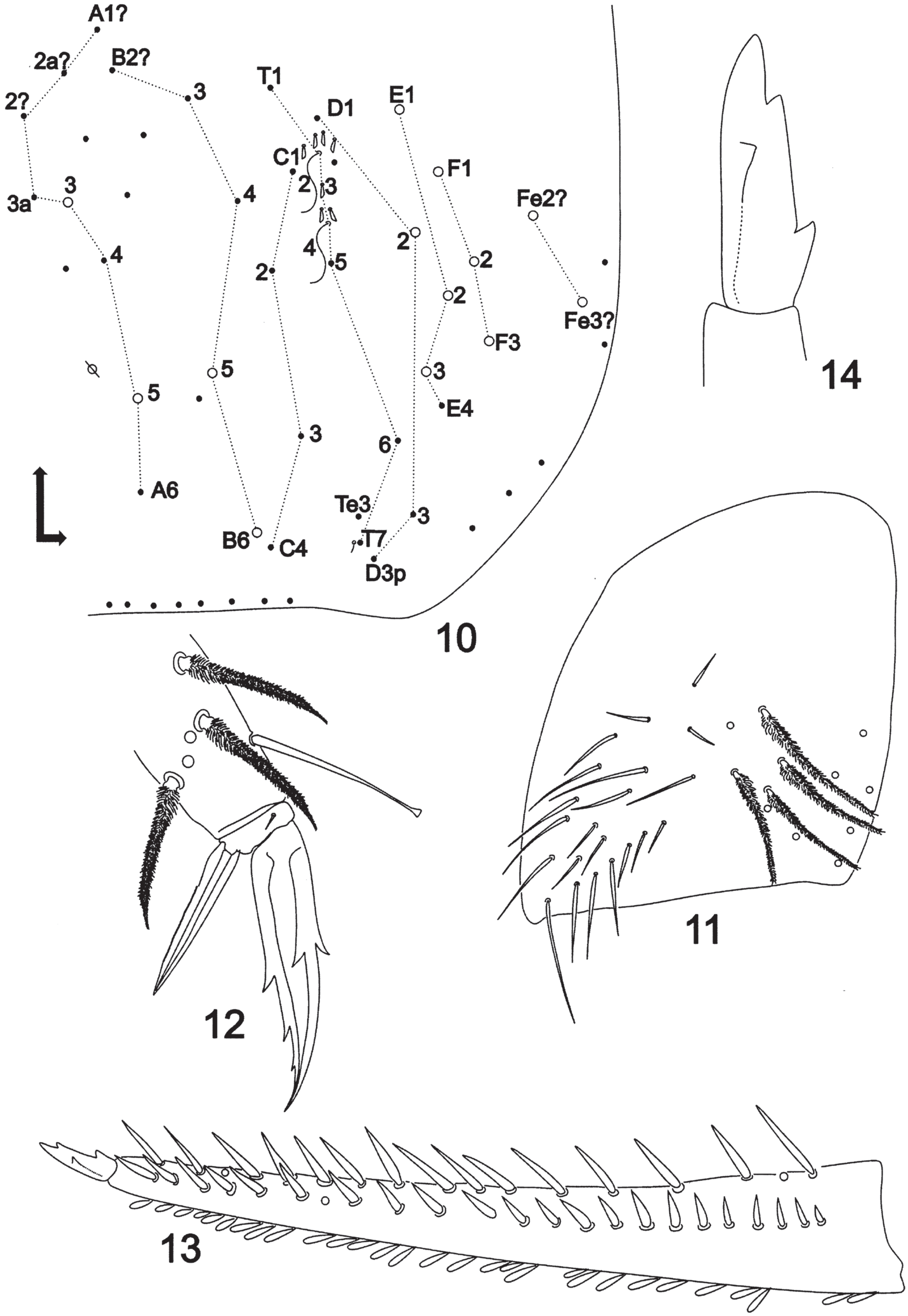
As pointed out by Deharveng & Bedos (1995), transference of *L. incerta* (Mari Mutt) to *Lepidonella* created a junior homonym of *L. incerta* (Handschin). The new name honors José Mari Mut, who originally described the species.

