



The Heteromurini Absolon & Ksenemann (Collembola, Entomobryidae): a review of the genera status and diagnoses, keys for species of *Alloscopus* Börner and *Heteromurtrella* Mari Mutt and description of a new species

NIKOLAS GIOIA CIPOLA^{1,4}, FABIO GONÇALVES DE LIMA OLIVEIRA²,
JOSÉ WELLINGTON DE MORAIS¹ & BRUNO CAVALCANTE BELLINI³

¹Laboratório de Sistemática e Ecologia de Invertebrados do Solo, Instituto Nacional de Pesquisas da Amazônia – INPA, CPEN, Avenida André Araújo, 2936, Aleixo, CEP 69011–970, Cx. Postal 478, Manaus, AM, Brazil. E-mail: nikolasgc@gmail.com

²Departamento de Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto da Universidade de São Paulo. CEP 14040–901, Ribeirão Preto, São Paulo, Brasil

³Programa de Pós-graduação em Sistemática e Evolução, Centro de Biociências, Universidade Federal do Rio Grande do Norte. Rodovia BR 101, Lagoa Nova, Campus Universitário, 59072–970 Natal, RN, Brazil

⁴Corresponding author

Abstract

The status of Heteromurini Absolon & Ksenemann is analyzed and a new diagnosis is proposed to the tribe. New chaetotaxic characters were added to distinguish *Dicranocentrus* Schött and *Pseudodicranocentrus* Mari Mutt. *Alloscopus* Börner, *Heteromurtrella* Mari Mutt and *Verhoeffiella* Absolon, originally proposed as subgenera of *Heteromurus* Wankel, are reviewed and a new diagnosis and generic status are proposed. The presence of the postantennal organ becomes the main characteristic to distinguish *Alloscopus* (present) and *Heteromurtrella* (absent). *Alloscopus yosiius* Mari Mutt, anteriorly synonymized with *Alloscopus tenuicornis* Börner, is revalidated. The absence of S0 macrochaeta on head of *Heteromurus* is reported now as a characteristic also shared with *Heteromurtrella*. *Heteromurtrella zairensis* Tshelnokov **comb. nov.** is transferred from *Heteromurus* by the presence of macrochaetae on abdomen I. *Heteromurtrella anae* **sp. nov.** from Brazilian Amazon is described and illustrated, including detailed dorsal chaetotaxy. This is the first record of *Heteromurtrella* in Brazil. *Heteromurus* now has 17, *Alloscopus* 10 and *Heteromurtrella* 20 valid species worldwide. An identification key and diagnosis for the six genera of Heteromurini and species of *Alloscopus* and *Heteromurtrella* are provided.

Key words: Chaetotaxy, Heteromurinae, Neotropical Region, Orchesellinae, taxonomy

Introduction

Heteromurini Absolon & Ksenemann, 1942 is a tribe of entomobryids widely distributed in the world and highly diverse in the tropics, currently with about 120 described species (Bellinger *et al.* 1996–2015). Traditionally Heteromurini species are distinguished from other tribes by the presence of strongly striated apically rounded or truncate scales on body and five antennal segments (Mari Mutt 1980a), but other current classification suggests that some members of the tribe are devoid of scales (Soto-Adames *et al.* 2008). However Zhang *et al.* (2014) recently proposed a new classification for Heteromurini, suggesting these characteristics appeared independently from other Entomobryidae and therefore added *Dicranocentrus* Schött, 1893 and *Pseudodicranocentrus* Mari Mutt, 1981 (in:1981b) in Heteromurini (Zhang *et al.* 2014, Zhang & Deharveng 2015).

Heteromurus Wankel, 1860 is the type genus of Heteromurini, with 54 described species widely distributed (Bellinger *et al.* 2015). Pantropical taxa as *Alloscopus* Börner, 1906, *Heteromurtrella* Mari Mutt, 1979 (in: 1979b) and *Verhoeffiella* Absolon, 1900 restricted to Africa and Europe, are ambiguously considered as: generic levels of Heteromurini (Thibaud & Massoud 1973, Hopkin 1997, Soto-Adames *et al.* 2008); or subgenera of *Heteromurus* (Mari Mutt 1977, 1980a, Lučić *et al.* 2007b, 2008).

At the same time, the diagnoses of these taxa are confusing. For example, in *Alloscopus* Mari Mutt the

presence of spines on dens is diagnostic, but they also occur in some species of *Heteromurtrella*, which is originally diagnosed by the absent of such spines (Mari Mutt 1979b, 1983, 1985a, 1985d). The same occurs with *Heteromurus* that is diagnosed by absent of S0 head macrochaeta, although this chaeta is also absent in some species of *Heteromurtrella* (Barra 1968; Mari Mutt 1979b, 1980b).

Therefore the taxonomic position and diagnosis of part of Heteromurini taxa needs to be re-evaluated and established in the light of current taxonomical knowledge.

Herein we provide: a new diagnosis for Heteromurini including its new status, an identification key and revised diagnoses for the current genera of the tribe, an identification key for the species of *Alloscopus* and *Heteromurtrella* and the description of a new species of *Heteromurtrella* from Brazil, including its detailed dorsal chaetotaxy.

Material and methods

The analyses of morphological characteristics were based on original descriptions and redescrptions. The nomenclature of the head dorsal chaetotaxy applied on the genera of Heteromurini is based in Mari Mutt (1979a) and Soto-Adames (2008) and body dorsal chaetotaxy follows Szeptycki (1979) based in secondary and primary chaetae of *Heteromurus*. Concerning some possible confusing characters, on head we named the sutural chaetae S0–S7, following Mari Mutt (1979a), and on Th II we labeled the three linear chaetae under the pseudopore as p1, p2 and p3 (as shown in Figs 11–12, 31) following Szeptycki (1979, pg. 137). The labial chaetotaxy system used in *Alloscopus* and *Heteromurtrella* follows Gisin (1964).

The description of the new species of *Heteromurtrella* follows Zhang & Deharveng (2015) for trunk specialized chaetae (S-chaetae). The subcoxae chaetotaxy follows Yosii (1959) based in *Lepidocyrtus* and labial papillae follows Fjellberg (1999).

The specimens of the new species were collected in fragments of Amazon Forest of “Reserva Ducke”, Amazonas State, Northern Brazil, from Berlese extractors. Specimens were firstly preserved in 92% ethanol and latter mounted on glass slides in Hoyer’s medium following the procedures described by Bonet (1931). Specimens were photographed in ethanol gel using a stereomicroscope (M165C) attached to a DFC420 digital camera. Photographs were digitally corrected using Application Suite V3.4.1. The material examined is deposited in the Invertebrate Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil.

Abbreviations: Ant—antennae; Abd—abdomen; mac—macrochaeta(e); PAO—postantennal organ; PLQ—Post-labial quadrangle; Th—Thorax. Symbols used to depict the chaetotaxy are presented in Figure 29. Chaetae of uncertain homology are followed by a question mark (?).

Systematics

Family Entomobryidae Tömösvary, 1882

Subfamily Heteromurinae *sensu* Zhang & Deharveng, 2015

Tribus: Heteromurini Absolon & Ksenemann, 1942

Diagnosis. Strongly striated apically rounded or truncate scales present on body, antennae, legs and furcula (Figs 24–28); Ant with 5 (Ant I subdivided in Ia and Ib) or 6 segments (Ant II also subdivided in IIa and IIb), Ant III–IV annulated or not (Figs 1–3); eyes 0+0 to 3+3, 6+6 or 8+8; PLQ with 2+2 chaetae (Figs 19–21); PAO present or absent (more common) (Fig. 8); head dorsal macrochaetotaxy with or without mac in series postsutural (Ps) and postoccipital (Pa, Pm and Pp) (Fig. 8); body dorsal mac reduced (e.g. *Heteromurus* s. lat.) or relatively dense (e.g. *Dicranocentrus* and *Pseudodicranocentrus*); Abd II–IV bothriotracha formula 2, 3, 2 (Figs 11–12); Th II to Abd V with S-chaeta formula 1, 0| 1, 0, 1, 0, 0 (ms) and 2, 2| 1, 3, 3, -, 3(4) (Figs 31–36, 38); Abd IV 1.2–1.5 times the length of Abd III in the midline (Figs 2–3, 22); trochanteral organ with at least 12 spine-like chaetae (Fig. 56); dental spines present or absent (Figs 15, 17); mucro bidentate with or without basal spine (Fig. 18).

Remarks. Heteromurini resembles other tribes of Entomobryidae as Orchesellini (Orchesellinae) and

Mastigocerini (Heteromurinae) by Ant with 5–6 segments, trochanteral organ with more than 15 chaetae, Th II to Abd III with S-chaeta (ms) formula 1, 0| 1, 0, 1, and mucro bidentate (see Zhang & Deharveng 2015). However the Heteromurini is distinguished from these tribes by presence of scales apically rounded or truncate on body, while in Mastigocerini scales are fusiform and in Orchesellini they are absent. Also, the chaetotaxy of tergal sensilla is 33-3(4) in Abd II–V of Heteromurini and Mastigocerini, while in Orchesellini the number is higher (see Zhang & Deharveng 2015).

In Heteromurini several characteristics are shared and can add support to the diagnosis of the tribe as: four prelabral chaetae, generally simple and smooth (Figs 10, 44), with exception of *Pseudodicranocentrus* in which they are bifurcate (see Mari Mutt 1981b); labral formula 4, 5, 5, smooth chaetae, four anterior chaetae (a1–a2), five median (m0–m2) and five posterior (p0–p2) (Fig. 45); head dorsal macrochaetotaxy with up to 8 series of chaetae (An, A, M, S, Ps, Pa, Pm, Pp), M, Ps, Pa; Pm and Pp present or absent (Figs 8, 30); tibiotarsi with or without rows of smooth chaetae; tenent hairs apically acuminate or capitate; unguis with one (medial) or two (medial and apical) unpaired teeth present or absent; unguiculi acuminate with or without outer tooth (Figs 12–14, 57–58); posterior face of manubrium and dens with or without rows of smooth chaetae (Fig 60) (Tab. 1) (Mari Mutt 1979a, 1979b, 1980b & c, 1981b, 1985d).

Key to world genera of Heteromurini

- 1 Antennae with 6 segments, Ant II subdivided (IIa and IIb); unguis with two paired basal inner teeth, never wing-like (Figs 1, 13) 2
- Antennae with 5 segments, Ant II not subdivided; unguis with two basal inner teeth or with two basal wing-like paired teeth (Figs 2, 13–14) 3
- 2 Head with A1 and Ps2 mac; prelabral chaetae bifurcate; dens base commonly with 3 groups of circularly arranged compound spines; dental spines absent (Figs 8, 9, 15–17) *Pseudodicranocentrus* Mari Mutt, 1981 (in: 1981b)
- Head without A1 and Ps2 mac; prelabral chaetae not bifurcate; dens base without compound spines; dental spines rows present or absent (Figs 8, 10, 15–17) *Dicranocentrus* Schött, 1893
- 3 Ant III not annulated (Fig. 3) 4
- Ant III annulated (Fig. 2) *Verhoeffiella* Absolon, 1900
- 4 Abd I with at least 1+1 mac (Fig. 12) 5
- Abd I without mac *Heteromurus* Wankel, 1860
- 5 Head posterior region without postoccipital mac; PAO present; dental spines always present (Figs 8, 15) *Alloscopus* Börner, 1906
- Head posterior region with postoccipital mac; PAO absent; dental spines usually absent (Figs 8, 15, 38) *Heteromurtrella* Mari Mutt, 1979 (in: 1979b)

Genus *Dicranocentrus* Schött, 1893

Dicranocentrus Schött, 1893: 21–22. Type species: *Dicranocentrus gracilis* Schött, 1893: 23, pl. 7, figs 1–6 (orig. descr.).

Dicranocentrella Wray, 1953, synonymized by Salmon 1964: 131

Heteromuricus Imms, 1912, synonymized by Mari Mutt 1979a: 17

Diagnosis. Antennae with 6 segments, Ant III–IV annulated (Fig. 1); eyes 8+8; four smooth prelabral chaetae not bifurcated (Fig. 10); PLQ with smooth chaetae (Figs 19–21); head dorsal macrochaetotaxy without A1 and Ps2 mac, S2 mac present (*sundanensis* group) or absent (other groups), postoccipital series (Pa, Pm and Pp) with up to 9+9 mac (other groups) or absent (*marias* group) (Fig. 8); Th II–III respectively with 5+5 to 17+17 central mac and 6+6 to 14+14 central mac; Abd I with 2+2 to 6+6 mac or absent; Abd II with 2+2 central mac (m3 and m3e); Abd III with 1+1 to 3+3 central mac (a2, m3 and m3e); Abd IV commonly with 2+2 to 5+5 central mac; Abd V with 4 sensilla; unguis with two paired basal inner teeth (Fig. 13); dens base without groups of compound spines; dental spines present or absent (Figs 15–17); mucro with basal spine (Fig. 18; Tab. 1).

Distribution. Pantropical.

Remarks. *Dicranocentrus* resembles another genera of Heteromurini, specially *Pseudodicranocentrus*, by antennae with 6 segments, tibiotarsi with or without smooth chaetae rows; tenent hair apically acuminate or capitate, unguis with two paired basal inner teeth, and mucro with basal spine (see Mari Mutt 1979a, 1981b). However *Dicranocentrus* differs from this genus by reduction of dorsal macrochaetotaxy, as head without A1 and

Ps2 mac; Th II with one to three central mac (m1, m2 and m2i), while in *Pseudodicranocentrus* there are always three, Abd II without a2 mac, and Abd III without extra central mac, while in *Pseudodicranocentrus* all these mac are present (see Mari Mutt 1979a, pg. 41–47). Other characteristics which characterize *Dicranocentrus* are: prelabral chaetae simple (bicurcated in *Pseudodicranocentrus* (Mari Mutt 1981b)), dental base without compound spines (present in most *Pseudodicranocentrus* spp.), and dental spines usually present. The coloration patterns of *Dicranocentrus* and *Pseudodicranocentrus* are shared and specimens of both genera can present blue or violet pigments on body, or be depigmented (Mari Mutt 1979a; Mari Mutt 1981b; Bellini *et al.* 2013; Xu & Zhang 2014). Finally *Dicranocentrus* and *Pseudodicranocentrus* share similar empodial complex morphology: the unguis present one unpaired medial tooth (typical), and one unpaired apical tooth (which can be also be absent in both genera) (Mari Mutt 1979a; Mari Mutt 1981b). The unguiculi are lanceolate and generally with small outer tooth, although some *Dicranocentrus* species may rarely present an outer smooth edge (e.g. *D. inermoides* (Uchida, 1944); *D. indicus* and *D. liuae* Xu & Zhang 2014).

The diagnosis of *Dicranocentrus* presented here does not include *D. pilosus* Mari Mutt, 1980 (in: Mari Mutt & Bhattacharjee, 1980), since this species has some distinct characteristics as head ‘M’ series with more than 5+5 mac, ‘S’ series with an extra mac (S6i?) and Ps2 present; Th II with 5+5 central mac, Th II with 15+15 posterior mac; Th III with 14+14 mac; Abd II with 4+4 central mac (a2, a3, m3 and m3e); Abd IV with 10+10 central mac; unguis smooth, without paired teeth at baseline; and tenent hair very short (see Mari Mutt & Bhattacharjee 1980). Due to its particular morphology, *D. pilosus* possibly belongs to a new genus in need of a full revision to be described.

Genus *Pseudodicranocentrus* Mari Mutt, 1981

Pseudodicranocentrus Mari Mutt, 1981b: 91–93. Type species: *Dicranocentrus circulatus*, 1979: 21–22, figs 15, 39, 63, 90, 103, Southern Mexico and Guatemala (orig. descr.).

Diagnosis. Antennae with 6 segments, Ant III–IV annulated (Fig. 1); eyes 8+8; four prelabral chaetae smooth and bifurcated (Fig. 9); chaetae of PLQ ciliated; head dorsal macrochaetotaxy with A1 and Ps2 mac, S2 mac absent (Fig. 8), postoccipital series (Pa, Pm and Pp) with more than 14+14 mac; Th II–III respectively with at least 17+17 and 14+14 central mac; Abd I with 4+4 or 5+5 mac; Abd II with 3+3 central mac (a2, m3 and m3e); Abd III with 3+3 or 4+4 central mac (a3, m3, m3e plus one unnamed); Abd IV with 7+7 to 8+8 central mac; unguis with two paired basal inner teeth; unguiculi lanceolate with outer tooth (Fig. 13); dental base with or without 3 groups of circularly arranged compound spines (Fig. 16); dens without spines; mucro with basal spine (Fig. 18; Tab. 1).

Distribution. Mexico and Guatemala.

Remarks. *Pseudodicranocentrus* is a small genus originated from the revision of *Dicranocentrus*, currently with three Neotropical species, mainly characterized by three features: prelabral chaetae bifurcate, head dorsal macrochaetotaxy with A1 and Ps2 mac and dental base generally with 3 groups of circularly arranged compound spines (Mari Mutt 1981b, 1984). This last characterized is present only in this genus, so the absence of such characteristic should be investigated in *P. niger* (see Mari Mutt, 1984).

The S-chaeta formula of Th II to Abd V in *Pseudodicranocentrus* is unknown, so this also needs to be investigated to clarify its relationship with *Dicranocentrus* and other Heteromurini.

Other information on *Pseudodicranocentrus* see remarks of *Dicranocentrus* and Table 1.

Genus: *Heteromurus* Wankel, 1860

Heteromurus Wankel, 1860: 203. Type species: *Heteromurus margaritarius* Wankel, 1860: 203, synonymized as *Podura nitida* Templeton, 1836: 94 by Bellinger & Ellis 1972: 213.

Ptenura Templeton, 1842, synonymized by Bellinger & Ellis 1972: 212–214.

Templetonia Lubbock, 1862, synonymized by Theobald 1911: 11.

Euheteromurus Börner, 1901 synonymized by Salmon 1964: 131.

Heteromurodes Absolon, 1901 synonymized by Mari Mutt 1980b: 31.

Propemesira Salmon, 1942 synonymized by Salmon 1964: 131.

Diagnosis. Antennae with 5 segments (Fig. 3), Ant IV annulated; eyes 0+0 to 3+3 or 8+8; PLQ with smooth or ciliated chaetae; head dorsal macrochaetotaxy without mac S0, S2 and Ps2, postoccipital series with 4+4, Pa3 and Pm3 present or absent (Fig. 8); Th II–III respectively with 6+6 to 9+9 and 4+4 central mac; Abd I without mac; Abd II with 2+2 central mac (m3 and m3e); Abd III with 0+0 to 2+2 central mac (m3 and m3e); Abd IV with 2+2 central mac (A3 and B5), A6 absent (Fig. 11); Abd V with 3 sensilla; unguis with two paired basal inner teeth (Fig. 13); unguiculi lanceolate with a small outer tooth; dens without spines; mucro with or without basal spine (Tab. 1).

Distribution. Holarctic.

Remarks. *Heteromurus* resembles *Verhoeffiella* in several characters such as: antennae with 5 segments, Ant IV annulated, head macrochaetotaxy without S0 mac, postoccipital series of head with 4+4 mac (pa2, Pa3, Pa5, Pp5), Abd I without mac and Abd V with 3 sensilla (see Mari Mutt 1980b, 1985b; Lukić *et al.* 2015).

Currently the annulated of Ant III is the main characteristic to distinguish *Heteromurus* (absent) from *Verhoeffiella* (present) (see Lukić *et al.* 2015), although some characteristics can complement the diagnoses of both genera (Tab. 1). The overall chaetotaxy of *Heteromurus* and *Verhoeffiella* are quite similar, but the Abd IV of *Heteromurus* always has 2+2 mac (see Mari Mutt 1980b; Mari Mutt & Stomp 1980), while in *Verhoeffiella* may eventually have 3+3 mac (see Loksa & Bogojević 1967, pg. 146). Species as *V. constantius* Ćurčić & Lučić, 2007 (in Lučić *et al.* 2007b), present the chaetotaxy of head to Abd II more complex (see Lucic *et al.* 2007b, pg. 71), so this should be investigated at the generic level.