MATERIAL EXAMINED

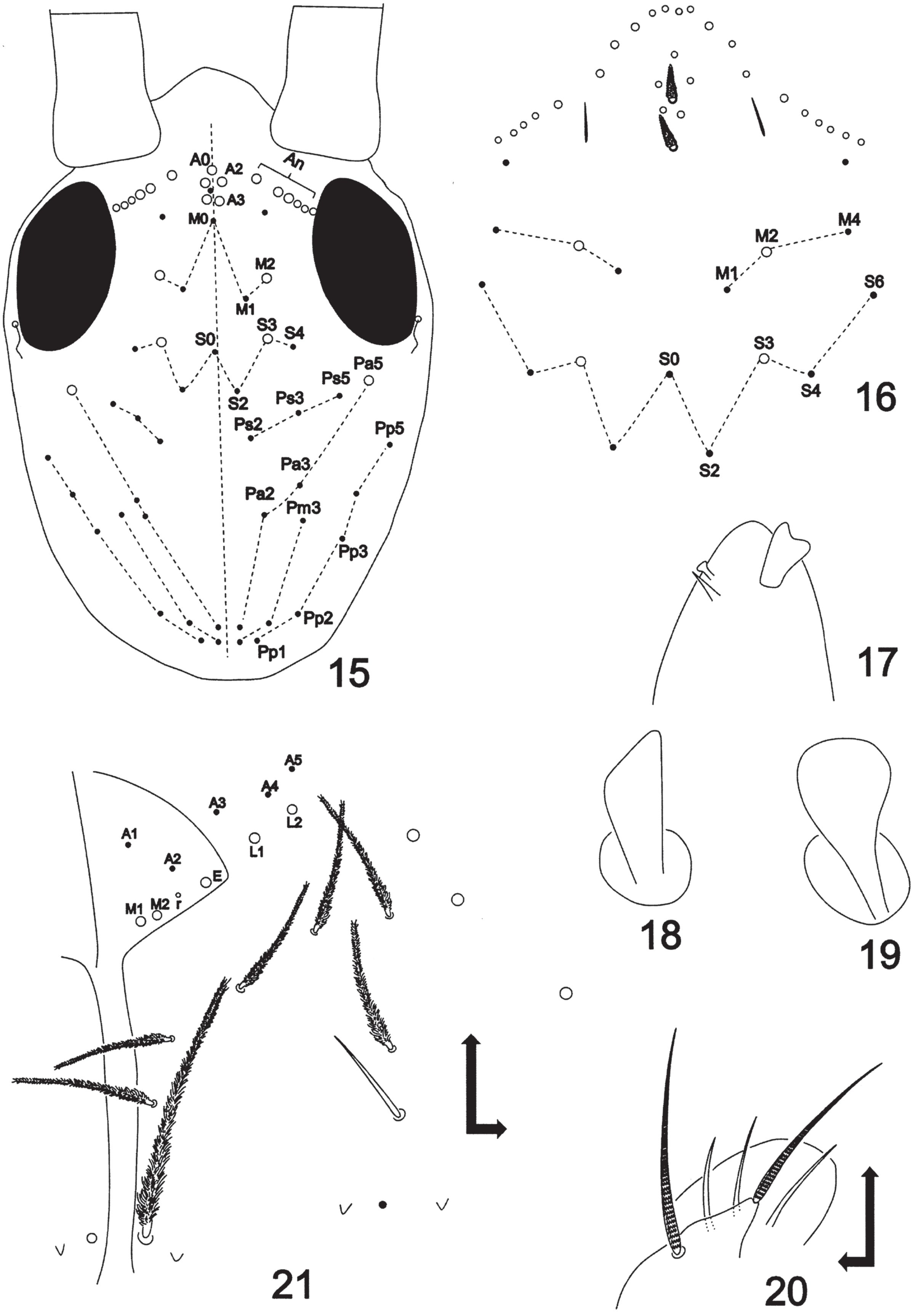
Puerto Rico, Isabela, Guajataca Commonwealth Forest, Road 446, N 18.41396 W - 66.97029, leaf litter top of *mogote*, 15.V.2009, F. Soto, 2 individuals in preparation; as above, but N 18.41714 W - 66.96459, along Nico's Trail, 25.IV.2010, F. Soto, 1 individual in preparation. Orocovis, Rd. 155 near Km 22.2, beating grasses along roadside, 19.VI.2001, F. Soto, 3 individuals in preparation.

US Virgin Islands, St. John, Cinnamon Trail, leaf litter, 30.VI.2000, F. Soto, 1 individual in preparation.

Dominican Republic, Pedernales, Sierra de Baoruco, Aceitillar, 25.2 Km ENE Pedernales, N 18.09957 W - 71.52112, 1272m, dense broadleaf and pine forest, yellow pan trap, sample DR42262B, 14.VI.2003, C. Young, J. Rawlings, C. Núñez, R. Davidson, P. Acevedo, M. de la Cruz, 1 individual in preparation. La Vega, Cordillera Central, Valle Nuevo Station, 5.2 Km ESE Valle Nuevo, N 18.77777 W - 70.64056, 2288m, open pine forest on slope, yellow pan trap, sample DR23162B, 23.V.2003, C. Young, J. Rawlings, C. Núñez, R. Davidson, P. Acevedo, 1 individual in preparation.



Figs. 10-14. *Lepidonella zeppelinii* **sp. nov**.; (10) Dorsal chaetotaxy of abdomen 4; (11) Trochanteral organ; (12) Metathoracic claw complex; (13) Dens and mucro; (14) Detail of mucro.



Figs. 15-21. *Lepidonella marimuti*; (15) complete dorsal chaetotaxy of head; (16) Detail of anterior chaetotaxy of head; (17) Apical bulb and subapical sense organ of antennal segment 4; (18-19) Sensilla of antennal segment 3 sense organ in different individuals; (20) Maxillary palp and sublobal plate; (21) Chaetotaxy of labial triangle and postlabium, 'v' symbols represent scales.

Key to World Species of the genus *Lepidonella*

The following key and the notes to the key account for all species assigned to *Lepidonella* by Deharveng & Bedos (1995). It is possible that more species from the African, Oriental and Oceania regions described during the first half of the 20th century and originally assigned to *Paronella* or *Pseudoparonella* belong in *Lepidonella*. However, the description of most species named before the 1960's are so incomplete by current standards that proper generic determination is not possible without examination of types or fresh material. Even most species currently assigned to *Lepidonella* are incompletely described and species diagnoses are based exclusively on color pattern, claw complex morphology and shape of mucro. Species identification in the following key is based on the characters listed above. It is recommended that some specimens be retained in alcohol, without clearing, to observe the color pattern.

1. Unguiculus truncate (Fig. 25-26) 2

—. Unguiculus lanceolate (Fig. 24) 8

2. Mucro elongate (Fig. 27) 3

—. Mucro compact (Fig. 28) or square (Fig. 29) 4

3. Unguis with 2 inner teeth; Pattern as in Fig. 30 . . . . *L. kei* (Yoshii and Suhardjono, 1992a)

—. Unguis with 4 inner teeth; Pattern as in Fig. 31 . . . . *L. duodecimoculata* (Prabhoo, 1971)

4. Mucro compact (Fig. 28) 5

—. Mucro square (Fig. 29) 6

5. Basal teeth of unguis inserted on basal fourth of distal half of inner edge (Fig. 26); mucro with 3 teeth; Abd. 4 only with posterolateral spots (Fig. 32) . . . . *L. oudemansi* (Yoshii, 1983)

—. Basal teeth of unguis inserted on distal half of inner edge (Fig. 25); mucro with 4 teeth; Abd. 4 with lateral longitudinal bands (Fig. 33) . . . . *L. nigrofasciata* (Handschin, 1928)

6. Unguis with 3 inner teeth; Abd. 4 with broken medial transversal band and paired latero-posterior spots (Fig. 34) . . . *L. tokiokai* Yosii, 1960

—. Unguis with 4 inner teeth; Abd. 4 transversal band, when present, unbroken (Figs. 35-37) 7

7. Abdomen 3 uniformly pigmented (Fig. 35) . . . . *L. ceylonica* (Yosii, 1966)

—. Abdomen 3 unpigmented (Figs. 36-37) . . . . *L. annulicornis* (Oudemans, 1890)

8. Mucro with 3 teeth; Ant. 4 apical papilla present . . . . *L. marimuti* Soto-Adames & Bellini, new name

—. Mucro with 4-5 teeth; Ant. 4 apical papilla absent 9

9. Unguis with 3 inner teeth; color pattern includes a large lateral spot on Abd. 3 and a transversal band on Abd. 4 (Fig. 38) . . *L. subcarpenteri* (Denis, 1948)

—. Unguis with 4 inner teeth; evenly yellow or white, with at most a wash of blue 10

10. Scales present on Ant. 1-2 and all leg segments; labial triangle setae M2 and E, ciliate (Fig. 6); Abd. 4 with 4 inner macrosetae; posterior edge of unguiculus finely serrate. . . . . *L. zeppelinii* Soto-Adames & Bellini, **sp. nov.**

—. Scales present only on body; labial triangle setae M2 and E smooth (Fig. 39); Abd. 4 with 3 inner macrosetae; posterior edge of unguiculus smooth . . . . *L. lecongkieti* Deharveng and Bedos, 1995

SPECIES NOT INCLUDED IN THE KEY

Lepidonella incerta (Handschin, 1925). This species shares the compact mucro of *L. nigrofasciata* and *L. oudemansi*. The original species description is very brief, and the color pattern described suggests that *L. incerta* may be a senior synonym of *L. oudemansi*.