The coloration pattern is variable in both genera, fully pigmented, restricted to antennae and eyepatches, or pigments totally absent on whole body (Martynova 1974; Mari Mutt 1980b; Nosek & Paoletti 1985; Lukic *et al.* 2015)

Heteromurus has tibiotarsi with (e.g. *H. nitidus* (Templeton, 1836), *H. peyerimhoffi* Denis, 1937) or without (*H. sexoculatus* Brown, 1926) two or three rows of smooth chaetae, while *Verhoeffiella* presents two rows of smooth chaetae or these elements are totally absent (see Mari Mutt 1985b; Lukić *et al.* 2015). At last both genera can have two forms of unguis: robust with one paired basal inner teeth (*H. gigans* Mari Mutt & Stomp, 1980; *V. longicornis*); or slender with one pair of small teeth (*V. dallai* Nosek & Paoletti 1985). However, the tenent hair in *Heteromurus* is apically capitate (*H. nitidus*, *H. major* (Moniez, 1889)) or acuminate (*H. noseki* Mari Mutt & Stomp, 1980), while in *Verhoeffiella* is always acuminate (Nosek & Paoletti 1985).

Genus *Verhoeffiella* Absolon, 1900

Typhlopodura (*Verhoeffiella*) Absolon, 1900: 429. Type species: *Typhlopodura* (*Verhoeffiella*) *cavicola* Absolon, 1900: 430–431, fig. 2 (orig. descr.).

Verhoeffiella; Börner, 1903: 179 (key).

Heteromurus (*Verhoeffiella*); Gisin, 1960: 237 (key).

Typhlopodura Absolon, 1900 synonymized by Mari Mutt 1980b: 31.

Diagnosis. Antennae with 5 segments, Ant III–IV annulated (Fig. 2); eyeless; PLQ with smooth chaetae; head dorsal macrochaetotaxy without mac S0 and S2, postoccipital series with 4+4 mac (Pa2, Pa5, Pm3 and Pp5), Pa3 absent (Fig. 8); Th II–III respectively with 7+7 to 9+9 and 4+4 central mac; Abd I without mac; Abd II with 2+2 central mac (m3 and m3e); Abd III with 1+1 central mac (m3); Abd IV with 2+2 or 3+3 central mac and at least 4+4 lateral mac (Fig. 11); Abd V with 3 sensilla; tibiotarsi without smooth chaetae rows; tenent hair acuminate; unguis with two paired basal inner teeth (Fig. 13); manubrium posteriorly with rows of smooth chaetae; dens without spines; mucro with basal spine (Fig. 18; Tab. 1).

Distribution. Holarctic.

Remarks. Almost all *Verhoeffiella* species were identified by shape of the unguis teeth and presence of annulations on Ant III (Nosek & Paoletti 1985) so the species of the genus should be investigated to reveal possible exclusive characters.

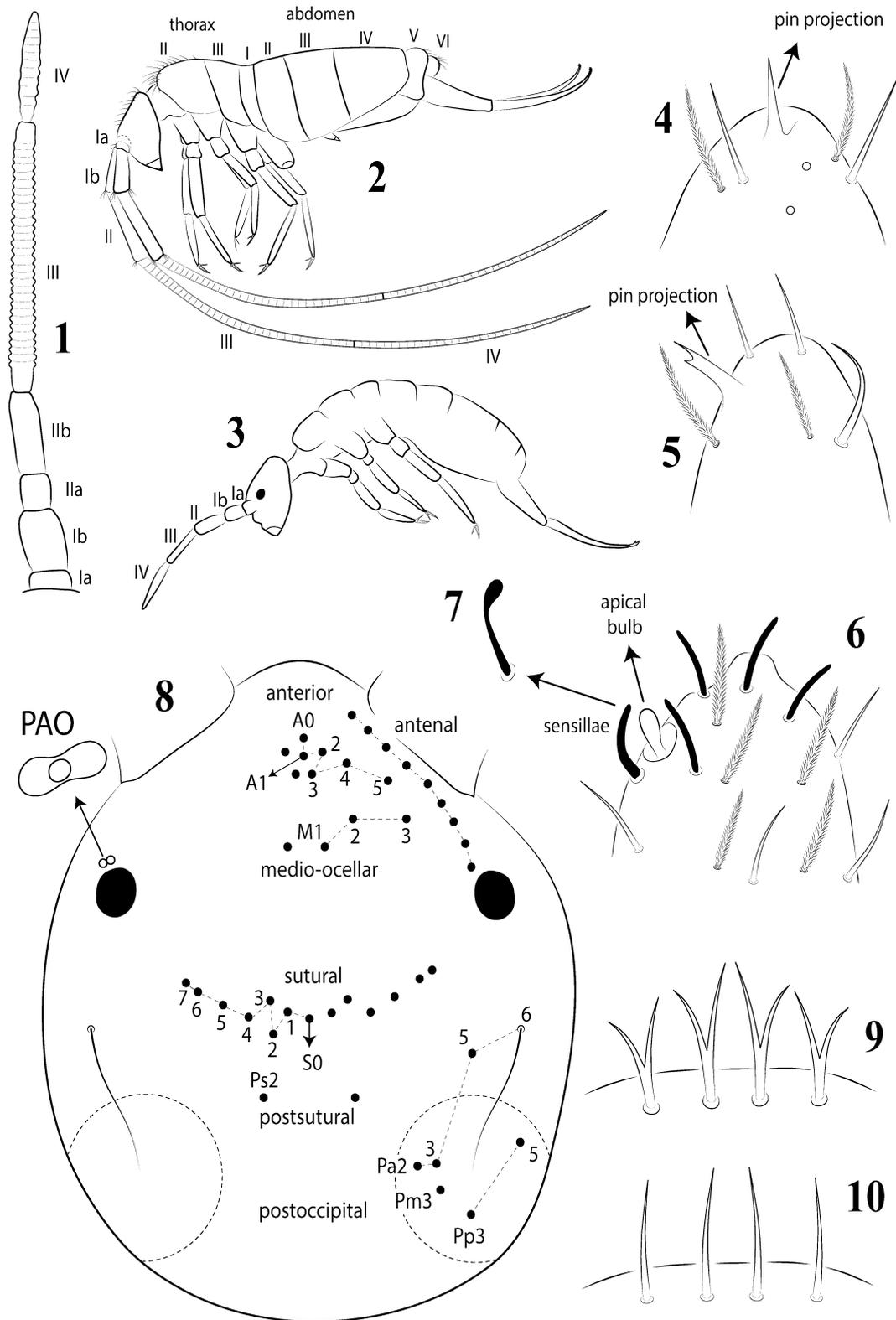
The record of *Verhoeffiella* Absolon, 1900 to Brazil in Bellini (2014) is incorrect and belongs to an epiedaphic eyed species of Heteromurini. This species resembles *Verhoeffiella* spp. in several diagnostic features (chaetotaxy not entirely evaluated) with exception of the presence of eyes.

Other information on *Verhoeffiella* see remarks of *Heteromurus* and Table 1.

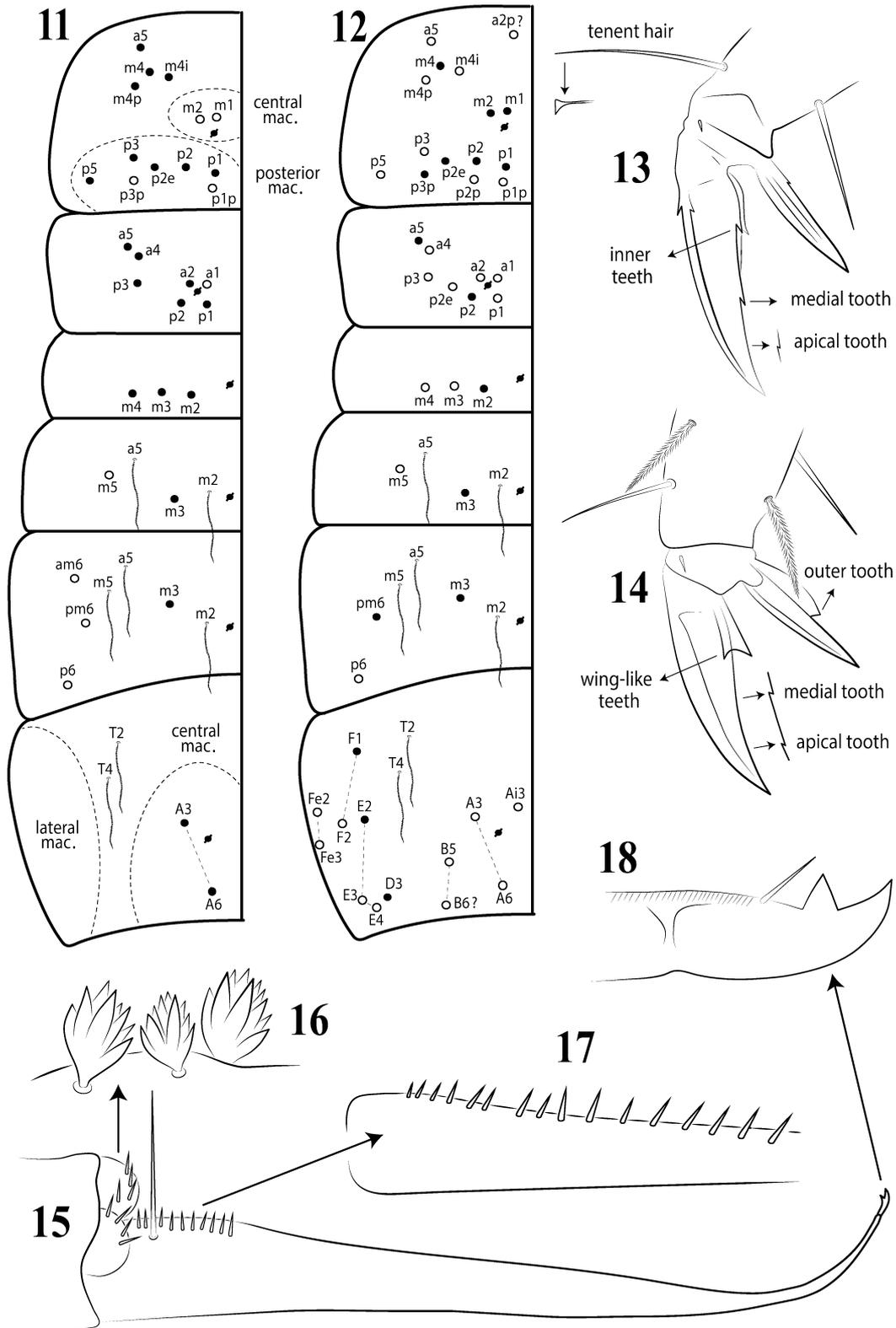
TABLE 1. Morphological characteristics of the genera of Heteromurini.

Characteristics	Genera					<i>Verhoefiella</i> 2, 4, 5, 21, 24, 29, 30, 34
	<i>Alloscopus</i> 3, 7, 17, 23, 26	<i>Dicranocentrus</i> 1, 8, 12, 15, 22, 26, 31, 32, 33	<i>Heteromurus</i> 4, 6, 10, 11, 13, 27, 28, 33	<i>Heteromurtella</i> 9, 14, 18, 20, 25	<i>Pseudodicranocentrus</i> 8, 16, 19	
Ant IV annulated	+	+	+	+ or -	+	+
Ant III annulated	-	+	-	-	+	+
Ant II subdivided (IIa and IIb)	-	+	-	-	+	-
Prelabral chaetae	smooth	smooth	smooth	smooth	Bifurcated	smooth
Number of eyes	0+0 to 3+3	8+8	0+0 to 3+3 or 8+8	0+0 to 2+2 or 6+6	8+8	0+0
Postantennal organ	+	-	-	-	-	-
A1	-	-	-	-	+	-
A5	+	+ or -	-	+ or -	+	?
S0 dorsal	+	+	-	+ or -	+	-
S2 macrochaetae	-	+ or -	-	-	-	-
Ps2	-	-	-	-	+	-
Series Pa, Pm, Pp	0+0 or 1+1	0+0 to 9+9	4+4	3+3 to 6+6	10+10 or more	4+4
PLQ chaetae 2+2	smooth or ciliated	smooth	smooth or ciliated	smooth	Ciliated	smooth
Th II central mac	10+10 to 13+13	5+5 to 17+17	6+6 to 9+9	7+7 to 15+15	17+17 or more	7+7 to 9+9
Th III central mac	6+6 or 7+7	6+6 to 14+14	4+4	2+2 to 8+8	14+14 or more	4+4
Abd I central mac	3	0+0 or 2+2 to 6+6	-	1+1 to 3+3	4+4 or 5+5	-
Abd II central mac	1+1	2+2	2+2	1+1	3+3	2+2
Abd III central mac	1+1	1+1 to 3+3	0+0 to 2+2	1+1	3+3 or 4+4	1+1
Number of S-chaetae on Abd V	?	4	3	3	?	3
Row of smooth chaetae on tibiotarsi	+ or -	+ or -	+	+ or -	+ or -	+
Tenent hairs apex	acuminate	acuminate or capitate	acuminate or capitate	acuminate	acuminate or capitate	acuminate
Paired basal teeth in unguis	wing-like	inner	inner	wing-like	inner	inner
Outer tooth in unguiculi	+ or -	+ or -	+	+ or -	+	+ or -
Smooth chaetae on manubrium	+	+ or -	+ or -	+	-	+
Compound spines groups on dens base	-	-	-	-	+ or -	-
Spines on dens	+	+ or -	-	+ or -	-	-
Mucronal spine	+ or -	+	+ or -	+ or -	+	+

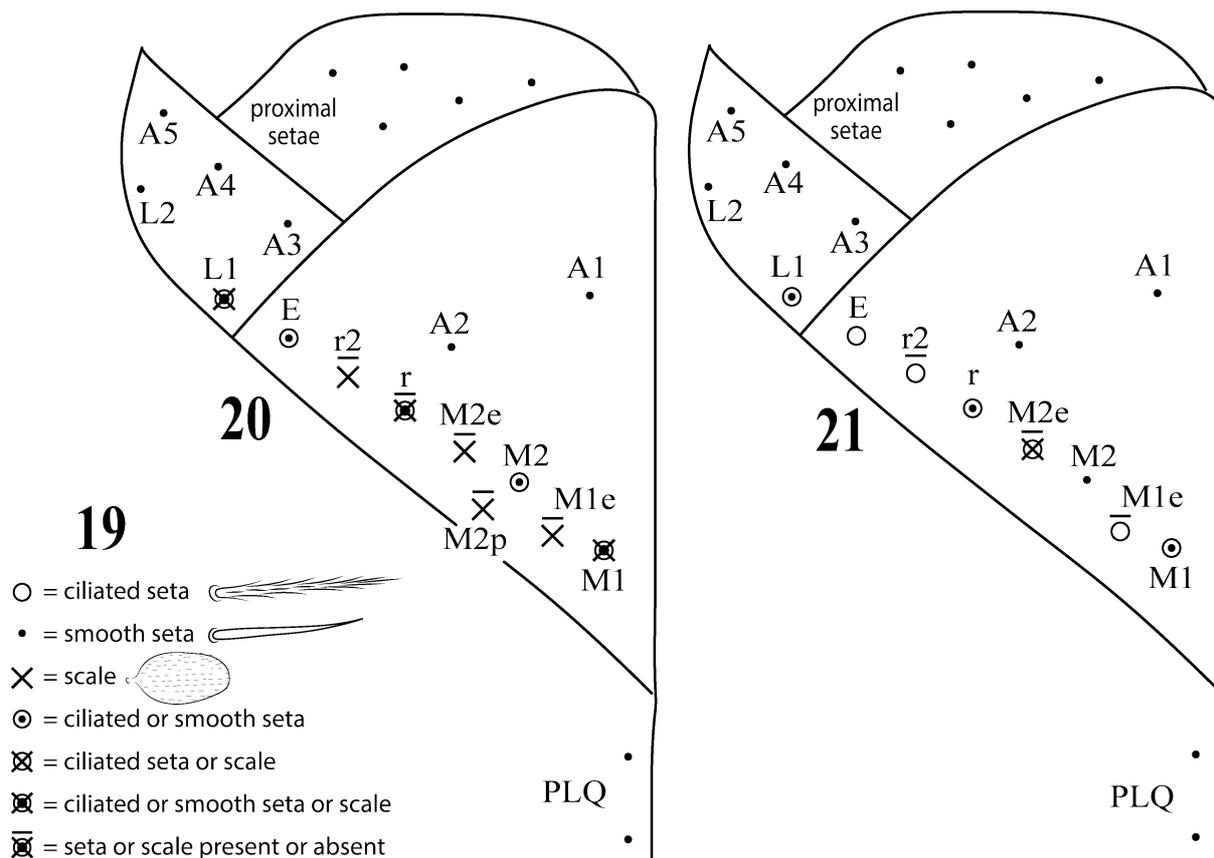
Symbols used to represent the morphological characteristics: Ant—antenna; Abd—abdomen; Th—thorax; mac—macrochaeta; PLQ—Post-labial quadrangle; ‘?’—unknown. Reference: ⁽¹⁾Schött 1893; ⁽²⁾Absohon 1900; ⁽³⁾Bömer 1906; ⁽⁴⁾Bonet 1931; ⁽⁵⁾Loksa & Bogojevic 1967; ⁽⁶⁾Martynova *et al.* 1974; ⁽⁷⁾Mari Mutt 1979a; ⁽⁸⁾Mari Mutt 1977; ⁽⁹⁾Mari Mutt 1979b; ⁽¹⁰⁾Szeptycki 1979; ⁽¹¹⁾Mari Mutt 1980b; ⁽¹²⁾Mari Mutt & Bhattacharjee 1980; ⁽¹³⁾Mari Mutt & Stomp 1980; ⁽¹⁴⁾Mari Mutt 1980c; ⁽¹⁵⁾Mari Mutt 1981a; ⁽¹⁶⁾Mari Mutt 1981b; ⁽¹⁷⁾Mari Mutt 1982; ⁽¹⁸⁾Mari Mutt 1983; ⁽¹⁹⁾Mari Mutt 1984; ⁽²⁰⁾Mari Mutt 1985a; ⁽²¹⁾Mari Mutt 1985b; ⁽²²⁾Mari Mutt 1985c; ⁽²³⁾Mari Mutt 1985d; ⁽²⁴⁾Nosek & Paoletti 1985; ⁽²⁵⁾Najt *et al.* 1988; ⁽²⁶⁾Yoshii & Suhardjono 1989; ⁽²⁷⁾Lucic *et al.* 2002; ⁽²⁸⁾Lucic *et al.* 2007a; ⁽²⁹⁾Lucic *et al.* 2007b; ⁽³⁰⁾Lucic *et al.* 2008; ⁽³¹⁾Bellini *et al.* 2013; ⁽³²⁾Xu & Zhang 2014; ⁽³³⁾Zhang & Deharveng 2015; ⁽³⁴⁾Lucic *et al.* 2015.



FIGURES 1–10. General morphology of Heteromurini: 1, antenna of *Dicranocentrus marias* (after Mari Mutt 1979b); 2, habitus of *Verhoeffiella longicornis* (after Absolon 1900); 3, habitus of *Heteromurtrella puertoricensis* (after Mari Mutt 1979b); 4–6, Antenna V apex: 4, *Alloscopus thailandensis* (after Mari Mutt 1985b); 5, *Alloscopus tihuiensis* (after Mari Mutt 1985a); 6, *Heteromurtrella mirifica* (after Salmon 1954); 7, antenna V apical sensilla of *Heteromurtrella stannardi* (after Mari Mutt 1980c); 8, head dorsal chaetotaxy of Heteromurini (modified of *Alloscopus* sensu Yoshii & Suhardjono 1989); 9–10, prelabral chaetotaxy: 9, *Pseudodicranocentrus circulatus* (after Mari Mutt 1981b), 10, *Dicranocentrus luzonensis* (after Mari Mutt 1985c).



FIGURES 11–18. General morphology of Heteromurini: **11–12** , dorsal chaetotaxy synthesis of Th II to Abd IV: **11**, *Alloscopus*; **12**, *Heteromurtrella*, black circles indicates present macrochaetae, open circles present or absent macrochaetae; **13–14**, empodial complex III: **13**, *Dicranocentrus colombiensi* (after Mari Mutt 1981b); **14**, *Heteromurtrella greensladeae* (after Mari Mutt 1987); **15**, dens and mucro of *Heteromurtrella tihuiensis* (after Mari Mutt 1985a); **16**, compound spines on dental lobe of *Pseudodicranocentrus circulatus* (after Mari Mutt 1981b); **17**, dental spines of *Alloscopus multispinatus* (modified of Mari Mutt 1982); **18**, mucro of *Dicranocentrus paramoense* (after Mari Mutt 1983).



FIGURES 19–21. Chaetotaxy scheme of the labial region: **19**, symbols used in detailed chaetotaxy schemes; **20**, *Alloscopus*; **21**, *Heteromurtrella*.