Lepidonella vivieni (Barra, 1969) and *L. monomaculata* (Barra, 1969). These species from Gabon were originally described in *Microparonella* and transferred to *Lepidonella* by Deharveng & Bedos (1995). The description and illustrations in Barra (1969) show that both species carry 2,3,3 bothriotricha on Abd. 2-4 and that, at least *L. vivieni*, lacks head setae Ps3. The number of bothriotricha on Abd. 4 and the absence of head seta Ps3 place the Gabonese species in *Trogolaphysa*, sensu Soto-Adames et al. (2014). Thus, we propose the following new combinations:

Trogolaphysa vivieni (Barra, 1969) **new combination**
Trogolaphysa monomaculata (Barra, 1969) **new combination**

DORSAL CHAETOTAXY OF *LEPIDONELLA*

Head (Figs. 3, 15-16)

Row A includes 2-3 unpaired and 3 paired setae. The organization of this row is typical of most entomobryoid species reported in the literature. As in other scaled paronellids, the homology of A5 is uncertain. In the species examined A0, A2 and A3 may be developed into macrosetae whereas A5 is a microseta. *Lepidonella zeppelinii* **sp. nov.** carries a supplementary microseta anterior to A1 absent in *L. marimuti.*

The number of setae in Row M differs between the 2 species. *Lepidonella zeppelinii* **sp. nov.** has 4 paired setae and M0 is absent, whereas *L. marimuti* carries 1 unpaired and 3 paired setae. The identity of lateral setae in this row is difficult to ascertain. Comparison with first instar *Pseudosinella* (Barra 1974) *Seira* (Soto-Adames 2008) and *Homidia* (Pan et al. 2011) suggests that the anterior, inner seta is M2

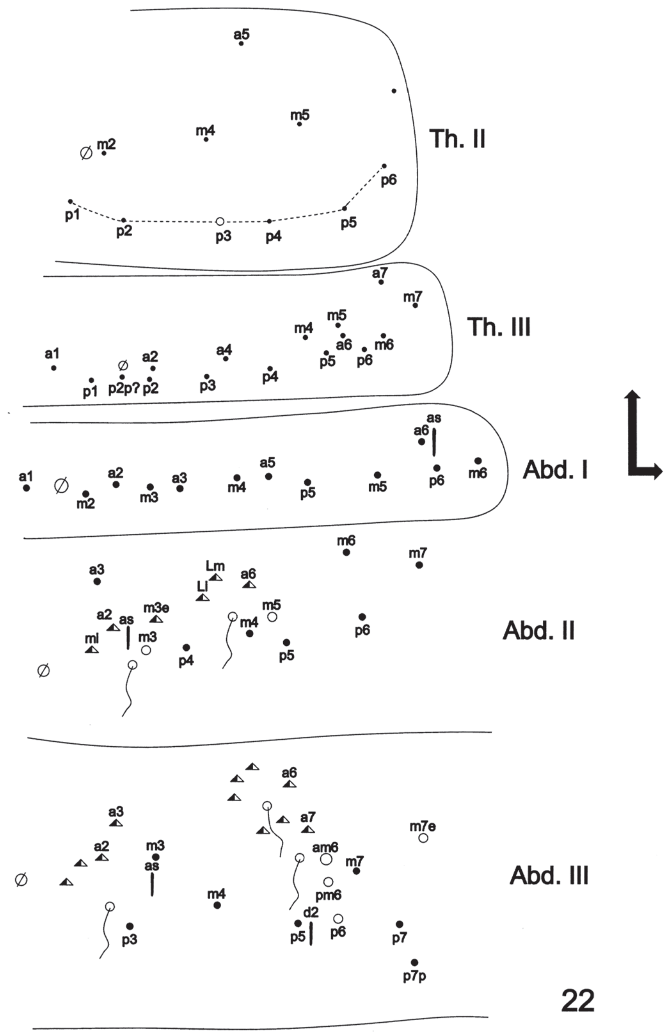


Fig. 22. *Lepidonella marimuti,* dorsal chaetotaxy of thorax 2 to abdomen 3.

instead of M3 as designated in *Trogolaphysa* and *Troglopedetes* (Soto-Adames & Taylor 2013; Soto-Adames et al. 2014). Following the chaetotaxy of *L. zeppelinii* **sp. nov**., the external seta is homologous to M4 instead of M3, seta M4 is always present and M3 may be present or absent. The two *Lepidonella* species also differ in the development of setae: *L. zeppelinii* **sp. nov.** carries macroseta M4, whereas in *L. marimuti* the macroseta present is M2.

The homology of lateral setae in Row S is also problematic. *Lepidonella marimuti* carries 1 unpaired and 4 paired setae, whereas in *L. zeppelinii* **sp. nov.** this row is greatly reduced and includes only 3 paired setae. When compared with Lepidocyrtini, (e.g., Barra 1974, Soto-Adames 2010) the lateral setae in *L. marimuti* appear homologous to S4 and S6, whereas S5 is absent. Based on the homologies indicated for *L. marimuti*, the setae present in *L. zeppelinii* sp. nov. are Ps2, Ps4 and Ps6. Irrespective of whether homology of the elements has been correctly assessed, the reduction in number of setae in *L. zeppelinii* **sp. nov.** is unique among species for which the head chaetotaxy is known.

Rows Ps, Pa, Pm, and Pp have 3, 5, 3 and 5 setae, respectively. These rows show an almost full complement of setae. Seta Pm2 is absent in the first instar of *Homidia*, *Seira*, or *Pseudosinella* and its presence in *Lepidonella* appears to be an apomorphy instead of the retention of a primitive character.

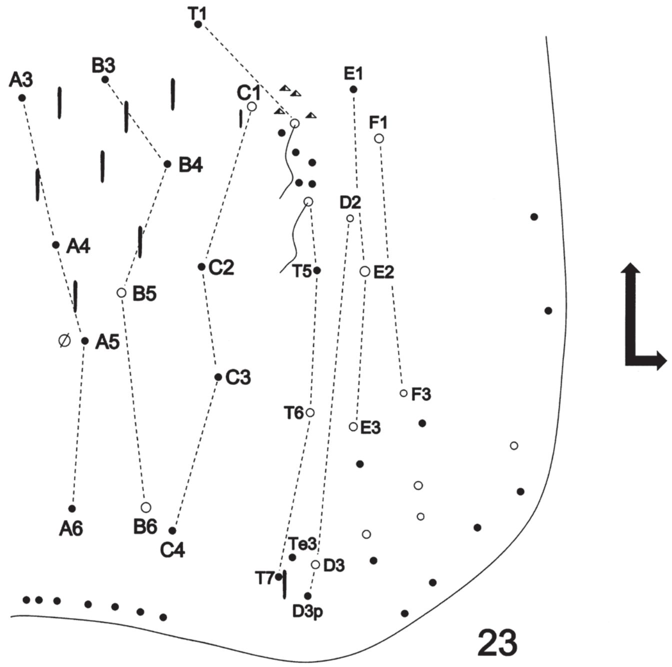


Fig. 23. *Lepidonella marimuti,* dorsal chaetotaxy of abdomen 4.

Mesothorax (Figs. 9, 22)

Rows a, m and p include 1, 4 and 6-7 setae, respectively. *Lepidonella zeppelinii* **sp. nov**. has 3 macrosetae on row p, likely corresponding to p4 and a duplicated p3, but otherwise is similar to *L. marimuti*. The chaetotaxy of this segment shows an almost identical arrangement in *Lepidonella* and Lepidocyrtini.

Metathorax (Figs. 9, 22)