Genus *Alloscopus* Börner, 1906

Heteromurus (*Alloscopus*) Börner, 1906: 177. Type species: *Heteromurus* (*Alloscopus*) *tenuicornis* Börner, 1906 (orig. descr.). *Alloscopus*; Handschin 1928: 267.

Indoscopus Prabhoo, 1971, synonymized by Soto-Adames *et al.* 2008: 512

Diagnosis. Antennae with 5 segments, Ant IV annulated (Figs 2–3); eyes 0+0 to 3+3; PAO present (Fig. 8); PLQ with smooth or ciliated chaetae; head dorsal macrochaetotaxy with S0 mac, S2 absent, postoccipital series with Pa5 mac present or absent (Fig. 8); Th II with 9+9 to 13+13 mac, p2p absent; Th III with 6+6 or 7+7 mac, p2e absent; Abd I with 3+3 mac (m2–4); Abd II–III with 1+1 central mac (m3); Abd IV with 2+2 central mac (A3 and A6) (Fig. 12); tenent hair acuminate; unguis with two basal wing-like teeth (Fig. 14); manubrium with rows of smooth chaetae; dental spines present; mucro with (Fig. 18) or without basal spine (Tab. 1–2).

Distribution. Pantropical.

Remarks. *Alloscopus* resembles other genera of Heteromurini as *Heteromurus* and *Heteromurtrella* by antennae with 5 segments, shorter than body, reduced macrochaetotaxy tibiotarsi with or without smooth chaetae rows, tenent hair generally acuminate and manubrium with smooth chaetae (see Tab. 2). However, *Alloscopus* can be distinguished from these genera by presence of PAO (absent in other genera), and dens always with spines rows (see Mari Mutt 1977, 1982, 1985d, Yoshii & Suhardjono 1989), although the latter characteristic can also be present in some species of *Heteromurtrella* (see Mari Mutt 1983, 1985a).

The dorsal macrochaetotaxy of *Alloscopus* differs by head with S0 mac (absent in *Heteromurus* and sometimes in *Heteromurtrella*), postoccipital series reduced, with no more than 1+1 (Pa5) mac. (3+3 or more in other genera); Th II–III lacking p2p and p2e mac respectively, and Abd II with 1+1 central mac (2+2 in *Heteromurus*) (Figs 8, 11; Tab. 1–3).

The color in these genera is variable, although it is often absent in *Alloscopus* and present in other genera (Mari

Mutt 1980b, c). Furthermore the posterior labial row in *Alloscopus* presents 5 to 6 chaetae (Fig. 20; Tab. 2), while in *Heteromurus* the labial chaetotaxy is more variable (see Mari Mutt 1980b), and in *Heteromurtrella* there are 6 or more chaetae.

Other generic characteristics are present in Tables 1 and 2.

***Alloscopus aspinosus* (Prabhoo, 1971) comb. nov.**

Indoscopus aspinosus Prabhoo, 1971: 35, 37, figs 167–170, Kerala, India (orig. descr.). Mari Mutt, 1977: 248 (cit.)

Diagnosis. Presence of black pigmentation on eyepatches, 2+2 eyes; PAO semidivided; Th II with 9+9 mac (a5, m4, m4i, m4p, p1, p2, p2e, p3 and one unnamed); Th III with 3+3 mac (a4, p1 and p2); Abd I with 2+2 mac (m2–3); Abd II with 1+1 mac (m3); Abd III with 4+4 mac (m3, am6, pm6 and p6) (Fig. 11); unguis without unpaired teeth (Fig. 14); unguiculi with smooth edges; mucro without basal spine (Tab. 2).

Distribution. India.

***Alloscopus deharvengi* Mari Mutt, 1985**

Heteromurus (Alloscopus) deharvengi Mari Mutt, 1985d: 338, figs 17–22, Wau, Papua New Guinea (orig. descr.).

Diagnosis. Eyes and pigmentation absent; Ant IV with one simple pin projection (Fig. 4); PAO small and irregular; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 3+3 mac (M1–3), Pa5 mac Absent (Fig. 8); Th II with 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2e, p3 and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 11); tibiotarsi with two rows of smooth chaetae; unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 4 smooth chaetae; dens with 3–5 spines in one row (Tab. 2).

Distribution. Papua New Guinea.

***Alloscopus fallax* Yoshii & Suhardjono, 1992**

Heteromurus (Alloscopus) fallax Yoshii & Suhardjono, 1992: 35–36, figs 20A–H, Indonesia (orig. descr.).

Diagnosis. Eyes 1+1; PAO semidivided; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 1+1 mac (M1); Pa5 mac absent (Fig. 8); Th II with 13+13 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2e, p3, p3p and p5); Th III with 7+7 mac (a1–2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3) (Fig. 11); tibiotarsi without smooth chaetae rows; unguis without unpaired teeth; unguiculi with smooth edges (Fig. 14); manubrium with two rows of 3 smooth chaetae; dens with 8 spines in one row; mucro without basal spine (Tab. 2).

Distribution. Indonesia.

***Alloscopus multispinatus* Mari Mutt, 1982**

Heteromurus (Alloscopus) multispinatus Mari Mutt, 1982: 86–89, figs 2–17, Guinea New Papua (orig. descr.). Mari Mutt 1985d: 338, 341, figs 23–28, Musgrave River, Guinea New Papua (descr.).

Alloscopus multispinatus; Yoshii & Suhardjono 1992: 34–35, figs 19A–H, Ternate, Indonesia (descr.).

Diagnosis. Black pigmentation on 1+1 eyes; Ant IV with one apical bulb; PAO semidivided or overlap; head ‘A’ series with 4 mac (A0, A2–A4), ‘M’ series with 3+3 mac (M1–M3), Pa5 mac present (Fig. 8); Th II with 11+11 or 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2e, p3 and p5), m1 present or absent; Th III with 7+7 mac (a1–2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6);

Abd IV with 2+2 central mac (A3 and A6) (Fig. 11); tibiotarsi without smooth chaetae rows; unguis with one unpaired medial tooth; unguiculi with outer tooth; manubrium with two row of 3+3 or 4+4 smooth chaetae; dens with 27–55 spines in two rows (Fig. 17); mucro without basal spine (Tab. 2).

Distribution. Indonesia and Papua New Guinea.

Alloscopus spinosus (Prabhoo, 1971) comb. nov.

Indoscopus spinosus Prabhoo, 1971: 35, figs 163–166, Kerala, India (orig. descr.). Mari Mutt, 1977: 248 (cit.)

Diagnosis. Black pigmentation on 2+2 eyes; PAO semidivided; Th II with 8+8 mac (a5, m4, m4i, m4p, p1, p2, p2e and p3); Th III with 5+5 mac (a4–5, p1–3); Abd I with 2+2 mac (m2–3); Abd II with 1+1 mac (m3); Abd III with 1+1 mac (m3) (Fig. 11); unguis without unpaired teeth (Fig. 14); unguiculi with smooth edges; mucro with basal spine (Fig. 18; Tab. 2).

Distribution. India.

Alloscopus strebeli Winter, 1966

Alloscopus strebeli Winter, 1966: figs 1–9, Rio Pastaza, Peru (orig. descr.). Winter 1963: 509, figs 36–45, Peru (*nomen nudum*). Izarra 1972: 539 (cit.).

Indoscopus strebeli; Mari Mutt, 1977: 248 (comb.). Mari Mutt 1982: 84 (cit.).

Heteromurus (Alloscopus) cf. strebeli; Mari Mutt 1982: 91, Figs 36–45, Province Morona-Santiago, Ecuador (descr. and comb.). Najt *et al.* 1988: 558–560, Figs 22–28, Napo province, Ecuador (descr. and del.).

Diagnosis. Black pigmentation on 3+3 eyes; Ant IV with one bifurcated pin projection (Fig. 5); PAO divided; head ‘A’ series with 4 mac (A0, A2–A4), ‘M’ series with 3+3 mac (M1–3) (Fig. 8); Th II with 11+11 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2e, p3 and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6) (Fig. 11); tibiotarsi without smooth chaetae; unguis with one unpaired medial tooth; manubrium with two rows of 3 smooth chaetae; dens with 4–6 spines in one row; mucro with basal spine (Fig. 18; Tab. 2).

Distribution. Peru and Ecuador.

Alloscopus tenuicornis Börner, 1906

Heteromurus (Alloscopus) tenuicornis Börner, 1906: 177, Tjibodas, West Java, Indonesia (orig. descr.).

Heteromurus tenuicornis; Imms, 1912: 120, Java, Indonesia (cat.).

Alloscopus tenuicornis; Handschin 1928: 267, Java and Sumatra, Indonesia (cat.).

Diagnosis. Black pigmentation on 1+1 eyes; Ant IV without modifications; PAO semidivided; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 2+2 mac (M1–2); Pa5 mac present (Fig. 8); Th II with 11+11 or 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2e, p3 and p5), p1p present or absent; Th III with 6+6 or 7+7 mac (a1–2, a4–5, p1–3), a1 present or absent; Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 11); tibiotarsi without smooth chaetae; unguiculi with outer tooth; manubrium with two rows of 4 smooth chaetae; dens with 5–14 spines in one row; mucro without basal spine (Tab. 2).

Distribution. Hawaii, Indonesia, Micronesia, Papua New Guinea, Philippines and Sumatra.

Alloscopus thailandensis Mari Mutt, 1985

Heteromurus (Alloscopus) thailandensis Mari Mutt, 1985d: 336, figs 1–10, Chiang Dao, Thailand (orig. descr.)

TABLE 2. Morphological characteristics of *Alloscopus* species of the world.

Characteristics	Species of <i>Alloscopus</i>									
	<i>aspinosus</i> IND 8	<i>deharvengi</i> PNG 5	<i>fullax</i> IDS 12	<i>multispinatus</i> INS, PNG 4,5,12	<i>spinosus</i> IND 8	<i>strebli</i> PER, ECU 4,7,9	<i>tenicornis</i> IDS, MIC, PHI 1-5,11	<i>thailandensis</i> THA 5	<i>tetracanthus</i> AUS, IDS, MAL, MIC, THA, PNG 1,3-6,10,11	<i>yosiius</i> IDS 5
Ocellar pigments	+	-	-	+	+	+	+ or -	+	-	+
Antennae IV annulated	+	?	+	+	+	+	+	?	+	?
Smooth chaetae on apex of Ant IV	?	+	?	+	?	+	?	+	?	?
Apical bulb on Ant IV	?	-	-?	1	?	-	-	-	-	-
Apex sensillae on Ant IV	?	1k	?	1h	?	3h, 1k	1h, 1k	-	1h	2h
Pin projection on Ant IV	?	1spl.	?	-	?	1bif.	-	1spl.	-	-
Number of eyes	2+2	0+0	1+1	1+1	2+2	3+3	1+1	0+0	1+1	1+1
Postantennal organ	semidivided	irregular	semidivided	semidivided or overlap	overlap	divided	semidivided	overlap	semidivided	semidivided or overlap
Size of the outer labral papillae in relation to inner	?	larger	equal	larger ⁴	?	larger	equal	lower	larger	larger
Shape of o.p.	?	conical	circular	conical	?	circular	conical	circular/conical	conical	conical
labral papillae	?	conical	circular	conical	?	conical	conical	conical	conical	conical
Head dorsal series	?	5	9	9	?	?	10	3	?	5
	?	5	5	4	?	4	5	5	4	5
	?	3	1	3	?	3	2	3	3	2
	?	7	7	7	?	7	7	7	7	7
	?	-	-	Pa5	?	?	Pa5	-	Pa5	-
	?	-	-	-	?	?	-	-	-	-
	?	-	-	-	?	?	-	-	-	-
	?	S	S	S	?	?	S	S	S	S
	?	C	C	C	?	?	C or S or E	C	C or S	C
	?	E?	E	E	?	?	-	-	-	E?
	?	S	S	S	?	?	C or S	S	S	S
	?	-	-	-	?	?	E	-	E or -	-
	?	-	E	E	?	?	-	-	E or -	E?
	?	E?	-	S	?	?	E	E	C or S	E?
	?	-	-	E	?	?	-	-	-	-
	?	S	S	S	?	?	C or S	S	S	S
	?	C or S	E	C or S	?	?	E	S	S	C
	?	S	S	S	?	?	S	S	S	S

...continued on the next page

TABLE 2. (continued)

Characteristics	<i>aspinosus</i> IND 8	<i>deharvengi</i> PNG 5	<i>fallax</i> IDS 12	<i>multispinatus</i> INS, PNG 4,5,12	<i>spinosus</i> IND 8	<i>strebli</i> PER, ECU 4,7,9	<i>tenuicornis</i> IDS, MIC, PHI 1-5,11	<i>thailandensis</i> THA 5	<i>tetracanthus</i> AUS, IDS, MAL, MIC, THA, PNG 1,3-6,10,11	<i>yosius</i> IDS 5
PLQ chaetae 2+2	?	S	?	S	?	?	C or S	S	?	S
Shape of the l.p. of papilla E	?	clavate	?	finger	?	finger	finger	conical	finger	finger
Length of the l.p. to papilla E	?	> 1/2	?	1/3	?	1/3	1/3	1/2	1/3	< 1/2
Appendices in papilla E	?	4	?	1	?	1	?	3	?	4
Th II central mac	9	12	13	11-12	8	11	11-12	12	10-12	11
Th III central mac	3	6	7	7	5	6	6-7	6	6	6
Abd I dorsal mac	2	3	3	3	2	3	3	3	3	3
Abd II dorsal mac	1,0	1,0	1,0	1,0	1,0	1,1	1,1	1,0	1,0	1,0
Abd III dorsal mac	1,3	1,2	?	1,2	1,0	1,2	1,2	1,2	1,2	1,2
Abd IV dorsal central mac	1	2	?	2	1	?	2	2	2	2
Trocanteral organ spines	?	17	30	30-40	?	18	25	15	15	25
Rows of smooth chaetae on tibiotarsi	?	2	-	-	?	-	-	-	2	-
Unpaired teeth in unguis	-	-	-	1	-	1	0-2	2	0-2	-
Teeth in unguiculi	-	+	-	+	-	+ or -	+	+	+	+
Smooth chaetae on lateral anal valve	?	2+2	?	0-1	?	?	-	-	2+2 or 3+3	0-1
Dorsal smooth chaetae on manubrium	?	4+4	3+3	3+3 or 4+4	?	3+3	4+4	4+4	3+3 or 4+4	4+4 (5+5?)
Number of rows of spines on dens	?	1+1	1+1	2+2	?	1+1	1+1	1+1	1+1	1+1
Number of spines on dens	?	3-5	8	27-55	?	4+4 to 6+6	5-14	3-6	3-7	6-10
Lobe on dens base	?	-	+	+	?	+	+	-?	-	-?
Smooth chaeta on dens base	?	-	-	-	?	3+3	-	?	1+1	?
Spines on dens base	?	-	-	-	?	1+1	1+1	-	-	-
Mucronal spine	-	?	-	-	+	+	-	-	-	-

Symbols used to represent the morphological characteristics: Ant—antenna; Abd—abdomen; Th—thorax; 'C'—ciliated; 'S'—smooth; 'E'—scales; 'Ip.'—lateral process; mac—macrochaeta; o.p.—outer papillae; i.p.—inner papillae; PLQ—Post-labial quadrangle; spl.—simple; bif.—bifurcated; h—hooked; k—knobbed; '+'—present; '-'—absent; '?'—unknown. Reference species: (1) Börner 1906; (2) Handschin 1925; (3) Mari Mutt 1977; (4) Mari Mutt 1982; (5) Mari Mutt 1982; (6) Mari Mutt 1985d; (7) Najt *et al.* 1988; (8) Prabhoo 1971; (9) Winter 1966; (10) Yosii 1959; (11) Yoshii & Suhardjino 1989; (12) Yoshii & Suhardjino 1992. Abbreviations of locations: AUS—Australia; ECU—Ecuador; IND—India; IDS—Indonesia; MAL—Malaysia; MIC—Micronesia; PER—Peru; PHI—Philippines; PNG—Papua New Guinea; THA—Thailand.

Diagnosis. Eyes and pigmentation absent; Ant IV with one simple pin projection; PAO overlap; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 3+3 mac (M1–3), Pa5 mac absent (Fig. 8); Th II with 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2e, p3 and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 11); tibiotarsi without smooth chaetae; unguis with two unpaired teeth; unguiculi with outer tooth; manubrium with two rows of 4 smooth chaetae; dens with 3–6 spines in one row; mucro without basal spine (Tab. 2).

Distribution. Thailand.

Alloscopus tetracanthus Börner, 1906

Heteromurus (Alloscopus) tetracantha Börner, 1906: 177, Forest of Tjompea, Java, Indonesia (orig. descr.).

Heteromurus tetracantha; Imms 1912: 120, Java, Indonesia (cat.).

Alloscopus tetracanthus; Handschin 1928: 267, Java, Indonesia (cat.).

Diagnosis. Black pigmentation on 1+1 eyes, Ant IV without modifications; PAO semidivided; head ‘A’ series with 4 mac (A0, A2–A4), ‘M’ series with 3+3 mac (M1–3), Pa5 mac present (Fig. 8); Th II with 10+10 to 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2e, p3 e p5), m1 and p1p present or absent; Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 11); tibiotarsi with two smooth chaetae rows; unguiculi with outer tooth; manubrium with two rows of 3+3 or 4+4 smooth chaetae; dens with 3–7 spines in one row; mucro without basal spine (Tab. 2).

Distribution. Australia, Indonesia, Malaysia, Singapore, Papua New Guinea, India, New Britain, Micronesia and Thailand.

Alloscopus yosiius Mari Mutt, 1985 status revalidated

Heteromurus (Alloscopus) yosiius Mari Mutt, 1985d: 336–338, figs 11–16, Java, Bogor, Indonesia (orig. descr.). Suhardjono 1989: 19, Indonesia (cat.).

Heteromurus (Alloscopus) yosiius synonymized with *Heteromurus (Alloscopus) tenuicornis* Börner, 1906 by Yoshii & Suhardjono 1989: 64.

Diagnosis. Black pigmentation on 1+1 eyes; Ant IV without modifications; PAO semidivided or overlap; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 2+2 mac (M1–2), Pa5 mac absent (Fig. 8); Th II with 11+11 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2e, p3 and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 11); tibiotarsi without smooth chaetae; unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 4+4 (possibly also 5+5) smooth chaetae; dens with 6–10 spines in one row; mucro without basal spine (Tab. 2).

Distribution. Indonesia.

Remarks. *Alloscopus yosiius*, anteriorly synonymized with *A. tenuicornis* (sensu Yoshii & Suhardjono 1989), is herein revalidate by its distinct dorsal chaetotaxy when compared to the second species. The differences are in: head without Pa5 mac (present in *H. tenuicornis*); Th II–III respectively with 11+11 and 6+6 mac (up to 12+12 and 7+7 in *H. tenuicornis*); Abd II without lateral mac (m5); and dental base without spines (present in *H. tenuicornis*).

Identification key for species of *Alloscopus*

- | | | |
|---|---|--------------------------------------|
| 1 | Eyes absent | 2 |
| - | Eyes present | 3 |
| 2 | Tibiotarsi I–III with two rows of smooth chaetae; unguis without unpaired teeth (Fig. 14); lateral anal valve with 2+2 smooth chaetae | <i>A. deharvengi</i> Mari Mutt, 1985 |

-	Tibiotarsi I–III without smooth chaetae rows; unguis with two unpaired teeth (Fig. 13); lateral anal valve without smooth chaetae	<i>A. thailandensis</i> Mari Mutt, 1985
3	Eyes 1+1 or 2+2; dens base with 0+0 or 1+1 smooth chaetae	4
-	Eyes 3+3; dens base with 3+3 smooth chaetae	<i>A. strebeli</i> Winter, 1966
4	Eyes 2+2	5
-	Eyes 1+1	6
5	Th II–III respectively with 9+9 and 3+3 mac; mucro without basal spine	<i>A. aspinosus</i> (Prabhoo, 1971)
-	Th II–III respectively with 8+8 and 5+5 mac; mucro with basal spine (Fig. 18)	<i>A. spinosus</i> (Prabhoo, 1971)
6	Tibiotarsi without smooth chaetae rows	7
-	Tibiotarsi with two smooth chaetae rows	<i>A. tetracanthus</i> Börner, 1906
7	Postoccipital anterior series of head with mac Pa5 (Fig. 8)	8
-	Postoccipital anterior series of head without mac Pa5	9
8	Head anterior series with A5 mac and medio-ocellar series without M3 mac; Abd II with 1+1 lateral mac (m5); trocanteral organ with up to 25 spine-like chaetae; dens dorsally with 5–14 spines in 1 row (Figs 8, 11, 15, 17)	<i>A. tenuicornis</i> Börner, 1906
-	Head anterior series without A5 mac and medio-ocellar series with M3 mac; Abd II without lateral mac; trocanteral organ with 30–40 spine-like chaetae; dens dorsally with 27–55 spines in 2 rows (Figs 8, 11, 15, 17)	<i>A. multispinatus</i> Mari Mutt, 1982
9	Head ‘M’ series with 1+1 mac (M1); Th II–III respectively with 13+13 and 7+7 mac; manubrium dorsally with 3+3 smooth chaetae (Figs 8, 11)	<i>A. fallax</i> Yoshii & Suhardjono, 1992
-	Head ‘M’ series with 2+2 mac (M1–2); Th II–III respectively with 11+11 and 6+6 mac; manubrium dorsally with 4+4 or 5+5 smooth chaetae (Figs 8, 11)	<i>A. yosiius</i> Mari Mutt, 1985

Genus *Heteromurtrella* Mari Mutt, 1979

Heteromurus (*Heteromurtrella*) Mari Mutt, 1979b: 214. Type species: *Heteromurus* (*Heteromurtrella*) *puertoricensis* Mari Mutt, 1979 (orig. descr.).