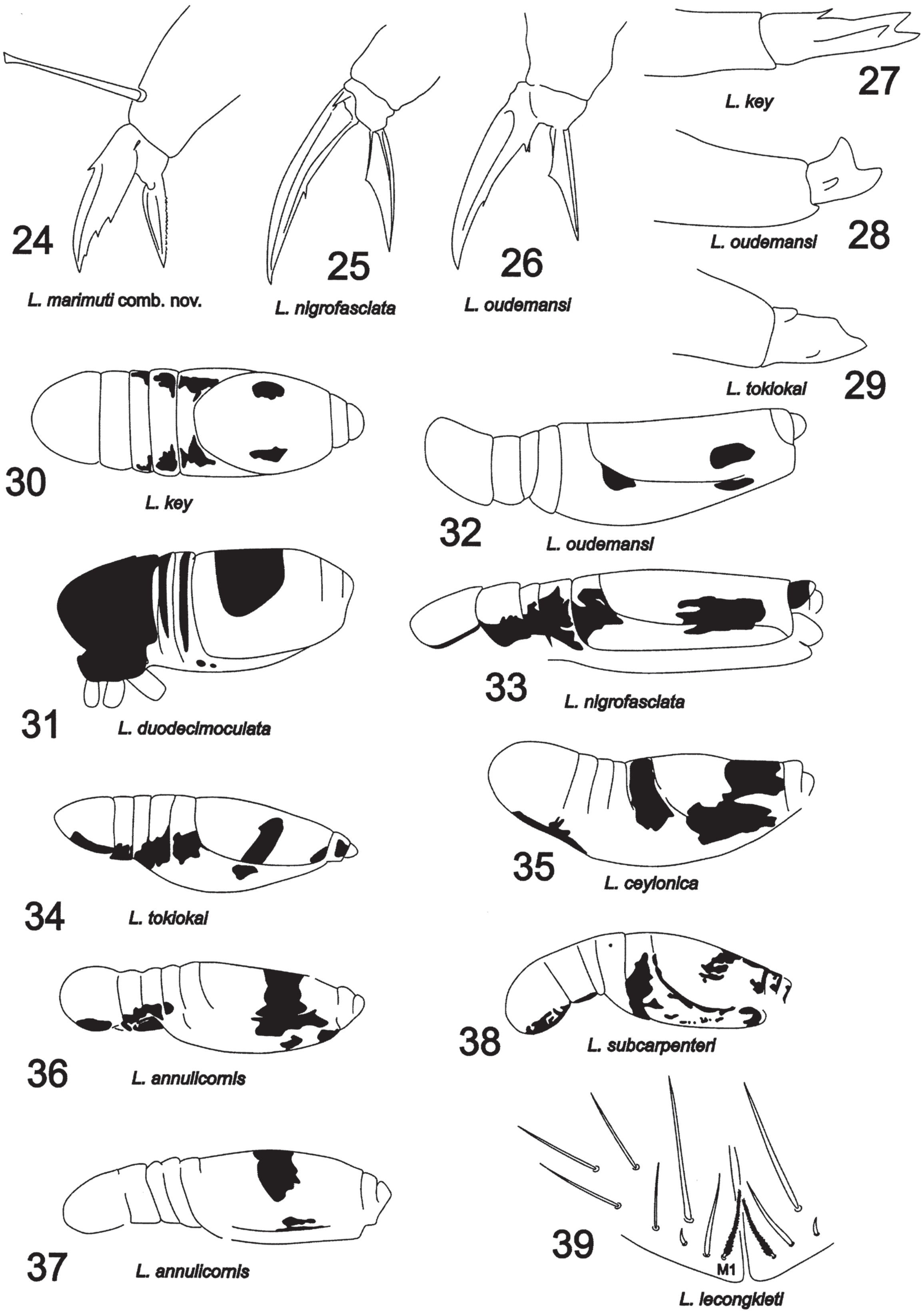
The metathorax carries 15-16 setae, 14 of which are present in both species. Setae p2 and p2p are absent in *L. zeppelinii* **sp. nov.** whereas m6a? is absent in *L. marimuti*. The general organization of the chaetotaxy is very similar to that in Lepidocyrtini, but *Lepidonella* lack setae m2 and m3, have the group of setae between p4 and p6 clumped and displaced laterally, and as it is typical in adults of other entomobryoids, seta a6 is inserted posterior to m5. The homology of seta a2 is unclear. In Lepidocirtini, the seta just external to the pseudopore is m2 whereas a2 is inserted clearly on the anterior row. However, in Paronellini seta a2 moves posteriorly in interspecific comparisons, sometimes ending in a similar position as that in *Lepidonella*.

First Abdominal Segment (Figs. 9, 22)

This segment carries 9-12 regular setae and one sensillum. The 12 setae present in *L. marimuti* are arranged as in the most generalized Lepidocyrtini, whereas *L. zeppelinii* sp. nov. has a reduce chaetotaxy and setae a1, a2 and a3 are absent.