Heteromurtrella; Hopkin 1997: 213 (classification).

Diagnosis. Ant with 5 segments (Fig. 3), Ant IV annulated or not; eyes 0+0 to 2+2 or 6+6; PAO absent; PLQ with smooth chaetae (Fig. 21); head dorsal macrochaetotaxy with A0 (atypical), A2a, A5 and S0 present or absent, S2 absent; postoccipital series with 3+3 to 6+6 mac (Pa2–3, Pa5, Pm3, Pp3 and Pp5), Pa2, Pm3 and Pp3 present or absent (Figs 8, 30); Th II chaetotaxy with 7+7 to 15+15 mac; Th III with 2+2 to 8+8 mac; Abd I with 1+1 to 3+3 mac; Abd II with 1+1 or 2+2 mac; Abd III with 2+2 or 3+3 mac; Abd IV with up to 5+5 central mac present or absent, but never devoid, and 3+3 to 8+8 lateral mac, E3–4, F2 and Fe2–3 present or absent (Fig. 12); Abd V with 3 sensilla (Fig. 38); tenent hair acuminate; unguis with two basal wing-like teeth (Fig. 14); manubrium with rows of smooth chaetae (Fig. 60); dens generally without spines; mucro with or without basal spine (Fig. 18; Tab. 1–3).

Distribution. Pantropical.

Remarks. Some species of *Heteromurtrella* species resemble *Alloscopus* by the presence of dental spines, such as *H. echinata* (Mari Mutt, 1983) and *H. tihuiensis* (Mari Mutt, 1985), therefore these species may be confused between the two genera (see Liu & Li 1999, pg. 248; Bellinger *et al.* 2015). In the other hand *Heteromurtrella* is readily distinguished from *Alloscopus* by the absence of PAO (Fig. 8). Also, the dorsal chaetotaxy of *Heteromurtrella* differs by S0 mac present or absent (always present in *Alloscopus*), postoccipital series of head with at least 3+3 mac (Pa3?, Pa5, Pp5), Th II always with m1 and m2 mac and Abd IV with up to five mac (Ai3, A3, A6, B5, B6?), while in some species of *Alloscopus* these mac may be absent (see Prabhoo 1971: 34; Mari Mutt 1977: 244).

Heteromurtrella species can have the body with coloration variable, fully pigmented, or restricted black pigment to eyepatches, anterior head and antennae; diffuse or absent (Mari Mutt 1979b, 1980c).

Other generic characteristics are present on Tables 1 and 3.

Heteromurtrella abrupta (Salmon, 1951)

Ptenura abrupta Salmon, 1951: 137–138, figs 28–32, Singapore (orig. descr.). Salmon 1964: 478 (compared).

Heteromurus (*Heteromurtrella*) *abruptus*; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 22–23 (diagnosis).

Diagnosis. Body with bluish pigmentation; eyepatches black on 6+6 eyes; unguis with one medial unpaired tooth; unguiculi with smooth edges; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Singapore.

***Heteromurtrella affinis* Mari Mutt, 1987**

Heteromurus (Heteromurtrella) affinis Mari Mutt, 1987: 575, figs 12–13, Sulawesi, Indonesia (orig. descr.).

Diagnosis. Body with light orange pigment or pale; black pigmentation on 1+1 eyes; head ‘A’ series with 4 mac (A0, A2–A4), ‘M’ series with 2+2 mac (M1–2), ‘S’ series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p); Th III with 7+7 mac (a2, a4–5, p1–2, p2e and p3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) and 3+3 lateral mac (D3, E2 and F1) (Fig. 12); unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 4 smooth chaetae; mucro without basal spine (Tab. 3).

Distribution. Indonesia.

***Heteromurtrella barrai* Mari Mutt, 1979**

Heteromurus (Heteromurtrella) barrai Mari Mutt, 1979b: 221–222, figs 2, 7, 12, Ipassa, Gabon (orig. descr.). Mari Mutt 1980c: 11–12 (cit. et key).

Diagnosis. Body pale; black pigmentation on 2+2 eyes; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 3+3 mac (M1–3), ‘S’ series with S0 mac, postoccipital series with 3+3 mac (Pa3, Pa5 and Pm3) (Fig. 8); Th II with 11+11 mac (a5, m1–2, m4, m4i, p1, p2, p2e, p3, p3p and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 1+1 central mac (A3) and 6+6 lateral mac (D3, E2, E3, E4, F1–2) (Fig. 12); unguiculi with outer tooth; manubrium with two rows of 2 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Gabon.

***Heteromurtrella caeca* Najt, Thibaud & Mari Mutt, 1988**

Heteromurus (Heteromurtrella) caecus Najt *et al.*, 1988: 560–561, figs 29–38, Napo, Ecuador (orig. descr.).

Diagnosis. Body and eyepatches pale, eyes absent; head ‘A’ series with 4 mac (A0, A2–A4), ‘M’ series with 2+2 mac (M1–2), ‘S’ series with S0 mac, postoccipital series with 4+4 mac (Pa2–3, Pa5 and Pm3) (Fig. 8); Th II with 12+12 mac (m1–2, m4, m4i, m4p, p1, p1p, p2, p2p, p2e, p3 and p3p); Th III with 7+7 mac (a2, a4–5, p1–2, p2e and p3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 4+4 central mac (A3, A6, B5–B6?) and 7+7 lateral mac (D3, E2, E3, E4, F1, Fe2–3) (Fig. 12); unguis with one medial unpaired tooth; unguiculi with outer tooth; manubrium with two rows of 3–4 smooth setae; mucro without basal spine (Tab. 3).

Distribution. Ecuador.

***Heteromurtrella diommata* (Denis, 1931)**

Heteromurus diommatus Denis, 1931: 143–145, figs 147–151, San Jose, Costa Rica (orig. descr.). Mari Mutt, 1977: 242 (compared).

Ptenura diommata; Salmon 1964: 479 (comb.).

Heteromurus (Heteromurtrella) diommatus; Mari Mutt, 1979b: 214 (comb.). Mari Mutt 1980c: 23–24, figs 4, 7, 23 (redescr.).

Diagnosis. Body violet; black pigmentation on 2+2 eyes; head 'A' series with 4 mac, 'M' series with 3+3 mac (M1–3), 'S' series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); unguis with one medial unpaired tooth; unguiculi with outer tooth (Fig. 14); manubrium with smooth chaetae of uncertain number; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Costa Rica.

***Heteromurtrella dubia* (Delamare-Deboutteville, 1952)**

Heteromurus dubius Delamare-Deboutteville, 1952 in Delamare-Deboutteville & Paulian 1952: 68, figs 22–24, Dabou, Ivory Coast (orig. descr.). Barra 1968: 110–112, figs 4A–F (redescr.). Mari Mutt, 1977: 242, (compared).

Ptenura dubia; Salmon 1964: 479 (comb.).

Heteromurus (Heteromurtrella) dubius; Mari Mutt 1979b: 214 (comb). Mari Mutt 1980c: 22, figs 5, 15, 18, Abidjan, Ivory Coast (redescr.).

Diagnosis. Body pale; black pigmentation on 2+2 eyes; head 'A' series with 4 mac (A0, A2–A4), 'M' series with 2+2 mac (M1–2), 'S' series with S0 mac, postoccipital series with 4+4 mac (Pa2–3, Pa5 and Pm3) (Fig. 8); Th II with 11+11 mac (m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 12); tibiotarsi with one smooth chaetae row; unguis with 1–2 unpaired teeth, apical tooth present or absent; unguiculi with smooth edges; manubrium with two rows of 4 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Ivory Coast.

***Heteromurtrella echinatus* Mari Mutt, 1983**

Heteromurus (Heteromurtrella) echinatus Mari Mutt, 1983: 158–163, figs 4, 23–35, 37, 39, Mérida State, Venezuela (orig. descr.). Mari Mutt 1985a: 145–146, figs 7–8 (compared).

Diagnosis. Body light salmon ochre to olive green, with dark pigments covering Ant IV–V, black pigmentation on 2+2 eyes; head 'A' series with 5 mac (A0–4), A1 atypical; 'M' series with 3+3 mac (M1–3), 'S' series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 11+11 or 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p), p2p present or absent; Th III with 6+6 or 7+7 mac (a1–2, a4–5, p1–3), a1 present or absent; Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV 2+2 or 3+3 central mac (Ai3?, A3 and A6), Ai3? present or absent, and 3+3 lateral mac (D3, E2 and F1) (Fig. 12); unguis without unpaired teeth; unguiculi with smooth edges; manubrium with two rows of 3 smooth chaetae; dens with up to 10 spines in one row; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Venezuela.

***Heteromurtrella greensladeae* Mari Mutt, 1987**

Heteromurus (Heteromurtrella) greensladeae Mari Mutt, 1987: 572–575, figs 1–11, 14, Sulawesi, Indonesia (orig. descr.).

Diagnosis. Body light orange or pale, black pigmentation on 1+1 eyes; head 'A' series with 4 mac (A0, A2–4), 'M' series with 2+2 mac (M1–2), 'S' series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 13+13 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2p, p2e, p3 and p3p); Th III with 7+7 mac (a2, a4–5, p1–2, p2e and p3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 1+1 central mac (A6) and 3+3 lateral mac (D3, E2 and F1) (Fig. 12); unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 4 smooth chaetae; mucro without basal spine (Tab. 3).

Distribution. Indonesia.

TABLE 3. Morphological characteristics of *Heteromurtrella* species of the world.

Characteristics	<i>abrupta</i> SIN 6, 11	<i>affinis</i> IDS 9	<i>anae</i> sp. nov. BRA	<i>barrai</i> GAB 1, 5	<i>caeca</i> ECU 10	<i>diommata</i> CR 3, 5-6	<i>dubia</i> IC 2, 5-6	<i>echinata</i> VEN 7	<i>greenladeae</i> IDS 9	<i>livida</i> UGA 6, 12
Body pigmentation	+ or -	+ or -	-	-	-	+	-	+	+ or -	+
Ocellar pigmentation	+	+	+	+	-	+	+	+	+	+
Antennae IV annulated	+	-?	+ or -	+	+	+	+	?	-?	+
Smooth chatae on apex of Ant IV	-	+	+	?	+	?	?	?	+	?
Apical bulb on Ant IV	-	-	-	-	-	?	-	?	-	-
Apical sensilla on Ant IV	1h	1h	7h	1k	2h	?	1k	?	1h	1k, +h
Pin projection of Ant IV	-	-	-	-	-	?	-	?	-	-
Number of eyes	6+6	1+1	2+2	2+2	0+0	2+2	2+2	2+2	1+1	2+2
Size of the outer labral papillae in relation to inner	?	larger	larger	equal	equal	larger	larger	larger	larger	?
Shape of labral papillae	?	circular	conical	hooked	circular	circular	circular	domed	domed	?
	?	conical	conical	hooked	conical	conical	conical	conical	conical	?
	?	13	9-11	6	6	?	?	8	13	?
Head dorsal series	?	4	6	5	4	4	4	4	4	?
	?	2	-	3	2	3	2	3	2	?
	?	7	6	7	7	7	7	7	7	?
	?	Pa2-3,5	Pa2-3,5	Pa3,5	Pa2-3,5	Pa2-3,5	Pa2-3,5	Pa2-3,5	Pa2-3,5	?
	?	Pm3	Pm3	Pm3	Pm3	Pm3	Pm3	Pm3	Pm3	?
	?	Pp5	Pp5	-	-	Pp5	-	Pp5	Pp5	?
	?	S	S	?	S	?	S	S	S	?
	?	C	C	?	C	?	C	S	C	?
	?	-	-	?	-	?	-	C	-	?
	?	S	S	?	S	?	S	S	S	?
	?	E	-	?	-	?	C	C	E	?
	?	E?	C	?	S	?	C	C	E?	?
	?	-	-	?	-	?	-	C	-	?
	?	S	S	?	S	?	S	S	S	?
	?	C	C	?	C	?	?	S	C	?
	?	S	S	?	S	?	?	S	S	?
	?	L1	L1	?	L1	?	?	S	C	?
	?	L2	L2	?	L2	?	?	S	S	?

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TABLE 3. (Continued)

Characteristics	<i>abrupta</i> SIN 6, 11	<i>affinis</i> IDS 9	<i>anae</i> sp. nov. BRA	<i>barrai</i> GAB 1, 5	<i>caeca</i> ECU 10	<i>ditommata</i> CR 3, 5-6	<i>dubia</i> IC 2, 5-6	<i>echinata</i> VEN 7	<i>greensladeae</i> IDS 9	<i>livida</i> UGA 6, 12
PLQ chaetae 2+2	?	S	S	?	?	S	?	S	S	?
Shape of the l.p. of papilla E	?	finger	finger	?	finger	?	finger	finger	finger	?
Length of the l.p. to papilla E	?	<1/3	1/3	?	3/4	?	3/4	<1/2	<1/3	?
Appendices in papilla E	?	5	4	?	2	?	?	2-3	5	?
Th II central mac	?	12	14	11	12	?	11	11-12	13	?
Th III dorsal mac	?	7	6	6	7	?	6	6-7	7	?
Abd I dorsal mac	?	3	3	3	3	?	3	3	3	?
Abd II dorsal mac	?	1, 1	1, 1	1, 1	1, 1	?	1, 0	1, 1	1, 1	?
Abd III dorsal mac	?	1, 2	1, 2	1, 2	1, 2	?	1, 2	1, 2	1, 2	?
Abd IV dorsal mac	?	1, 3	2, 4	1, 6	4, 7	?	2, ?	2-3, 3	2, 3	?
Trocanteral organ	?	?	12	?	16	?	?	16-38	?	?
Rows of smooth chaetae on tibiotarsi	-	-	-	-	-	-	1	-	-	-
Unpaired teeth in unguis	1	-	1	0-1	-	1	1-2	-	-	-
Teeth in unguiculi	-	+	-	+	+	+	-	-	+	+
Dorsal smooth chaetae on manubrium	?	4+4	2+2	1+1	3+3 or 4+4	+	4+4	3+3	4+4	1+1
Number of rows of spines on dens	-	-	-	-	-	-	-	1+1	-	-
Number of spines on dens	-	-	-	-	-	-	-	0-10	-	-
Lobe on dens base	?	-	-	-	+	?	-	+	-	?
Smooth chaetae on dens base	?	1+1	1+1	-	1+1	?	?	1+1	1+1	?
Spines on dens base	?	-	-	-	-	?	-	2+2	-	-
Mucronal spine	+	-	+	+	-	+	+	+	-	+

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TABLE 3. (Continued)

Characteristics	<i>mirifica</i> UGA 6,12	<i>nitens</i> TOI 5-6,9,14	<i>pruinosa</i> VEN 7	<i>puertoricensis</i> PR 5	<i>schoetti</i> CR, GUA, PER, 5-6	<i>similis</i> GAB 1,5-6	<i>stannardi</i> SOI 4,5,6	<i>sububia</i> GAB 1,5-6	<i>tihuiensis</i> PR 8	<i>zairensis</i> ZAI 13
Body pigmentation	+	-	+	+	-	+	+	-	+	-
Ocellar pigmentation	+	-	-	-	-	+	-	-	+	-
Antennae IV annulated	+	+	?	+	+	+	+	+	?	?
Smooth chatae on apex of Ant IV	+	?	?	?	?	+	?	?	+	?
Apical bulb on Ant IV	+	?	?	-	-	-	-	-	-	?
Apical sensilla on Ant IV	1k	?	?	1k	1k	+h	1-2k	1k	1h	?
Pin projection of Ant IV	-	?	?	-	-	-	-	1spl.	1bif.	?
Number of eyes	2+2	1+1	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2
Size of the outer labral papillae in relation to inner	equal	larger	?	larger	equal	?	larger	larger	?	?
Shape of labral papillae	hooked	circular	?	circular	conical	?	circular	circular	domed	?
	hooked	conical	?	conical	conical	?	conical	conical	conical	?
Head	?	?	8	?	?	6	7	?	10-12	?
dorsal series	5	?	4	4	6	5	6	3	4	4
	3	?	2	3	-	3	-	3	3	3
	7	?	7	7	7	6	7	7	7	7
	Pa3?,5	?	Pa2-3,5	Pa2-3,5	Pa2-3,5	Pa3?,5	Pa2-3,5	Pa2-3,5	Pa2-3,5	Pa3?,5
	-	?	Pm3	Pm3	Pm3	-	Pm3	Pm3	Pm3	-
	Pp5	?	Pp3,5	Pp5	Pp5	Pp5	Pp5	Pp5	Pp5	Pp5
	S	?	S	S	S	?	S	?	S	S
	C	?	C or S	C	C	?	C	?	C?	C
	-	?	C	C	-	?	C	?	-	-
	S	?	S	S	S	?	S	?	C?	S
	C	?	C or -	-	C	?	-	?	-	-
	C	?	C	C	C	?	C	?	C?	-
	-	?	C	-	-	?	-	?	-	-
	S	?	S	S	S	?	S	?	C?	S
	C	?	C or -	-	C	?	-	?	-	-
	C	?	C	C	C	?	C	?	C?	-
	-	?	C	-	-	?	-	?	-	-
	S	?	S	S	S	?	S	?	-	S
	C	?	C or S	?	?	?	?	?	-	-
	C	?	C	C	C	?	C	?	C?	-
	-	?	C	-	-	?	-	?	-	-
	S	?	S	S	S	?	S	?	-	S
	?	?	C or S	?	?	?	?	?	-	?
	?	?	S	?	?	?	?	?	-	?
	?	?	S	?	?	?	?	?	-	?