Second Abdominal Segment (Figs. 9, 22)

Both species carry 18 setae, of which 16 are held in common and with the same general organization. The common setae include 2 bothriotricha, 2 macrosetae, one sensillum associated with bothriotrix m2 and 11 microsetae. Microseta a3 is internal to a2 in *L. marimuti* and external to a2 in *L. zeppelinii* sp. nov., and 2 setae are unique to either species: setae p4 and m4 are present only in *L. marimuti*, whereas *L.*



Figs. 24-39. Figs. 24-26 Metathoracic claw complex; (24) *L. marimuti*, after Mari Mutt 1987; (25) *L. nigrofasciata*; (26) *L. oudemansi*; Figs. 25-26 after Yoshii 1983. Figs. 27-29 Mucro; (27) *L. kei* after Yoshii and Suhardjono 1992a; (28) *L. oudemansi* after Yoshii 1983; (29) *L. tokiokai* after Yoshii 1960.Figs. 30-37 Color pattern; (30) *L. kei*, after Yoshii and Suhardjono 1992a; (31) *L. duodecimoculata* after Prabhoo 1971; (32) *L. oudemansi* after Yoshii 1983; (33) *L. nigrofasciata* after Handschin 1928; (35) *L. ceylonica* after Yoshii 1966; (35-37) *L. annulicornis* after Yoshii 1981; (38) *L. subcarpenteri* color pattern after Denis 1948; (39) *L. lecongkieti* chaetotaxy of labial triangle after Deharveng & Bedos 1995.

zeppelinii carries a supplementary seta anterior to m5 (which may be an anteriorly displaced m4) and one other seta of uncertain homology anterior and external to p5. The number, and organization of most setae on this segment are almost identical to that in *Lepidocyrtini*.

Third Abdominal Segment (Figs. 9, 22)

This segment carries 26-27 setae, of which 25 are shared and equally organized in both species. The common setae include 3 bothriotricha, 3 macrosetae (am6, pm6 and p6), 2 sensilla and 17 other setae. Setae a3, and p3 are present only in *L. marimuti*, whereas *L. zeppelinii* sp. nov. carries 2 supplementary setae between a6 and a7 that are absent in *L. marimuti*. *Lepidonella* differs from the Lepidocyrtini model only in the arrangement of lateral setae on Abd. 3. However, the lateral setae of Abd. 3 also shows variation in *Lepidocyrtus* (Mari Mutt 1987).

Fourth Abdominal Segment (Figs. 10, 23)

The chaetotaxy of this segment shows the highest degree of variation between the 2 species of *Lepidonella*. The 3 inner columns, bothriotrichal complex and presence of postero-lateral sensilla associated with T7 show the generalized organization present in most scaled Entomobryinae, but the number of inner setae assigned to zones 8-10 (Jordana 2012) differs between species. Columns B, C, T, D and E have the same number of setae, columns B and C have similar organization, but columns A and F differ in seta number and organization. The bothriotrichal complex in *L. marimuti* is most similar to the complex in *Lepidocyrtus* in having 4 anterior setae (homologous to a, m, s and D1) associated with bothriotrix T2, 3 setae (homologous to c1p, T3 and D1p) between bothriotricha T2 and T3, and 2 setae (Pi and Pe) anterior to T4. *Lepidonella zeppelinii* **sp. nov.** carries the same number of supplementary setae to T2 and T4 as *L. marimuti* but they differ in organization.

Discussion

Family Paronellidae is well characterized by the presence of cylindrical, smooth dens and variable but characteristic mucro. Paronellidae includes five major groups, subfamily Paronellinae with four tribes (Paronellini, Bromachanthini, Cremastocephalini, Callintrurini) and subfamily Cyphoderinae (Mitra 1993; Soto-Adames et al. 2008; Soto-Adames et al. 2014). The monophyly of the core Paronellinae lineages has never been seriously questioned, whereas placement of *Cyphoderus* and related genera in their own family is based on morphological adaptations to symbiotic life in ant and termite nests rather than detailed phylogenetic analysis. Recently Jantarit et al. (2014) have expressed the opinion that a short furcula and scale-like dental setae justify the recognition of family Cyphoderidae. This is an opinion on classification, not on phylogeny. The dens characters highlighted by Jantarit et al. (2014) are autapomorphies and do not help to solve the placement of *Cyphoderus* among Entomobryoidea. The reduced idiochaetotaxy in Paronellini and Cyphoderinae (see below) suggests a relationship between these two groups, a view espoused by Salmon's (1964) phylogenetic tree of Collembola relationships. Nevertheless, elucidation of the phylogenetic affinities of Cyphoderinae awaits formal evaluation.

Either including or excluding Cyphoderinae, the origin of the Paronellidae (s. lat.) remains unresolved. Two characters point at a close relationship between Paronellidae and Entomobryinae, the presence of modified supplementary setae associated with the bothriotrichal complexes of Abd. 2-4, and the similar habitus of *Lepidonella* and Lepidocyrtini. The genus *Lepidonella* sensu Deharveng & Bedos (1995) clearly belongs in Paronellidae, but the Lepidocyrtini-like organization of the eye patch and body shape have been pointed out from the inception of genus (Yosii 1960) as reflecting a possible phylogenetic relationship between the two groups. The idea that *Lepidonella* might be related to *Lepidocyrtus* was further reinforced by observations of the similarity in abdominal chaetotaxy between several *Lepidonella* species and members of Lepidocyrtini (Yoshii 1981; Mari Mutt 1987; Yoshii & Sujardjono 1992a; Mitra 1993).

Given the original observation of similarities in abdominal chaetotaxy between *Lepidonella* and Lepidocyrtini, the two questions to answer are: 1) do similarities in chaetotaxy between the taxa extend beyond those on Abd. 2-3?; and 2) do these similarities represent synapomorphies or symplesiomorphies?

To address the first questions, the present analysis confirms that similarities in chaetotaxy between *Lepidonella* and Lepidocyrtini extend beyond that of Abd. 2-3 to include Th. 2 and Abd. 4. The chaetotaxy of Abd. 1 in *L. marimuti* is identical to the basic plan in Lepidocyrtini, but *L. zeppelinii* **sp. nov.** shows an initial tendency towards a reduction in the number of setae. The chaetotaxy of Th. 3 in both species of *Lepidonella* shows a small reduction in the number of inner setae and characteristic arrangement of elements in the lateral field, more alike that in *Seira* (Soto-Adames 2008) than the undifferentiated chaetotaxy in Lepidocyrtini.

The second question may be address by considering the evolution of the chaetotaxy in scaled entomobryoids (Barra 1974; Szeptycki 1979; Soto-Adames 2008). Scaled entomobryoid genera display two trends in idiochaetotaxy development with respect to first instar nymphs, one leading to reduction in the number of setae, another leading to the evolution of multiplets (as defined by Szeptycki 1979). A trend towards a reduction in idiochaetotaxy on some or most segments of the trunk is evident in *Heteromurus* (Orchesellinae, Szeptycki 1979), *Metasinella* sp. (Lepidocyrtini, Soto-Adames 2002), Paronellini (Soto-Adames & Taylor 2013; Jantarit et al. 2013; Soto-Adames et al. 2014), and Cyphoderinae (Szeptyki 1979; Jantarit et al. 2014). A tendency to develop multiplets is evident in *Dicranocentrus* (Orchesellinae, Mari Mutt 1979; Mari Mutt & Bhattacharjee 1980); *Seira* (Seirini, Szeptycki 1979; Barra 2004; Soto-Adames 2008; Bellini et al. 2009; Cipolla et al. 2014) and *Callyntrura* (Callyntrurini, Mitra 1973, 1974; Yoshi 1982). Contrary to the two trends listed above, the number of dorsal trunk setae in *Lepidonella* and most species of Lepidocyrtini is the same found in the first instar of most other entomobryoids so far described (Barra 1974; Szeptycki 1979; Soto-Adames 2008; Pan et al. 2010). Molecular phylogenetic analyses of Collembola (Xiong et al. 2008) and Entomobryidae in particular (Zhang et al. 2014) place Lepidocyrtini at the base of the Entomobryinae tree, providing additional support to the interpretation that absence of significant idiochaetotaxy evolution is a primitive condition. Thus, we conclude that similarities in idiochaetotaxy between *Lepidonella* and Lepidocyrtini reflect a primitive, rather than a derived condition. This has important implications for the evolution and classification of Paronellidae.

The basal position of *Lepidonella* among scaled paronellids support previous views that the reduction in idiochaetotaxy in Paronellini (and Cyphoderinae) is a derived character (Soto-Adames et al. 2014). In addition, several characters, including the reduction in metathorax and first abdominal segment chaetotaxy in *L. zeppelinii* provide a path for the origin of Paronellini and Cyphoderinae from among *Lepidonella*-like ancestors. At the family level, determination of sister taxa relationship between *Lepidonella* and Lepidocyrtini would have provided evidence for an origin for Paronellidae from among Lepidocyrtini. Instead, current evidence leads to the hypothesis that Paronellidae was derived from an Orchesellinae-like ancestor (or an Heteromurini-like ancestor, according to Zhang et al. 2014) and is sister to Entomobryinae. Application of the hypothesis proposed here to the classification would result in either subsuming Paronellidae back into Entomobryidae as a subfamily, or elevating the individual units currently included in Orchesellinae to family. Further investigation on the origin of the family Paronellidae will require analysis of additional genera, including the genus *Metacoelura*, which retains a crenulate dens although other characters point to affinities with Paronellidae (Yoshii & Suhardjono 1992b).

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