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TABLE 3. (Continued)

Characteristics	<i>mirifica</i> UGA 6, 12	<i>nitens</i> TOI 5-6, 9, 14	<i>pruinosa</i> VEN 7	<i>puertoricensis</i> PR 5	<i>schoetti</i> CR, GUA, PER, 5-6	<i>similis</i> GAB 1, 5-6	<i>stannardi</i> SOI 4, 5, 6	<i>subdubia</i> GAB 1, 5-6	<i>tihuensis</i> PR 8	<i>zairensis</i> ZAI 13
PLQ chaetae 2+2	?	?	S	S	?	?	?	?	S	?
Shape of the l.p. of papilla E	finger	?	finger	finger	finger	?	finger	?	?	?
Length of the l.p. to papilla E	1/2	?	1/3	3/4	?	?	1/2	?	3/4	?
Appendices in papilla E	1	?	2	?	?	?	1	?	?	?
Th II central mac	10	7?	11-12	12	13	10	11	13	12	11
Th III dorsal mac	4	7	5-6	6	6	4	6	6	6	6
Abd I dorsal mac	1	3	3	3	3	2	2	3	3	3
Abd II dorsal mac	1, 1	1, 1	1, 1	1, 1	1, 0	1, 0	1, 1	1, 1	1, 1	1, 1
Abd III dorsal mac	1, 2	?	1, 2	1, 2	1, 2	1, 2	1, 1	1, 2	1, 2	1, 2
Abd IV dorsal mac	2, ?	?	3, 3	2, ?	2, ?	2, ?	1, ?	2, ?	2, 4	2, 5
Trocanteral organ	?	15	16-38	?	?	?	26	?	?	?
Rows of smooth chaetae on tibiotarsi	-	?	-	-	-	?	-	-	-	?
Unpaired teeth in unguis	1	1	-	1-2	0-2	1	-	1-2	-	-
Teeth in unguiculi	+	+	-	-	-	+	+	-	+	+
Dorsal smooth chaetae on manubrium	?	5+5	2+2	4+4	4+4	4+4	3+3	4+4	3+3 or 4+4	2+2
Number of rows of spines on dens	?	-	-	-	-	-	-	-	1+1	-
Number of spines on dens	?	-	-	-	-	-	-	-	11	-
Lobe on dens base	?	+	-	-	-	-	?	-	+	-
Smooth chaetae on dens base	?	1+1	1+1	1+1	1+1	1+1	1+1	1+1	2+2	1+1
Spines on dens base	?	-	-	-	-	-	-	-	-	-
Mucronal spine	+	+	+	+	+	+	-	+	+	+

Symbols used to represent the morphological characteristics: Ant—antenna; Abd—abdomen; Th—thorax; 'C'—ciliated; 'S'—smooth; 'E'—scales; l.p.—lateral process; mac—macrochaeta; o.p.—outer papillae; i.p.—inner papillae; PLQ—Post-labial quadrangle; spl.—simple; bif.—bifurcated; h—hooked; k—knobbed; *—restricted pigments in antennae and/or head anterior region, or diffuse on body; '+'—present; '?'—unknown. Reference species: (1)Barra 1968; (2)Delamare Deboutteville 1952; (3)Denis 1931; (4)Mari Mutt 1976; (5)Mari Mutt 1979; (6)Mari Mutt 1980c; (7)Mari Mutt 1983; (8)Mari Mutt 1985a; (9)Mari Mutt 1987; (10)Najt *et al.* 1988; (11)Salmon 1954; (12)Salmon 1951; (13)Tshelnokov 1977; (14)Yosii 1964. Abbreviations of locations: CR—Costa Rica; BRA—Brazil; ECU—Ecuador; GAB—Gabon; GUA—Guatemala; IC—Ivory Coast; IDS—Indonesia; PER—Peru; PR—Puerto Rico; SIN—Singapore; SOI—Solomon Islands; TOI—Tonga Islands; UGA—Uganda; VEN—Venezuela; ZAI—Zaire.

***Heteromurtrella livida* (Salmon, 1954)**

Ptenura livida Salmon, 1954: 125–126, figs 8–10, Ruwenzori, Uganda (orig. descr.). Salmon 1964: 479 (compared).
Heteromurus (*Heteromurtrella*) *lividus*; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 23 (redescr.).

Diagnosis. Body, antennae and legs blue, black pigmentation on 2+2 eyes; tibiotarsi without smooth chaetae rows; unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with 2+2 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Uganda.

***Heteromurtrella mirifica* (Salmon, 1954)**

Ptenura mirifica Salmon, 1954: 125–127, figs 11–17, Ruwenzori, Uganda (orig. descr.). Salmon 1964: 480 (compared).
Heteromurus (*Heteromurtrella*) *mirificus*; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 13–14, figs 1, 9–10, 24, 27 (redescr.).
Heteromurus mirificus; Barra, 1968: 114–116, figs 6A–G (misidentification), described as *Heteromurus* (*Heteromurtrella*) *barrai* by Mari Mutt (1979b).

Diagnosis. Body covered by diffuse brownish to yellowish pigment, black pigmentation on 2+2 eyes; Ant IV with one simple apical bulb; head ‘A’ series with 5 mac (A0, A2–5); ‘M’ series with 3+3 mac (M1–3), ‘S’ series with S0 mac, postoccipital series with 3+3 mac (Pa3?, Pa5 and Pp5) (Fig. 8); Th II with 10+10 mac (a5, m1–2, m4, m4p, p1, p2, p2e, p3 and p3p); Th III with 4+4 mac (a4–5, p1–2); Abd I with 1+1 mac (m2); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV 2+2 central mac (A3 and A6) (Fig. 12); unguis with one medial unpaired teeth; unguiculi with outer tooth; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Uganda.

***Heteromurtrella nitens* (Yosii, 1964)**

Heteromurus nitens Yosii, 1964: 14, figs 6A–H, Tonga Islands (orig. descr.). Barra 1968: 106, 110 (cit.). Mari Mutt 1976: 326 (compared).
Heteromurus (*Heteromurtrella*) *nitens*; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 14, 17 (compared). Mari Mutt 1987: 575 (compared). Najt *et al.* 1988: 561 (compared).

Diagnosis. Body and eyepatches pale, 1+1 eyes; Th II posteriorly with 7+7 mac (p1, p1p, p2, p2p, p2e, p3 and p3p); Th III with 7+7 mac (a2, a4–5, p1–2, p2e and p3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5) (Fig. 12); unguis with one medial unpaired tooth; unguiculi with outer tooth; manubrium with two rows of 5 smooth chaetae (Tab. 3).

Distribution. Tonga Islands.

***Heteromurtrella pruinosa* Mari Mutt, 1983**

Heteromurus (*Heteromurtrella*) *pruinus* Mari Mutt, 1983: 163–164, figs 29, 36, 38, 40–41, Merida State, Venezuela (orig. descr.).

Diagnosis. Body light salmon ochre to olive green, dark pigments covering Ant IV–V, black pigment absent on 2+2 eyes; head ‘A’ series with 4 mac (A0, A2–4); ‘M’ series with 2+2 mac (M1–2), ‘S’ series with S0 mac, postoccipital series with 6+6 mac (Pa2–3, Pa5, Pm3, Pp3 and Pp5) (Fig. 8); Th II with 11+11 or 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p), p3 present or absent; Th III with 5+5 or 6+6 mac (a2, a4–5, p1–3), p1 present or absent; Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV 3 central mac (Ai3?, A3 and A6) and 3+3 lateral mac (D3, E2 and F1) (Fig. 12); unguis without unpaired teeth; unguiculi with smooth edges; manubrium with two rows of 2 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Venezuela.

***Heteromurtrella puertoricensis* Mari Mutt, 1979**

Heteromurus (Heteromurtrella) puertoricensis Mari Mutt, 1979b: 220–221, figs 1, 3–6, 8–11, 13–16, Maricao, Puerto Rico (orig. descr.). Mari Mutt 1980c: 11–12 (cit. et key). Mari Mutt 1983: 162 (compared).

Diagnosis. Body light orange, black pigments on 2+2 eyes; head ‘A’ series with 4 mac (A0, A2–A4), ‘M’ series with 3+3 mac (M1–3), ‘S’ series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 12); unguis with 1–2 unpaired teeth; unguiculi with smooth edges; manubrium with two rows of 4 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Puerto Rico.

***Heteromurtrella schoetti* (Denis, 1931)**

Heteromurus schoetti Denis, 1931: 145–146, figs 152–157, Orizuaco, Costa Rica (orig. descr.). Denis 1933: 254–255, La Carpintera, Costa Rica (cat.). Barra 1968: 105, 107 (compared). Mari Mutt, 1977: 242 (compared).

Ptenura schoetti; Salmon 1964: 483 (comb.).

Heteromurus (Heteromurus) schoetti; Mari Mutt 1977: 242 (compared).

Heteromurus (Heteromurtrella) schoetti; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 17, 19, figs 2, 6, 11–12, 17, 22, 26, 30, Sacatepequez, Guatemala; Tingo Maria, Peru (redescr.).

Heteromurus bidentatus Denis, 1931: 146–147, figs 158–159, San Jose, Costa Rica, synonymized by Mari Mutt 1980c: 17.

Diagnosis. Body and eyepatches pale, 2+2 eyes; head ‘A’ series with 6 mac (A0, A2, A2a, A3–A5), ‘M’ series without mac, ‘S’ series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 13+13 mac (a5, m1–2, m4, m4i, m4p, p1, p1p, p2, p2p, p2e, p3 and p3p); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 12); unguis with or without 2 unpaired teeth; unguiculi with smooth edges; manubrium with two rows of 4 smooth chaetae (Tab. 3).

Distribution. Costa Rica, Guatemala, Peru.

***Heteromurtrella similis* (Barra, 1968)**

Heteromurus similis Barra, 1968: 112–114, figs 5A–G, Ipassa, Gabon (orig. descr.).

Heteromurus (Heteromurtrella) similis; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 14, figs 19, 28 (compared).

Diagnosis. Body pale, black pigments covering antennae and on 2+2 eyes; head ‘A’ series with 5 mac (A0, A2–A5), ‘M’ series with 3+3 mac (M1–3), ‘S’ series with 6+6 mac (S1, S3–7), S0 absent, postoccipital series with 3+3 mac (Pa3?, Pa5 and Pp5) (Fig. 8); Th II with 10+10 mac (a5, m1–2, m4, m4i, p1, p2, p2e, p3 and p3p); Th III with 4+4 mac (a5, p1–3); Abd I with 2+2 mac (m2–3); Abd II with 1+1 mac (m3); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 12); unguis with one medial unpaired tooth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 4 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Gabon.

***Heteromurtrella stannardi* (Mari Mutt, 1976)**

Heteromurus stannardi Mari Mutt, 1976: 326–329, figs 1–7, Guadalcanal, Solomon Islands (orig. descr.). Mari Mutt 1977: 242 (compared). Mari Mutt, 1978: 5 (cat. typ.).

Heteromurus (Heteromurtrella) stannardi; Mari Mutt 1979b: 214 (comb.). Mari Mutt 1980c: 13, figs 3, 13–14, 21 (redescr.).

Diagnosis. Body, antennae, legs and eyepatches black to violet, 2+2 eyes; head 'A' series with 6 mac (A0, A2, A2a, A3–5), 'M' series without mac, 'S' series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 11+11 mac (m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 2+2 mac (m2–3); Abd II with 1+1 mac (m3); Abd III with 2+2 mac (m3 and pm6); Abd IV with 1+1 central mac (A3) (Fig. 12); unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 3 smooth chaetae; mucro without basal spine (Tab. 3).

Distribution. Solomon Islands.

Heteromurtrella subdubia (Barra, 1968)

Heteromurus subdubius Barra, 1968: 108–110, figs 5A–E, Ipassa, Gabon (orig. descr.). Mari Mutt 1976: 326 (compared, misspelled as *subdubius*)

Heteromurus (Heteromurtrella) subdubius; Mari Mutt, 1979b: 214 (comb.). Mari Mutt 1980c: 19–21, figs 8, 16, 29 (compared).

Diagnosis. Body and eyepatches pale, 2+2 eyes; Ant IV with one simple pin projection; head 'A' series with 3 mac (A2–A4), A0 absent; 'M' series with 3+3 mac (M1–3), 'S' series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 13+13 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3, p3p and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) (Fig. 12); unguis with 1–2 unpaired teeth; unguiculi with smooth edges; manubrium with two rows of 4 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

Distribution. Gabon.

Heteromurtrella tihuiensis (Mari Mutt, 1985)

Heteromurus (Heteromurtrella) tihuiensis Mari Mutt, 1985a: 145–147, figs 1–6, Sierra de Luquillo, Puerto Rico (orig. descr.).

Diagnosis. Body light orange, black pigmentation on 2+2 eyes; Ant IV with one bifurcated pin projection (Fig. 5); head 'A' series with 4 mac (A0, A2–4); 'M' series with 3+3 mac (M1–3), 'S' series with S0 mac, postoccipital series with 5+5 mac (Pa2–3, Pa5, Pm3 and Pp5) (Fig. 8); Th II with 12+12 mac (a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3 and p3p); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV 2+2 central mac (A3 and A6) and 4+4 lateral mac (D3, E2, E3 and F1) (Fig. 12); unguis without unpaired tooth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 3–4 smooth chaetae; dens with 11+11 spines in one row (Fig. 15; Tab. 3).

Distribution. Puerto Rico.

Heteromurtrella zairensis (Tshelnokov, 1977) comb. nov.

Heteromurus zairensis Tshelnokov, 1977: 105–106, fig. 3, Virunga National Park, Zaire (orig. descr.).

Diagnosis. Body pale, black pigmentation on 2+2 eyes; head 'A' series with 4 mac (A0, A2–4); 'M' series with 3+3 mac (M1–3), 'S' series with S0 mac, postoccipital series with 3+3 mac (Pa3?, Pa5 and Pp5) (Fig. 8); Th II with 11+11 mac (a5, m1–2, m4, p1, p2, p2e, p3, p3p, p5 and one of uncertain homology); Th III with 6+6 mac (a1, a4–5, p2, p2e and p3); Abd I with 3+3 mac (m2–4); Abd II with 2+2 mac (m3 and m5); Abd III with 3+3 mac (m3, pm6 and p6); Abd IV 2+2 central mac (of uncertain homology) and 5+5 lateral mac (D3, E2–3, F1–2) (Fig. 12); unguis without unpaired teeth; unguiculi with outer tooth (Fig. 14); manubrium with two rows of 2 smooth chaetae; mucro with basal spine (Fig. 18; Tab. 3).

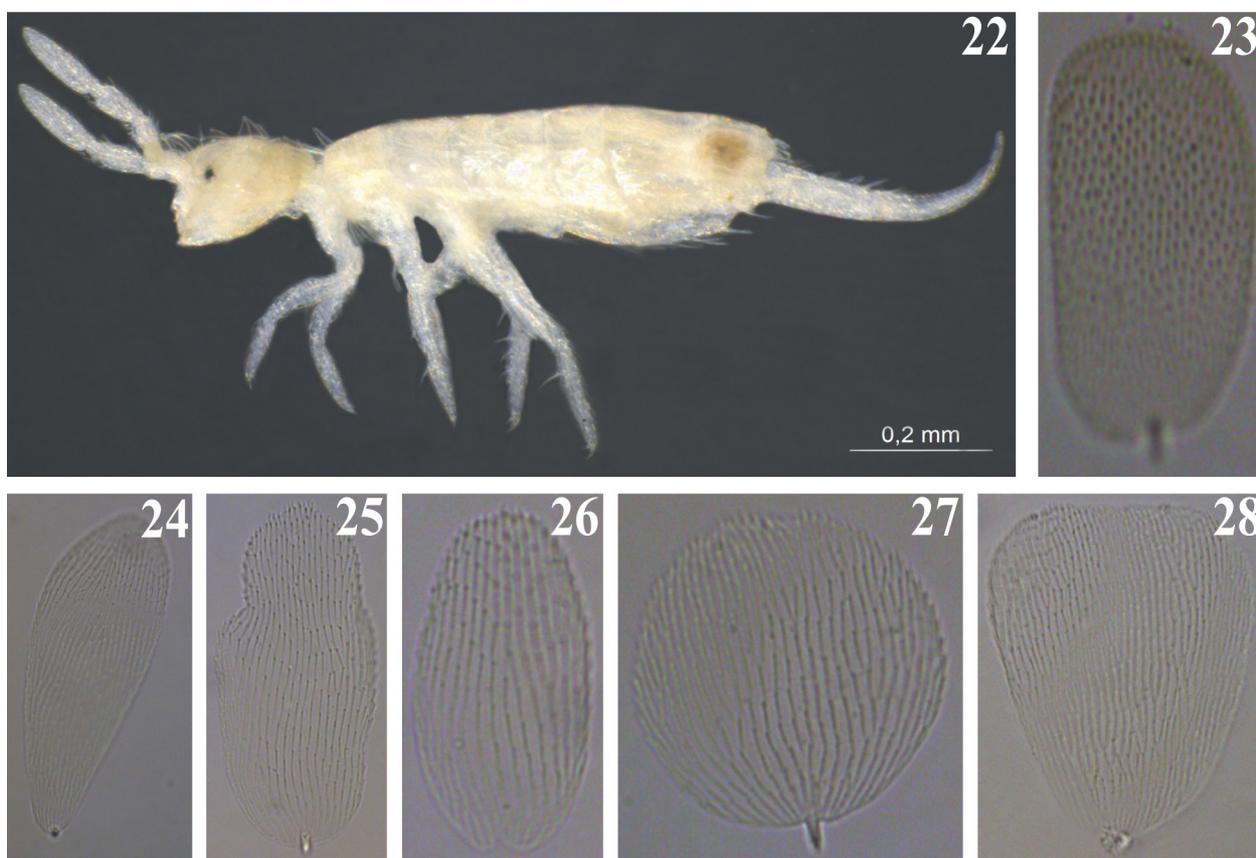
Distribution. Zaire.

Remarks. *Heteromurtrella zairensis* **comb. nov.** is herein transferred from *Heteromurus* to *Heteromurtrella* by the presence of S0 mac in head and 3+3 mac (M2–4) in Abd I (see Tshelnokov 1977, pg. 106). Such chaetal characters are diagnostically absent in *Heteromurus*.

***Heteromurtrella anae* sp. nov. Cipola**

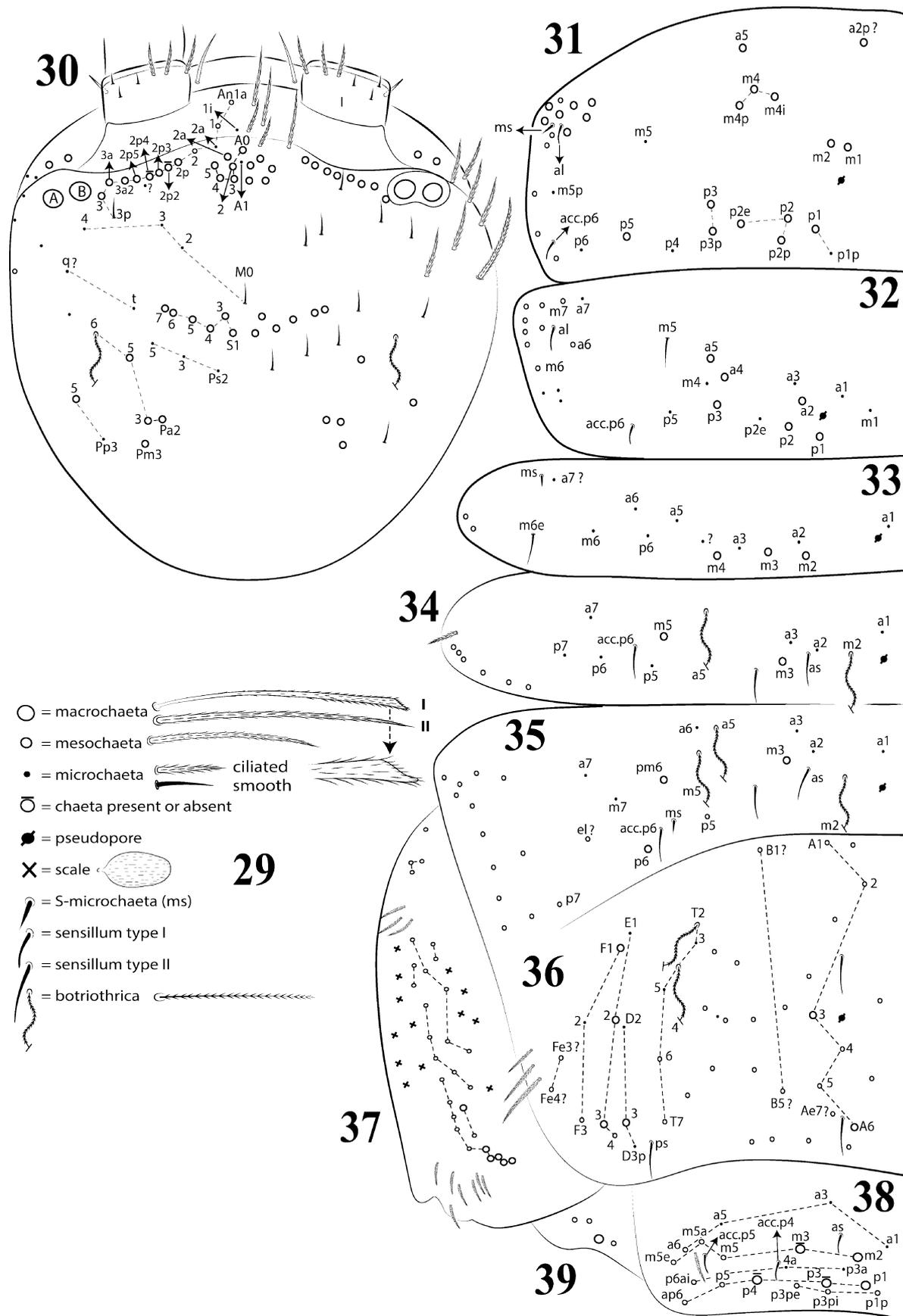
Figs 22–62

Type material. Holotype Female, Brazil, Amazonas, Manaus, Reserva Ducke, grid L6-500 (02°58'18"S; 59°57'28"W), xi.2011, extraction with Berlese, FGL Oliveira & JW Morais coll., on slide N° COLLE 038/INPA. Paratypes on slides N° COLLE 038A-M/INPA, 2 males, 9 females and 1 juveniles and 07 specimens in alcohol, same data as holotype, except grids L3-2500 (02°56'32"S; 59°56'39"W), L3-3500 (02°56'38"S; 59°56'39"W), L4-500 (02°57'13"S; 59°57'38"W), L5-500 (02°57'45"S; 59°57'33"W), L7-500 (02°58'49"S; 59°57'23"W), L8-1500 (02°59'16"S; 59°56'46"W), L8-3500 (02°59'05"S; 59°55'42"W).

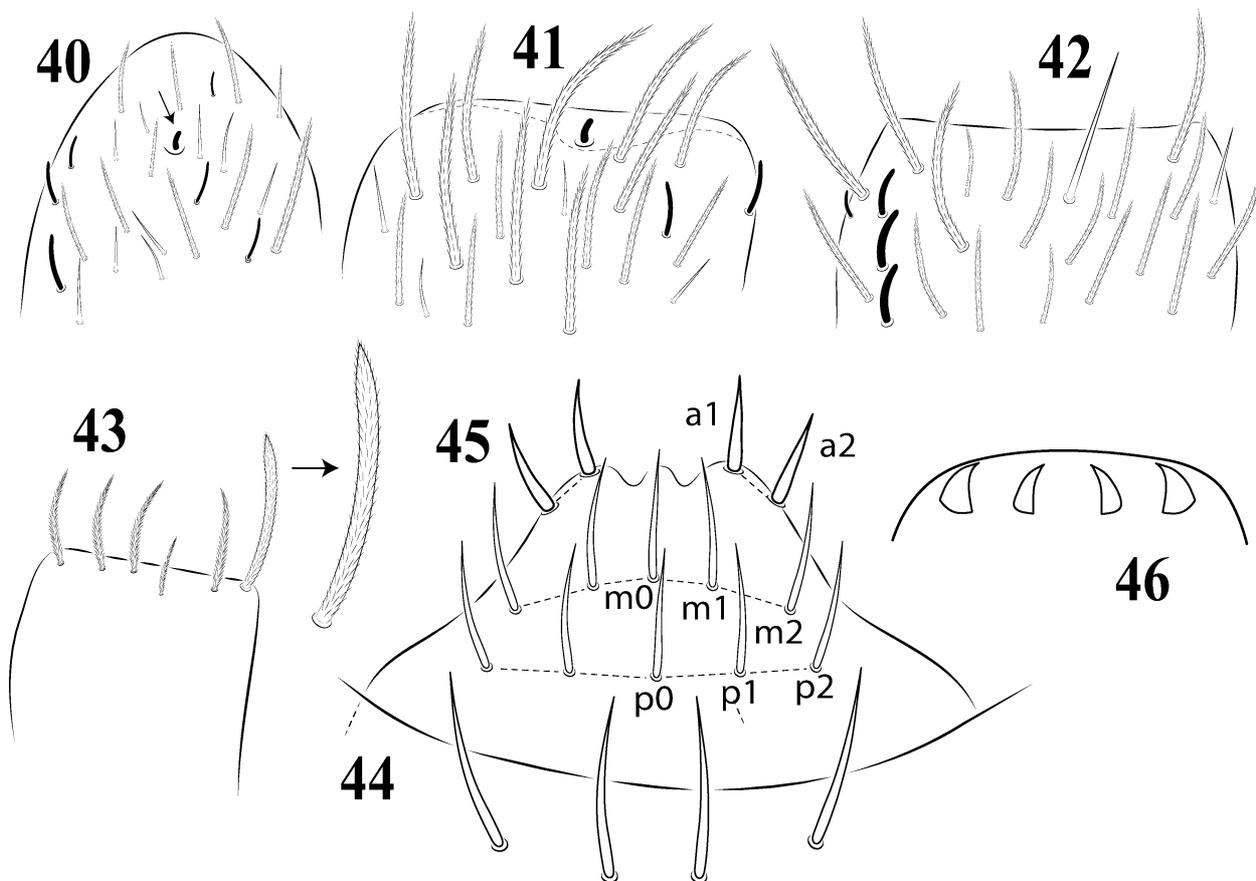


FIGURES 22–28. *Heteromurtrella anae* **sp. nov.**: **22**, habitus of a fixed adult specimen; **23–28**, different shapes of scales: **23**, rounded and strongly striated, **24**, elongate; **25**, irregular; **26**, oval; **27**, rounded; **28**, truncate.

Diagnosis. Black pigments restricted to 2+2 eyes; head ‘A’ series with 6 mac (A0, A2, A2a, A3–5); ‘M’ series without mac; ‘S’ series with 6+6 mac (S1, S3–7), S0 absent; ‘Pa’ series with 3+3 mac (Pa2–3 and Pa5), ‘Pm’ series with Pm3 mac, ‘Pp’ series with Pp5 mac; Th II with 14+14 mac (a2p?, a5, m1–2, m4, m4i, m4p, p1, p2, p2p, p2e, p3, p3p and p5); Th III with 6+6 mac (a2, a4–5, p1–3); Abd I with 3+3 (m2–4); Abd II with 2+2 (m3 and m5); Abd III with 3+3 (m3, pm6 and p6); Abd IV with 2+2 central mac (A3 and A6) and 4+4 lateral mac (D3, E2, E3 and F1); Abd V with 2+2 to 5+5 mac (m2, m3, p1, p3 and p4), m3, p3 and p4 present or absent; tibiotarsi without smooth rows of chaetae; unguis with one unpaired medial tooth; unguiculi I–II acuminate, III truncate, without tooth; manubrium dorsally with two rows of 2 smooth chaetae; dens dorsally without spines; dental base without lobe and spines, with 1+1 smooth chaetae; mucronal spine present (Figs 22, 30–36, 38, 40, 57–58, 60–62; Tab. 2).



FIGURES 29–39. *Heteromurtrella anae* sp. nov.: dorsal chaetotaxy. **29**, symbols used in detailed chaetotaxy schemes; **30**, head; **31**, Th II; **32**, Th III; **33**, Abd I; **34**, Abd II; **35**, Abd III; **36**, Abd IV; **37**, Abd III–IV lateral; **38**, Abd V; **39**, Abd V lateral.

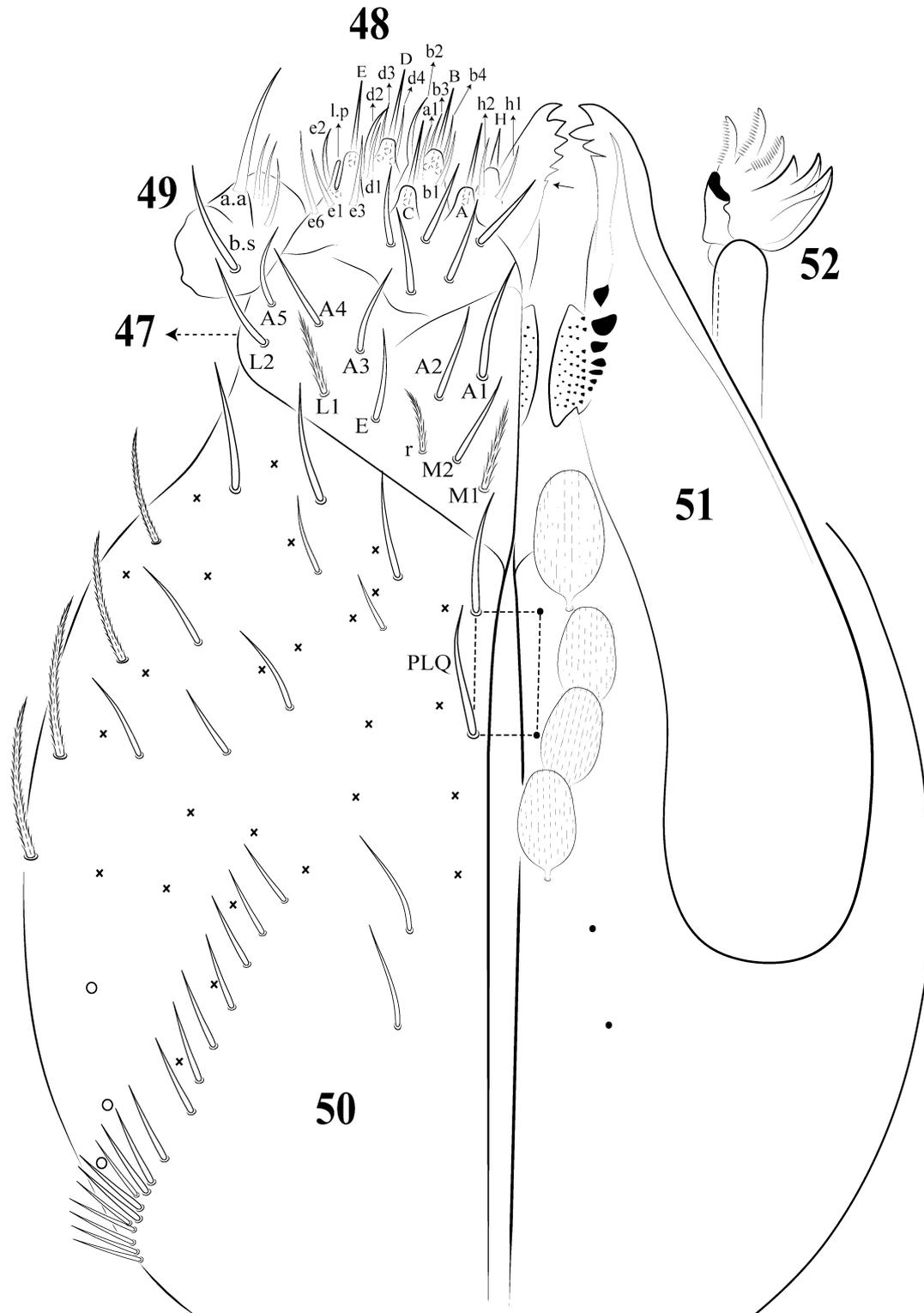


FIGURES 40–46. *Heteromurtrella anae* sp. nov.: 40, Ant IV apex, arrow indicates sense organ; 41, sense organ of Ant IV; 42, ventral face of Ant IV; 43, Ant II distal chaetotaxy; 44, prelabral chaetotaxy; 45, labral chaetotaxy; 46, labral papillae.

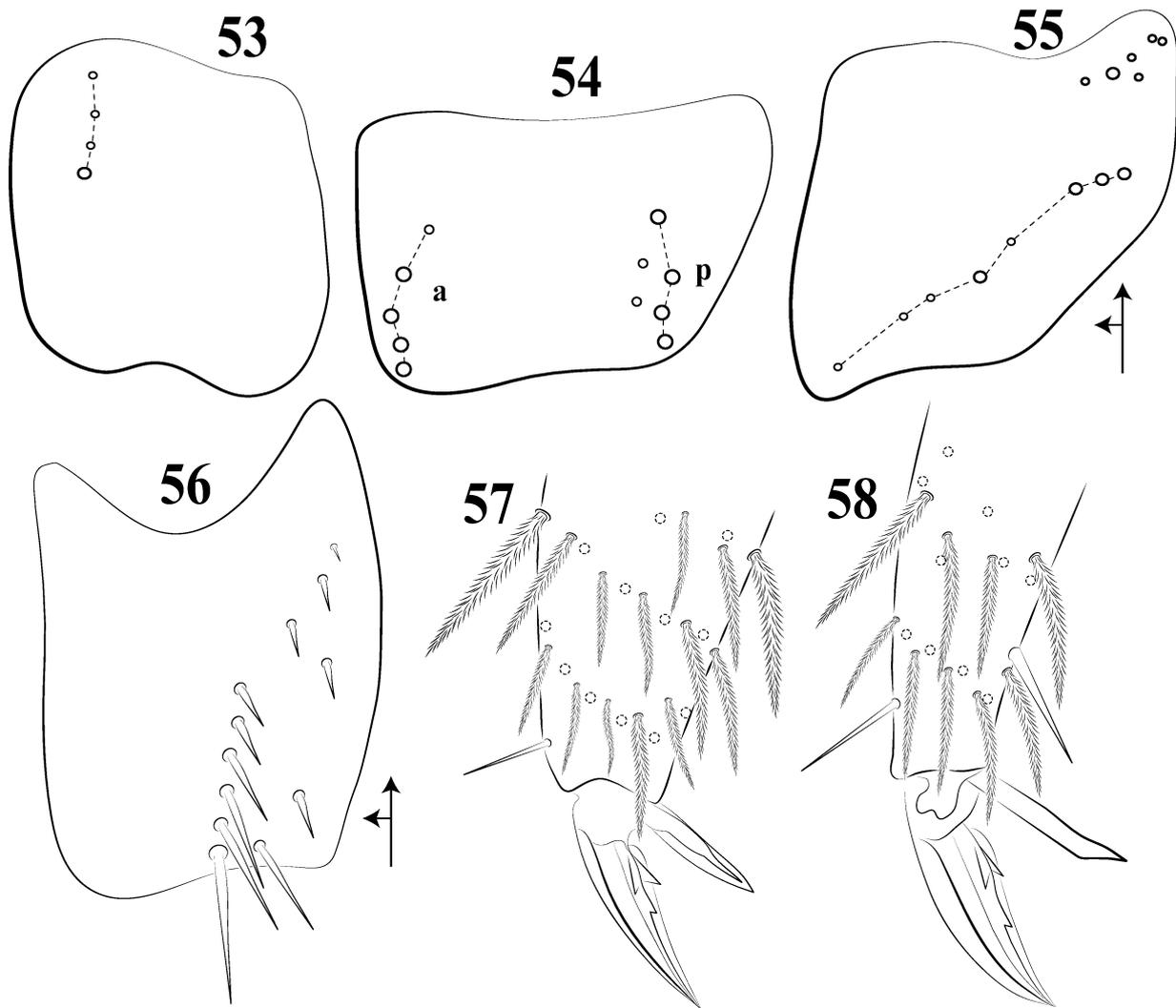
Description. Total length of holotype 1.24 mm. Habitus typical of Heteromurinae (Fig. 22). Color of specimens pale with black pigments limited to eyepatches (Fig. 22). Strongly striated apically rounded scales with stria rows unaligned covering thorax and abdomen (Fig. 23). Moderately striated scales with stria rows aligned with different shapes (apically elongated, irregular, oval, rounded or truncate) covering Ant I, II and III base of Ant IV, both faces head, thorax, abdomen, collophore posterior face, legs (except tibiotarsi), both manubrium faces and anterior face of dens (Figs 24–28).

Head. Ant IV annulated or normal, without apical bulb, with six s-blunt sensillae, one subapical organite, and ciliated and smooth chaetae (Fig. 40). Apical sense organ of Ant IV as in Fig. 41, with 1 rods (atypical) and 2 s-blunt sensillae; ventral face of Ant IV with 4 s-blunt sensillae, both faces with smooth and ciliated chaetae (Figs 41–42). Ant II external face with one rod-like short macrochaeta (Fig. 43). Eyes oval, with two subequal ocelli A and B (Fig. 30). Head dorsal chaetotaxy as in Fig. 30; antennal series ‘An’ with 12+12 to 14+14 chaetae (An2p, An2p2–5, An3a2, An3a and An3 as macrochaetae, An1a, An1 and An2 as mesochaetae, and An2a, An3p, An1i plus one unnamed microchaeta), An2p2, An2p4 present or absent; anterior series ‘A’ with 6 macrochaetae (A0, A2–5, and A2a) and A1 as microchaeta; medio-ocellar series ‘M’ with 4+4 microchaetae (M0, M2–4); sutural series ‘S’ with 6+6 macrochaetae (S1, S3–7), S0 and S2 absent; interocular series with 2+2 microchaetae (q? and t); post-sutural series ‘Ps’ with 3+3 microchaetae (Ps2–3 and Ps5); postoccipital anterior series ‘Pa’ with 4+4 chaetae (Pa2–3 and Pa5 as macrochaetae, Pa6 as bothrioticum); postoccipital media series ‘Pm’ with 1+1 macrochaetae (Pm3); postoccipital posterior ‘Pp’ series with 2+2 chaetae (Pp5 as macrochaeta and Pp3 as microchaeta). Prelabral/labral formula 4/ 5, 5, 4, all smooth chaetae, four anterior labral as spine-like chaetae (a1 and a2), five median (m0, m1 and m2) and five posterior (p0, p1 and p2) (Figs 44–45). Labral papillae cone-shaped, outer larger, inner smaller (Fig. 46). Labial region with chaeta r (smaller), M1 and L1 ciliated; A1, A2, A3, A4, A5, M2, E and L2 smooth (Fig 47). Labium with five smooth proximal chaetae. Labial palp with five papillae (A–E), A and C simple, B with five smooth appendages (a1, b1, b2, b3 and b4), D with four smooth appendage (d1, d2, d3 and d4). Papilla E with lateral process finger-shaped (l.p.) with length 2.3x smaller than the papilla, four

smooth appendages (e1, e2, e3 and e6), plus the main hypostomal chaeta (H) with two accessorial appendages (h1 and h2) (Fig. 48). Maxillary palp with apical appendage (a.a.) and basal chaeta (b.s.) smooth, subequal in length; sublobal plate with three smooth appendages (Fig. 49). PLQ with 2+2 smooth chaetae (Fig. 50). Head ventral chaetotaxy as in Fig. 50. Left mandible (ventral view) with five to six incisive teeth, one minute basal present or absent; right mandible with four teeth, the second teeth most developed; both mandibles with seven molar teeth (Fig. 51). Maxillae with three teeth, three lamellae and one projected sclerosed condyle (Fig. 52).



FIGURES 47–52. *Heteromurtrella anae* sp. nov.: ventral head: **47**, labial region; **48**, labial papillae and proximal chaetae; **49**, maxillary palp and sublobal plate; **50**, post labial chaetotaxy; **51**, left mandible; **52**, left maxilla (ventral view).



FIGURES 53–58. *Heteromurtrella anae* sp. nov.: **53**, subcoxa I; **54**, subcoxa II; **55**, subcoxa III; **56**, trochanteral organ; **57**, empodial complex I; **58**, empodial complex III.

Thorax. Th II dorsal chaetotaxy as in Fig. 31; anterior series ‘a’ with 2+2 macrochaetae (a2p? and a5); medial series ‘m’ with 7+7 chaetae (m1, m2, m4i, m4 and m4p as macrochaetae, m5 and m5p as microchaetae); posterior series ‘p’ with 10+10 chaetae (p1, p2, p2p, p2e, p3, p3p and P5 as macrochaetae, p1p, p4 and p6 as microchaetae); and 1+1 S-microsensillum (ms), 1+1 anterolateral sensilla (al) plus accessory sensilla (acc.p6) near to p6, the latter two type I. Th III dorsal chaetotaxy as in Fig. 32; series ‘a’ with 7+7 chaetae (a2, a4 and a5 as macrochaetae, a6 as mesochaeta, a1, a3 and a7 as microchaetae); series ‘m’ with 4+4 chaetae (m6–7 as mesochaetae, m5 as long smooth microchaeta, m1 and m4 as microchaetae); series ‘p’ with 5+5 chaetae (p1–3 as macrochaetae, p2e and p5 as microchaetae). Six extranumerary mesochaetae and three microchaetae on the side of tergite, anterolateral sensilla (al) and accessory sensilla (acc.p6) type I present.

Abdomen. Abd I dorsal chaetotaxy as in Fig. 33; series ‘a’ with 7+7 microchaetae (a1–3, a5–a7? and one extranumerary); series ‘m’ with 5+5 chaetae (m2–4 as macrochaetae, m6 as microchaeta, m6e long microchaeta); series ‘p’ with 1+1 microchaeta (p6). Two unnamed lateral mesochaetae, 1+1 S-microsensillum (ms), accessory sensilla (acc.p6) not seen. Abd II dorsal chaetotaxy as in figure 34; series ‘a’ with 5+5 chaetae (a1–3 and a7 as microchaetae, a5 as bothriotricum); series ‘m’ with 4+4 chaetae (m3 and m5 as macrochaetae, m2 as bothriotricum, m3e as microchaeta); series ‘p’ with 3+3 microchaetae (p5–7). Three sensillae present, one anterosubmedial (as), one accessory (acc.p6) and one unnamed, all type II. Six unnamed chaetae of different lengths present laterally. Abd III dorsal chaetotaxy as in Fig. 35; series ‘a’ with 6+6 chaetae (a1–3, a6–7 as microchaetae, a5 as bothriotricum); series ‘m’ with 5+5 chaetae (m3 as macrochaeta, m2 and m5 as bothriotrica, m4 and m7 as microchaetae); series ‘p’ with 4+4 chaetae (pm6 and p6 as macrochaetae, p5 and p7 as

mesochaetae). Three sensillae present, one anterosubmedial (as), accessory (acc.p6) and one unnamed, all type II, plus one S-microsensillum (ms). Chaetae el and about 12 unmaed antero-lateral mesochaetae present. Abd IV dorsal chaetotaxy as in Fig. 36; series 'A' with 6+6 chaetae (A3 and A6 as macrochaetae, A1–2, A4–5 as mesochaetae); series 'Ae' with Ae7? present as mesochaeta; series 'B' with 2+2 mesochaetae (B1? and B5?); series 'T' with 6+6 chaetae (T6–7 as mesochaetae, T2 and T4 as bothriotrica, T3 and T5 as microchaetae); series 'D' with 3+3 chaetae (D3 as macrochaeta, D2 and D3p as microchaetae); series 'E' with 4+4 chaetae (E2 and E3 as macrochaetae, E4 as mesochaeta, E1 as microchaeta); series 'F' with 3+3 chaetae (F1 as macrochaeta, F3 as mesochaeta, F2 as microchaeta); series 'Fe' with 2+2 mesochaetae (Fe3?–4?). Three sensilla type II (ps and two unnamed) present. Three unmaed mesochaetae present between the series 'Ai' to 'T'. Posterior margin with about four mesochaetae. Latero-posterior margin typically with three chaetae. Abd III–IV lateral chaetotaxy as in Fig. 37; series 'G' with G1 as mesochaeta; series 'H' with 3+3 mesochaetae (H1, H1e and H1p); series 'Ii' with 2+2 mesochaetae (Ii1–2); series 'I' with 5+5 mesochaetae (I1–4); series 'Ie' with 2+2 mesochaetae (Ie1–2); series 'J' with 5+5 mesochaetae (J1–3); series 'K' with 2+2 chaetae (K1 as macrochaeta, K3 as mesochaeta); series 'Ke' with 10+10 chaetae (Ke3p–5p as macrochaetae, Ke1–3 as mesochaetae); three unnamed ciliated microchaetae in latero-anterior region and seven in posterior region. Abd V dorsal chaetotaxy as in Fig. 38; series 'a' with 4+4 chaetae (a6 as mesochaeta, a1, a3 and a5 as microchaetae); series 'm' with 4+4 to 5+5 chaetae (m2 (present or absent) and m3 as macrochaetae, m5, m5a and m5e as mesochaetae); posteroanterior series 'pa' with 3+3 chaetae (p6ai as mesochaeta, p3a and p4a as microchaetae); series 'p' with 3+3 to 5+5 chaetae (p3, p4 (present or absent) and p1 as macrochaetae, p5 and ap6 as mesochaetae); posterior-posterior series 'pp' with 3+3 mesochaetae (p1p, p3pi and p3pe). One anterosubmedial sensillae (as) and two accessory sensillae (acc.p4 and acc.p5) present, all type I. Abd V lateral chaetotaxy as in figure 39, with 4+4 chaetae (1+1 macrochaeta and 3+3 mesochaetae).

Legs. Subcoxal chaetotaxy with type II macrochaeta; subcoxa I with a row of one macrochaeta and three mesochaetae; subcoxa II with an anterior row (a) of four macrochaetae and one mesochaeta, posterior row (p) of four macrochaetae plus two anterior mesochaetae; subcoxa III with an inferior row of four macrochaetae and four mesochaetae, superior group with a macrochaeta and five mesochaetae (Figs 53–55). Trochanteral organ V-shaped with approximately 12 spine-like chaetae (Fig. 56). Tibiotarsi I–III without smooth chaetae (with exception of one distal chaeta in tibiotarsus III). Unguis gently concave, toothless edges, with one pair of basal wing-like inner teeth and one unpaired tooth at the medial region. Unguiculi I–II acuminate, with smooth edges; unguiculi III truncate, with the outer edge slightly excavated. Tenent hairs acuminate with smooth edges (Figs 57–58). Tibiotarsus III with a smooth inner distal chaeta, near the empodium (Fig. 58).

Collophore. All smooth chaetae; posterior and anterior faces with eight chaetae; latero-posterior face with 11 chaetae (Fig. 59).

Furca. Dorsal face of manubrium with two rows of two erect smooth chaetae, two smaller in base and two larger near median region; ciliated chaetae on the base of manubrium smaller and on distal region larger, subapical region with 7+7 long ciliated chaetae in a transversal line; manubrial plate with 2+2 setae and 1+1 pseudopores (Figs 60–61). Both faces of manubrium with scales (Fig. 60). Base of the dens not subdivided, with 1+1 erect smooth chaetae; dental plate with 5+5 ciliated chaetae, lobe and spines absent. Complete chaetotaxy of manubrium and dens basal region in Figs 60 and 61. Mucro bidentate with a basal spine slightly surpassing the apex of the second tooth of mucro (Fig. 62).

Etymology. The new species is named after the beloved future wife of the first author, Ana Carolina Santos Xavier.

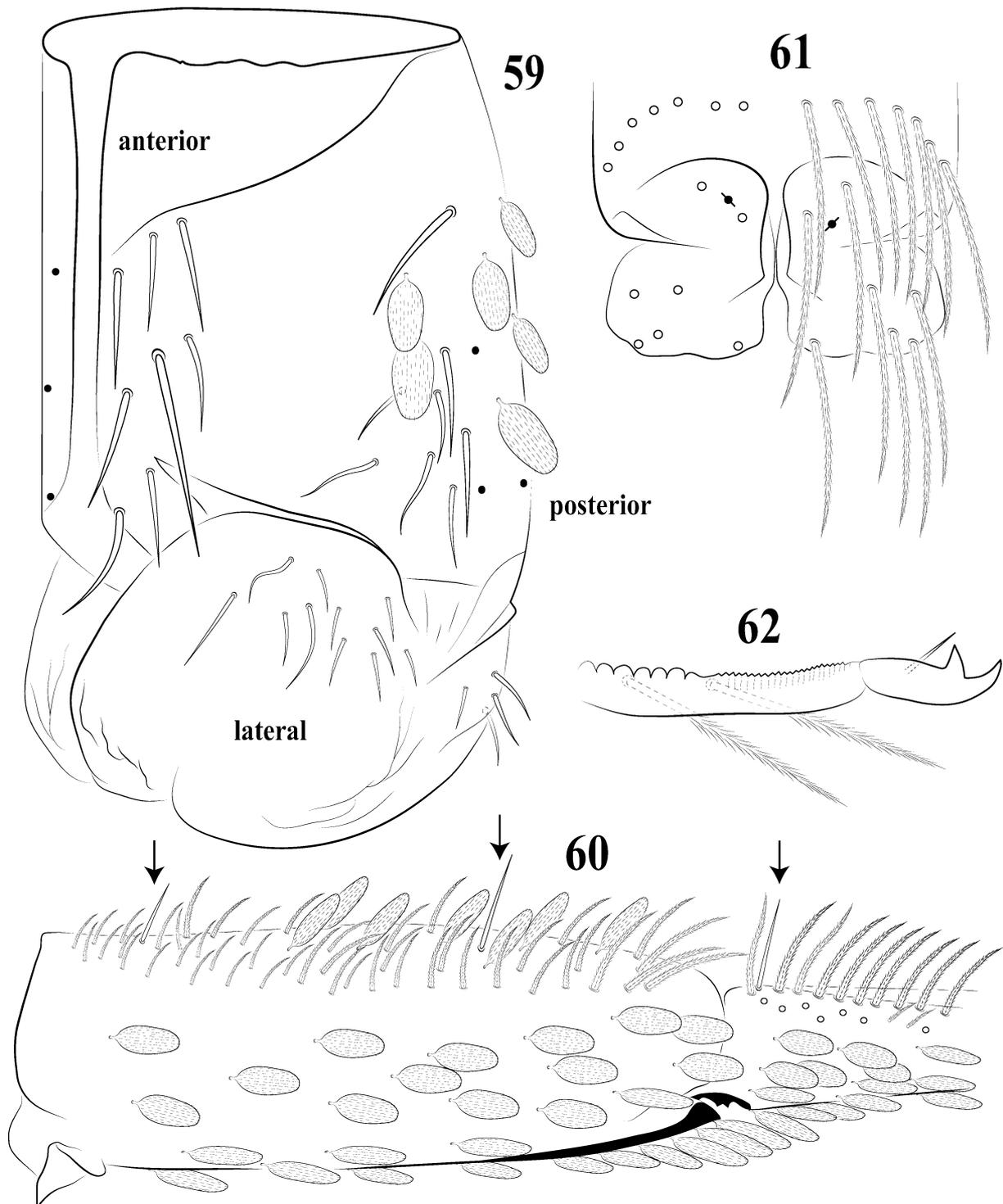
Distribution and habitat. The specimens were collected in hemiedaphic environments, a few centimeters into the soil of different areas of "Reserva Ducke", an forested area of Brazilian Amazon Forest, Amazonian Phytogeographic Domain, Neotropical Region. The site is located in Amazonas State and fits Good's biogeographic zone 26 (Good 1974). The climate of the area following the Köppen-Geiger system is "Am" tropical wet (or monsoon) climate, characterized by wet and dry seasons (Kottek *et al.* 2006). The new species represents the first record of *Heteromurtrella* in Brazil.

Remarks. *Heteromurtrella anae* **sp. nov.** resembles other species such *H. pruinosa* Mari Mutt from Venezuela, *H. puertoricensis* Mari Mutt from Puerto Rico, and *H. subdubia* (Barra) from Gabon, Africa, by absence of body pigment, 2+2 eyes, tibiotarsi without smooth setae rows, manubrium with two smooth rows of chaetae, and Abd I chaetotaxy with 3+3 mac (m2–4). However *H. anae* **sp. nov.** differs from these species by the presence of black pigment on eyepatches (absent in other species); head 'A' series with 6 mac (less in other species); head 'S' series

without S0 macand ‘M’ series without mac (present in other species); Th II with 14+14 mac (13+13 or less in other species); Th II with a2p? mac (absent in other species); Th III always with p1 mac (sometimes absent in *H. pruinosa*); unguis with one unpaired teeth (absent in *H. pruinosa*); manubrium dorsally with 2+2 smooth chaetae (4+4 in *H. puertoricensis* and *H. subdubia*).

The coxal chaetotaxy pattern and differentiated mac in Ant II of *H. anae* **sp. nov.** are also present respectively in *H. puertoricensis* and *H. nitens* (see Yosii 1964, pg. 15) and should be investigated in other species as they could be generic diagnostic characteristics.

Other morphological differences between *Heteromurtrella* species are provided in Table 2.



FIGURES 59–62. *Heteromurtrella anae* **sp. nov.**: **59**, colophore chaetotaxy; **60**, manubrium and dental base; **61**, manubrial plate and dental base; **62**, distal dens and mucro.

Identification key for species of *Heteromurtrella*

- 1 Eyes absent *H. caeca* (Najt, Thibaud & Mari Mutt, 1988)
 - Eyes present 2
 2 Dental spines absent (Figs 15, 17) 3
 - Dental spines present (Figs 15, 17) 19
 3 Eyes 1+1 or 2+2 4
 - Eyes 6+6 *H. abrupta* (Salmon, 1951)
 4 Eyes 1+1 5
 - Eyes 2+2 7
 5 Unguis without unpaired teeth (Fig. 14); manubrium dorsally with 4+4 smooth chaetae 6
 - Unguis with one medial unpaired tooth; manubrium dorsally with 5+5 smooth chaetae *H. nitens* (Yosii, 1964)
 6 Th II with 6+6 posterior mac, p1p absent; Abd IV with 1+1 central mac (A6) (Fig. 12) *H. affinis* (Mari Mutt, 1987)
 - Th II with 7+7 posterior mac, p1p present; Abd IV with 2+2 central mac (A3 and A6) (Fig. 12)
 *H. greensladeae* (Mari Mutt, 1987)
 7 Body pigments totally absent, or restricted to eyepatches, or restricted to anterior portion of head and antennae; or if diffused throughout head and body it is very light and visible only under magnification 8
 - Body pigment clearly 18
 8 Abd I with 1+1 or 2+2 mac (m2–3) (Fig. 12) 9
 - Abd I with 3+3 mac (m2–4) (Fig. 12) 11
 9 Abd I with 1+1 mac (m2) (Fig. 12) *H. mirifica* (Salmon, 1954)
 - Abd I with 2+2 mac (m2–m3) (Fig. 12) 10
 10 Head without S0 and Pm3 mac, head ‘M’ series with 3+3 mac (M1–3); Th III with 4+4 mac (a5, p1–3); Abd III com 2+2 lateral mac (pm6 and p6); Abd IV 2+2 central mac (A3 and A6) (Figs 8, 12) *H. similis* (Barra, 1968)
 - Head with S0 and Pm3 mac, head medial series without mac; Th III with 6+6 mac (a2, a4–5, p1–3); Abd III com 1+1 lateral mac (pm6); Abd IV 1+1 central mac (A3) (Figs 8, 12) *H. stannardi* (Mari Mutt, 1976)
 11 Abd IV 1+1 central mac (A3); manubrium with 1+1 dorsal smooth chaetae (Fig. 12) *H. barrai* (Mari Mutt, 1979)
 - Abd IV 2+2 central mac (A3 and A6) or more; manubrium with 2+2 dorsal smooth chaetae or more (Fig. 12) 12
 12 Manubrium with 2+2 dorsal smooth chaetae (Fig. 60) 13
 - Manubrium with 4+4 dorsal smooth chaetae 15
 13 Head without S0 mac, head ‘A’ series with 6+6 mac and ‘M’ series without mac; Th II with 14 mac (Figs 8, 12, 30)
 *H. anae* **sp. nov.** Cipola
 - Head with S0 mac, head ‘A’ series with 4+4 mac; Th II with 12 mac or less (Figs 8, 12) 14
 14 Head ‘M’ series with 3+3 mac (M1–3); Abd IV with 2+2 central mac and 5+5 lateral mac; unguiculi with outer tooth (Figs 8, 12, 14) *H. zairensis* **comb. nov.** (Tshelnokov, 1977)
 - Head ‘M’ series with 2+2 mac (M1–2); Abd IV with 3+3 central mac and 3+3 lateral mac; unguiculi without outer tooth (Figs 8, 12, 14) *H. pruinosa* (Mari Mutt, 1983)
 15 Th II with 11 mac; tibiotarsi with smooth rows of chaetae (Fig. 12) *H. dubia* (Delamare Deboutteville, 1952)
 - Th II with 12–13 mac; tibiotarsi without smooth chaetae (Fig. 12) 16
 16 Head ‘M’ series without mac; Abd II without lateral mac (Figs 8, 12) *H. schoetti* (Denis, 1931)
 - Head ‘M’ series with 3+3 mac (M1–3); Abd II with 1+1 lateral mac (m5) (Figs 8, 12) 17
 17 Head ‘A’ series with 4+4 mac (A0, A2–A4), A0 present; Th II with 12+12 mac (Figs 8, 12)
 *H. puertoricensis* (Mari Mutt, 1979)
 - Head ‘A’ series with 3+3 mac (A2–A4), A0 absent; Th II with 13+13 mac (Figs 8, 12) *H. subdubia* (Barra, 1968)
 18 Unguis with one unpaired tooth (Fig. 14) *H. diommata* (Denis, 1931)
 - Unguis without unpaired teeth (Fig. 14) *H. livida* (Salmon, 1954)
 19 Abd IV with 3+3 lateral mac (D3, E2 and F1); unguiculi without outer teeth; dental base with 1+1 smooth chaetae and 2+2 spines (Figs 12, 14–15) *H. echinata* (Mari Mutt, 1983)*
 - Abd IV with 4+4 lateral mac (D3, E2, E3 and F1); unguiculi with outer teeth; dental base with 2+2 smooth chaetae and without spines (Figs 12, 14–15) *H. tihuiensis* (Mari Mutt, 1985)

* Absence of dental spines in *H. echinata* was not considered as a key character since it only occurs in juveniles (see Mari Mutt 1983)

Discussion

The taxonomic status and diagnoses of the six Heteromurini genera presented here were vague in some points, and therefore it was necessary to improve the diagnosis of the tribe and its genera. According to Mari Mutt (1980a), Heteromurini species are characterized by the presence of dark scales, although species such as *H. anae* **sp. nov.** (Figs 23–28) and *A. tetracanthus* (Yosii 1959, pg. 38) bear hyaline scales. Therefore the coloration of scales should

not be taken as a diagnostic character to the Heteromurini. In the other hand the sculpturing of the scales is a characteristic that can possibly be useful to determine the groups of Entomobryidae (Zhang *et al.* 2014). In *Heteromurtrella* the scales can be strongly striated with unaligned rows of stria; or moderately striated with aligned rows of stria (Figs 23–28). This condition is similarly seen in other genera of the tribe and should be investigated due to its potential as a diagnostic feature (see Mari Mutt 1976, 1979a; Zhang *et al.* 2014, pg. 232).

Although the relationship between Heteromurini genera is uncertain, the generic level of taxa was supported using the new detailed diagnoses herein provided. In this context the dorsal chaetotaxy within the tribe create two distinct groups: *Dicranocentrus* and *Pseudodicranocentrus* with abundant macrochaetae and antennae with 6 segments; and *Heteromurus*, *Alloscopus*, *Heteromurtrella* and *Verhoeffiella* with reduction of macrochaetae and antennae with 5 segments (Mari Mutt 1977, 1979a, 1979b, 1980b, 1981b).

Among this second group, *Heteromurus* and *Verhoeffiella* species are the most similar with each other by reduction on some mac as S0 and Pa2 in the head, Th III with up to 4 mac, and Abd I without mac (Mari Mutt, 1985b). Both genera are currently distinguished especially by presence of annulations on Ant III (absent in *Heteromurus*), and *Verhoeffiella* species as cave-dweller organisms (Mari Mutt 1980a, 1980b), although further characteristics presented in Table 1 can also help to correctly identify the genera. We believe this non chaetotaxic characters could be expected troglomorphies and could obscure the real relationships between the two genera. Due to the absence of detailed dorsal chaetotaxy of most species of *Heteromurus* and *Verhoeffiella* a further a review is in need to elucidate their relationships with each other and the other Heteromurini (Bonet 1931, Salmon 1964, Nosek & Paoletti 1985, Lučić *et al.* 2007b, 2008).

From now additional chaetotaxic characters (Figs 11–12) can be used to distinguish *Heteromurus* from other similar genera such as: lack of 5 mac in Th II (m4, m4i, m4p, p1p and p5); 4 mac in Th III (a5, p1–3); Abd I without mac; m5 and A6 mac absent in Abd II and Abd IV respectively (present in *Alloscopus* and *Heteromurtrella*), and Abd III with one distinctive mac (m3e) (Mari Mutt 1980b).

The absence of head macrochaeta S0 was pointed as an exclusive characteristic of *Heteromurus* (Mari Mutt 1980b) but it is also absent in some species of *Heteromurtrella*, such as *H. anae* **sp. nov.** and *H. similis*. According to our revision Abd I macrochaetae distribution is the main characteristic to distinguish *Heteromurus* (absent) to *Heteromurtrella* (present) (Tab. 1 and 3). In the same sense the presence of dorsal spines in dens is not exclusive of *Alloscopus* as it is also present in *Heteromurtrella* as *H. echinata* and *H. tihuiensis*, so the presence of PAO and reduction of head postoccipital macrochaetae (Pa2, Pa3, Pm3 and Pp5) in *Alloscopus* is the main characteristic to distinguish it from other genera (Tabs 1–3).

Concerning chaetotaxy, other features can be used to separate Heteromurini genera. The labial chaetotaxy also distinguishes *Heteromurtrella* from *Alloscopus*, by posterior row with reduction of scales, r chaeta always present, E chaeta always smooth and M2 seta ciliated (Figs 20–21). The dorsal chaetotaxy separates *Heteromurtrella* from *Alloscopus* by presence of exclusive macrochaetae in *Heteromurtrella* as Th II with p2p mac, Th III with p2e mac, and Abd IV with 3+3 central mac (Ai3, B5 and B6) (Figs 11–12; Tab. 2 and 3). Also 11 macrochaetae may be present or absent only in *Heteromurtrella*: 5 in Th II (a5, m4i, m4p, p3 and p5), 4 in Th III (a2, a4, p1 and p3), and 2 in Abd I (m3–4), while in *Alloscopus* these macrochaetae are always present. *Heteromurtrella* also has six exclusive macrochaetae: 2 in Th II (a2p? and p2p), 1 in Th III (p2e), and 3 in Abd IV (Ai3, B5 and B6?), while *Alloscopus* only am6 mac on Abd III (Figs 11–12). On the other side 10 macrochaetae are invariable and shared among *Alloscopus* and *Heteromurtrella*, 4 in Th II (m4, p1, p2 and p2e), p2 and a5 in Th II, m2 in Abd I, m3 in Abd II, and m3 and pm6 in Abd III.

The dorsal chaetotaxy observed in Heteromurini indicate possible 22 homologous chaetae (most primary) that can be used in as diagnostic of the tribe as: head always with sutural 6+6 mac (S1, S3, S4, S5, S6 and S7), S6 and S7 always together; postoccipital series usually with at least Pa5 mac; Th II usually with 7+7 central mac (m1, m2, p1, p2, p2e, p3 and p3p); Th III with 2+2 mac (a4 and a5) always together; Abd I with at least 3+3 mac (m2, m3 and m4); Abd II–III usually with m3 mac, and Abd IV with at least A3 mac (Figs 8, 11–12) (Mari Mutt 1977, 1979a, 1979b, 1980b, 1981b).

Finally our review provides new numbers of species in different taxa of Heteromurini. Now *Heteromurus* has 17, *Alloscopus* 10 and *Heteromurtrella* 20 valid species.

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References

- Absolon, K. (1900) Über zwei neue Collembolen aus den Höhlen des österreichischen Occupationsgebietes. *Zoologischer Anzeiger Band*, 23 (9), 427–431.
- Absolon, K. (1901) Beiträge zur Kenntniss der mährischen Höhlenfauna. *Verhandlungen des naturforschenden Vereines in Brünn*, 39, 6–14 & 1 pl.
- Absolon, K. & Ksenemann, M. (1942) Troglopedetini. Vergleichende Studie über eine altertümliche höhlenbewohnende Kollembolengruppe aus den dinarischen Karstgebieten., *Studien aus dem Gebiete der allgemeinen Karstforschung, der wissenschaftlichen Höhlenkunde, der Eiszeitforschung und den Nachbargebieten*, 16, 5–57.
- Barra, J.A. (1968) Contribution a l'étude du genre *Heteromurus* Wankel, 1860 (Collemboles). *Biologia Gabonica*, 4, 104–107.
- Bellinger, P.F., Christiansen, K.A. & Janssens, F. (1996–2015) Checklist of the Collembola of the World. Available from: <http://www.collembola.org> (accessed 1 May 2015)
- Bellinger, P.F. & Ellis, W.N. (1972) *Ptenura* Templeton, 1844 (Insecta, Collembola): proposed suppression under the plenay powers. *Z.N.(S.) 2000. Bulletin of Zoological Nomenclature*, 29 (4), 212–214.
- Bellini, B.C. (2014) Fauna de Collembola (Arthropoda) em áreas úmidas do semiárido. In: Bravo, F. & Calor, A. (Org.), *Artrópodes do Semiárido, Biodiversidade e Conservação. 1st Edition*. Feira de Santana Printmídia, Feira de Santana, pp. 57–68.
- Bellini, B.C., Morais, J.W. & Oliveira, F.G.L. (2013) A new species of *Dicranocentrus* Schött (Collembola, Entomobryidae, Orchesellinae) from Brazilian Amazon. *Zootaxa*, 3709 (3), 296–300. <http://dx.doi.org/10.11646/zootaxa.3709.3.8>
- Börner, C. (1901) Zur Kenntnis der Apterygoten-Fauna von Bremen und der Nachbardistrikte: Beitrag zu einer Apterygoten-Fauna Mitteleuropas. *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen*, 17 (1), 1–140.
- Börner, C. (1906) Das System der Collembolen nebst Beschreibung neuer Collembolen des Hamburger Naturhistorischen Museums. *Mitteilungen aus den Naturhistorischen Museum in Hamburg*, 23, 147–188.
- Bonet, F. (1931) Estudios sobre colémbolos cavernícolas con especial referencia a los de la fauna Española. *Memorias de la Sociedad Española de Historia Natural*, 14, 231–403.
- Delamare-Deboutteville, C. (1952) Étude systématique. I. Collemboles. In: Delamare-Deboutteville, C. & Paulian, R. (Eds.), *Faune des nids et des terriers en Basse Côte d'Ivoire. Encyclopédie Biogéographique et Écologique*, 8, pp. 62–77.
- Denis, J.R. (1931) Contributo alla conoscenza del "microgenton" di Costa Rica. II. Collemboles de Costa Rica avec une contribution au species de l'ordre. *Bollettino. R. Laboratorio Entom. Agrario di Portici*, 25, 69–170.
- Denis, J.R. (1933) Contributo alla conoscenza del "microgenton" di Costa Rica. III. Collemboles de Costa Rica avec une contribution au species de l'ordre (deuxieme note). *Bollettino. R. Laboratorio Entom. Agrario di Portici*, 27, 222–322.
- Denis, J.R. (1937) Sur les Collemboles d'Afrique du Nord. *Bulletin Society History African North, Algiers*, 28, 85–87.
- Fjellberg, A. (1999) The Labial Palp in Collembola. *Zoologischer Anzeiger*, 237, 309–330.
- Gisin, H. (1960) *Collembolenfauna Europas*. Museum d'Histoire Naturelle, Genève, 312 pp.
- Gisin, H. (1964) Collemboles d'Europe. VII. *Revue Suisse de Zoologie*, 71 (36), 649–678.
- Good, R. (1974) *The geography of flowering plants. 4th Edition*. Longman Group, London, 574 pp.
- Handschin, E. (1925) Beiträge zur Collembolenfauna der Sundainseln. *Treubia*, 6 (3–4), 225–70.
- Handschin, E. (1928) Collembolen aus Java, nebst einem Beitrag zu einer Monographie der Gattung *Cremastocephalus* Schött. *Treubia*, 19 (2–3), 245–270.
- Hopkin, S.P. (1997) *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, Oxford, 330 pp.
- Imms, A.D. (1912) On some Collembola from India, Burma, and Ceylon, with a Catalogue of the Oriental Species of the Order. *Proceedings of the Zoological Society of London*, 82, 80–125. <http://dx.doi.org/10.1111/j.1469-7998.1912.tb07006.x>
- Izarra, D.C. (1972) *Alloscopus platensis*, una nueva especie de La Plata, Provincia de Buenos Aires, *Physis*, 31 (83), 537–39.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, 15, 259–263. <http://dx.doi.org/10.1127/0941-2948/2006/0130>
- Liu, Y. & Li, Z. (1999) A new subgenus and a new species of the genus *Heteromurus* in China (Collembola Entomobryidae). *Xinan Nongye Daxue Xuebao*, 21 (3), 248–250.
- Loksa, I. & Bogojevic, L. (1967) Einige neue Collembolenarten aus Jugoslawien. *Acta Zoologica Sciences Hungarica*, 13 (1–

2), 139-148.

- Lubbock, J. (1862) Notes on the Thysanura – Part II. Smythuridae. *Transactions of the Linnean Society of London*, 23, 589–601.
<http://dx.doi.org/10.1111/j.1096-3642.1860.tb00149.x>
- Lučić, L.R., Ćurčić, B.P.M., Mitić, B.M. & Ćurčić, S.B. (2002) On the biodiversity of Apterygota in FR Yugoslavia: *Heteromurus uzicensis* n. sp. (Collembola, Entomobryidae). *Archives of Biological Sciences, Belgrade*, 54 (3–4), 125–128.
<http://dx.doi.org/10.2298/ABS0204125L>
- Lučić, L.R., Ćurčić, B.P.M. & Mitić, B.M. (2007a) A new endemic cave springtail from the former Yugoslav Republic of Macedonia - *Heteromurus (Heteromurus) constantinellus* n.sp. (Collembola, Entomobryidae). *Archives of Biological Sciences, Belgrade*, 59 (4), 67–68.
<http://dx.doi.org/10.2298/ABS0704067L>
- Lučić, L.R., Ćurčić, B.P.M. & Tomić, V.T. (2007b) *Heteromurus (Verhoeffiella) constantius*, n. sp. (Collembola, Entomobryidae), from a cave in Herzegovina. *Archives of Biological Sciences, Belgrade*, 59 (4), 71–72.
<http://dx.doi.org/10.2298/ABS0704071L>
- Lučić, L.R., Tomić, V.T., Brajković, M.M. & Ćurčić, S.B. (2008) *Heteromurus (Verhoeffiella) anagastumensis* n. sp. (Collembola, Entomobryidae), a new cave springtail from Montenegro. *Archives of Biological Sciences, Belgrade*, 60 (2), 297–300.
<http://dx.doi.org/10.2298/ABS0802297L>
- Lukić, M., Porco, D., Bedos, A. & Deharveng, L. (2015) The puzzling distribution of *Heteromurus (Verhoeffiella) absoloni* Kseneman, 1938 (Collembola: Entomobryidae: Heteromurinae) resolved: detailed redescription of the nominal species and description of a new species from Catalonia (Spain). *Zootaxa*, 4039 (2), 249–275.
<http://dx.doi.org/10.11646/zootaxa.4039.2.3>
- Mari-Mutt, J.A. (1976) A new species of *Heteromurus* from the Solomon Islands (Collembola: Entomobryidae). *The Pan-Pacific Entomologist*, 52, 326–330.
- Mari-Mutt, J.A. (1977) The taxonomic status of *Alloscopus* and redescription of its two species. *The Pan-Pacific Entomologist*, 53 (4), 241–249.
- Mari-Mutt, J.A. (1979a) A revision of the genus *Dicranocentrus* Schött (Insecta: Collembola: Entomobryidae). *Agricultural Experiment Station Bulletin*, 259, 1–79.
- Mari-Mutt, J.A. (1979b) *Heteromurtrella*, a new tropical subgenus of *Heteromurus* with descriptions of two new species (Insecta: Collembola: Entomobryidae). *The Journal of Agriculture of the University of Puerto Rico*, 63 (2), 214–222.
- Mari-Mutt, J.A. (1980a) A classification of the Orchesellinae with a key to tribes, genera and subgenera (Collembola: Entomobryidae). *Annals of the Entomological Society of America*, 73 (4), 455–459.
<http://dx.doi.org/10.1093/aesa/73.4.455>
- Mari-Mutt, J.A. (1980b) A Revision of *Heteromurus* s. str. (Insecta: Collembola: Entomobryidae). *Transactions of the Illinois State Academy of Science*, 72 (3), 29–50.
- Mari-Mutt, J.A. (1980c) Descriptive notes for nine species of *Heteromurus* (s.g. *Heteromurtrella*) and a key to the species (Collembola: Entomobryidae). *The Pan-Pacific Entomologist*, 56 (1), 11–25.
- Mari-Mutt, J.A. (1981a) A new species and complements to the descriptions of nine African or Oriental *Dicranocentrus* (Collembola: Entomobryidae). *The Journal of Agriculture of the University of Puerto Rico*, 65 (2), 160–170.
- Mari-Mutt, J.A. (1981b) New genus, a new species, and complements to the descriptions of seven Neotropical *Dicranocentrus* (Collembola: Entomobryidae: Orchesellinae). *The Journal of Agriculture of the University of Puerto Rico*, 65 (2), 90–107.
- Mari-Mutt, J.A. (1982) A new species of *Heteromurus (Alloscopus)* from Papua New Guinea and descriptive notes for the other species of the subgenus (Collembola: Entomobryidae: Orchesellinae). *Pacific Insects*, 24 (1), 84–94.
- Mari-Mutt, J.A. (1983) Four new species of *Dicranocentrus* and *Heteromurus* from the State of Mérida, Venezuela (Collembola: Entomobryidae). *Journal of Agriculture of the University of Puerto Rico*, 67 (2), 148–164.
- Mari-Mutt, J.A. (1984) Five new species of Orchesellini from Central Mexico (Collembola: Entomobryidae: Orchesellinae). *Proceedings of the Entomological Society of Washington*, 86 (4), 808–820.
- Mari-Mutt, J.A. (1985a) A new species of *Heteromurus* from Puerto Rico (Collembola: Entomobryidae). *Entomological News*, 96 (4), 145–147.
- Mari-Mutt, J.A. (1985b) Contribución al conocimiento de tres especies de Orchesellinae descritas por F. Bonet y redescipción de *Orchesellides sinensis* (Denis) (Collembola). *Eos*, 61, 189–198.
- Mari-Mutt, J.A. (1985c) Eight new species of *Dicranocentrus* and redescipciones for *D. thaicus* and *D. pilosus* (Collembola: Entomobryidae: Orchesellinae). *Journal of Agriculture of the University of Puerto Rico*, 69 (3), 297–322.
- Mari-Mutt, J.A. (1985d) Three new species of *Heteromurus (Alloscopus)* and descriptive notes for species of the subgenus (Collembola: Entomobryidae). *The Florida Entomologist*, 68 (2), 335–346.
<http://dx.doi.org/10.2307/3494370>
- Mari-Mutt, J.A. (1987) Two new species of *Heteromurus* from Sulawesi Utara (Celebes) and a new record for *H. tenuicornis* Börner (Collembola: Entomobryidae). *Journal of the New York Entomological Society*, 95 (4), 572–576.
- Mari-Mutt, J.A. (1988) A new *Dicranocentrus* from Thailand, redescription of *D. fasciatus* Yosii and records for two other species of Orchesellinae (Collembola: Entomobryidae). *Journal of the Kansas Entomological Society*, 61 (2), 179–185.
- Mari-Mutt, J.A. & Bhattacharjee, R.K. (1980) Four new species of *Dicranocentrus* from northeast India and Nepal (Collembola: Entomobryidae: Orchesellinae). *Pacific Insects*, 22 (1–2), 162–170.
- Mari-Mutt, J.A. & Stomp, N. (1980) Two new species of *Heteromurus* s. str. from Portugal and Romania (Insecta, Collembola,

- Entomobryidae). *Archives d' Institut Grand-Ducal de Luxembourg, Section des Sciences naturelles, physiques et mathématiques*, 38, 183–189.
- Martynova, E.F., Chelnokov, V.G & Rasulova, Z.K. (1974) Species of the genus *Heteromurus* Wankel, 1860 (Collembola, Entomobryidae, s. l.) in the USSR fauna. *Vestnik Zoologii*, 2, 66–71.
- Moniez, R. (1899) Notes sur les Thysanoures – I: Espèces qui vivent aux Açores. *Revue Biologique du Nord de la France*, 2, 24–31.
- Najt, J., Thibaud, J.-M. & Mari-Mutt, J.A. (1988) Collemboles (Insecta) de l'Équateur, III. Entomobryidae : Orchesellinae. *Bulletin du Muséum National d'Histoire Naturelle*, 4 (3), 553–561.
- Nosek, J. & Paoletti, M.G. (1985) *Heteromurus (Verhoeffiella) dallaii* sp. n. a new cave-dwelling springtail (Collembola: Entomobryidae). *Revue suisse Zoologie*, 92, 271–274.
<http://dx.doi.org/10.5962/bhl.part.81615>
- Prabhoo, N.R. (1971) Soil and litter collembola of South India. *Oriental insects*, 5, 1–46.
<http://dx.doi.org/10.1080/00305316.1971.10433988>
- Salmom, J.T. (1942) New genera and species of New Zealand Collembola. *Records of the Dominion Museum*, 1, 55–60 & 2 pls.
- Salmon, J.T. (1951) Some Collembola from Malaya. *Proceedings of the Royal Society of London*, 20 (11–12), 131–141.
<http://dx.doi.org/10.1111/j.1365-3113.1951.tb01010.x>
- Salmon, J.T. (1954) Orchesellini (Collembola) from East Africa. *Annals & Magazine of Natural History*, 12 (7), 122–127.
<http://dx.doi.org/10.1080/00222935408651704>
- Salmon, J.T. (1964) An Index to the Collembola. *Bulletin of the Royal Society of New Zealand*, 7 (1–2), 1–644.
- Schött, H. (1893) Beiträge zur Kenntnis der Insektenfauna von Kamerun. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 19, 5–28.
- Soto-Adames, F.N. (2008) Postembryonic development of the dorsal chaetotaxy in *Seira dowlingi* (Collembola, Entomobryidae); with an analysis of the diagnostic and phylogenetic significance of primary chaetotaxy in *Seira*. *Zootaxa*, 1683, 1–31.
- Soto-Adames, F.N., Barra, J.A., Christiansen, K. & Jordana, R. (2008) Suprageneric Classification of the Entomobryomorph Collembola. *Annals of the Entomological Society of America*, 101 (3), 501–513.
[http://dx.doi.org/10.1603/0013-8746\(2008\)101\[501:SCOCE\]2.0.CO;2](http://dx.doi.org/10.1603/0013-8746(2008)101[501:SCOCE]2.0.CO;2)
- Suhardjono, Y.R. (1989) Revised check list of Collembola from Indonesia and its adjacent Regions. *Acta Zoologica Asiae Orientalis*, 1, 1–22.
- Szeptycki, A. (1979) *Chaetotaxy of the Entomobryidae and its phylogenetical significance. Morpho-systematic studies on Collembola. IV.* Polska Akademia Nauk, Zakład Zoologii Systematycznej i Doświadczalnej, Państwowe Wydawnictwo Naukowe, Warszawa, Kraków, 219 pp.
- Theobald, F.V. (1911) Springtails (Collembola). Their economic importance with notes on some unrecorded instances of damage. *Ier Congrès International D'Entomologie, Bruxelles Memoires*, 2, 1–18.
- Thibaud, J.-M. & Massoud, Z. (1973) Essai de classification des Insectes Collemboles cavernicoles européens. *Comptes Rendus Academie Sciences*, 277, 2137–2140.
- Tömösvary, O. (1882) Adatok hazánk Thysanura-Faunájához. *A Magyar Tudományos Akadémia Matematikai és Természettudományi Közlemények*, 18, 1–131.
- Tshelnokov, V.G. (1977) Some new and little known species of Collembola in the fauna of equatorial Africa. In: Skarlato, O.A., Kryzhanovskii, O.L. & Galkin, A.K. (Eds.), *Systematics and faunistics of insects*. Akademiya Nauk SSSR, Leningrad, pp. 103–112. [in Russian]
- Uchida, H. (1944) Collembola von Mikronesien. *Bulletin of the Tokyo Science Museum*, 74, 1–23.
- Wankel, H. (1860) Beiträge zur fauna der Mährischen Höhlen. *Lotos*, Prague, 10, 201–206.
- Winter, C. (1963) Zur Ökologie und taxonomie der neotropischen Bodentiere. II. Zur Collembolenfauna Perus. *Zoologische Jahrbücher Jena*, 90, 393–520.
- Winter, C. (1966) Beiträge zur Kenntnis der neotropischen Collembolenfauna. *Entomological Zeitung*, 76, 165–169.
- Xu, G.-L. & Zhang, F. (2014) A new species of *Dicranocentrus* from China with comments on the systematic position of the genus. *ZooKeys*, 417, 1–8.
<http://dx.doi.org/10.3897/zookeys.417.7373>
- Yoshii, R. & Suhardjono, Y.R. (1989) Notes on the Collembolan Fauna of Indonesia and its vicinities. I. Miscellaneous Notes, with special references to Seirini and Lepidocyrtini. *Acta Zoologica Asiae Orientalis*, 1, 23–90.
- Yoshii, R. & Suhardjono, Y.R. (1992) Notes on the Collembolan Fauna of Indonesia and its Vicinities. II. Collembola of Irian Jaya and Maluku Islands. *Acta Zoologica Asiae Orientalis*, 2, 1–52.
- Yosii, R. (1959) Studies on the Collembolan Fauna of Malay and Singapore with special reference to the Genera: *Lobella*, *Lepidocyrtus* and *Callyntrura*. *Contributions from the Biological Laboratory Kyoto University*, 10, 1–65.
- Yosii, R. (1964) Some Collembola of the Tonga Islands. *Kontyû*, 32 (1), 9–17.
- Zhang, F. & Deharveng, L. (2015) Systematic revision of Entomobryidae (Collembola) by integrating molecular and new morphological evidence. *Zoologica Scripta*, 44, 298–311.
<http://dx.doi.org/10.1111/zsc.12100>
- Zhang, F., Chen, Z., Dong, R.-R., Deharveng, L., Stevens, M.I., Huang, Y.-H. & Zhu, C.-D. (2014) Molecular phylogeny reveals independent origins of body scales in Entomobryidae (Hexapoda: Collembola). *Molecular Phylogenetics and Evolution*, 70, 231–239.
<http://dx.doi.org/10.1016/j.ympev.2013.09.024>