

Checklist of the *Clubiona japonica*-group spiders, with the description of a new species from China (Araneae, Clubionidae)

Hao Yu^{1,3}, Jianshuang Zhang², Jian Chen³

1 College of Chemistry and Life Sciences, Integrated Mountain Research Institute, Guizhou Education University, Guiyang, Guizhou, China **2** School of Life Sciences, Guizhou Normal University, Guiyang, Guizhou, China **3** Centre for Behavioural Ecology and Evolution (CBEE), College of Life Sciences, Hubei University, Wuhan, Hubei, China

Corresponding authors: Hao Yu (insect1986@126.com); Jian Chen (chen.jian_hb@foxmail.com)

Academic editor: Cor Vink | Received 22 June 2017 | Accepted 18 October 2017 | Published 9 November 2017

<http://zoobank.org/9873F0E2-011F-4EDE-AB64-B9F56BFAE9AC>

Citation: Yu H, Zhang J, Chen J (2017) Checklist of the *Clubiona japonica*-group spiders, with the description of a new species from China (Araneae, Clubionidae). ZooKeys 715: 1–16. <https://doi.org/10.3897/zookeys.715.14645>

Abstract

In the present paper, a worldwide checklist of *Clubiona japonica*-group spiders is provided based on published literature and authors' collections. A new *japonica*-group species, *Clubiona grucollaris* **sp. n.** (♀♂) from Guizhou Province and Hainan Island of China is diagnosed, described, and illustrated. A distribution map of this species is given.

Keywords

catalogue, *Japoniona*, Sac spiders, taxonomy

Introduction

The genus *Clubiona* Latreille, 1804 contains 495 catalogued species and is widespread throughout most of the tropics and temperate regions of the world (World Spider Catalog 2017). Due to the high species diversity of *Clubiona*, several infrageneric classifications have been proposed by taxonomists, and therefore *Clubiona* species were assigned to a series of species-groups and/or subgenera (Simon 1932; Gertsch 1941;

Lohmander 1944; Edwards 1958; Dondale and Redner 1976, 1982; Mikhailov 1990, 1991, 1995, 2002; Deeleman-Reinhold 2001; Wunderlich 2011).

Japoniona was established as a subgenus by Mikhailov (1990), including only one species-group: *japonica*-group. Later, the subgenus *Japoniona* was suppressed by Deeleman-Reinhold (2001) and reverted to *japonica* species-group. In the same book, Deeleman-Reinhold (2001) carried out intensive research on this group's limits, supplemented some characters to support the monophyly of the group, and provided a checklist of *C. japonica*-group species from Southeast Asia. During the past decade, at least nine species belonging to the *japonica* species-group were reported and described from southeast Asia, China, and India (Dankittipakul and Singtripop 2008; Jäger and Dankittipakul 2010; Dankittipakul et al. 2012; Keswani and Vankhede 2014; Wu and Zhang 2014). However, a few other known species are not assigned, although they exhibit typical *japonica*-group features. The first goal of this paper is to provide a checklist as complete as possible of the current *japonica*-group species.

Various field collections in Guizhou Province, China were carried out by the colleagues of Hubei University in 2014 and 2016. Four males and 20 females were collected in these field explorations, among which one pair were captured during mating; thus, they are conspecific. Additionally, one male collected from Hainan Island was examined, and no differences from the Guizhou specimens were observed. All specimens possess certain characters associated with the *japonica*-group, but can be easily distinguished from the other *japonica*-group species. This species is new to science and is described under the name of *Clubiona grucollaris* sp. n.

Materials and methods

The checklist is based on an examination of specimens deposited in the "Centre for Behavioural Ecology and Evolution" (CBEE) and reviews of the published literature, including several recent world catalogues of spiders (Lin and Li 2016; World Spider Catalog 2017).

Spiders were fixed and preserved in 80% ethanol. Specimens were examined with an Olympus SZX7 stereomicroscope; details were studied with an Olympus BX51 compound microscope. Male palps and female epigynes were examined and illustrated after being dissected. Spermathecae were cleared in boiling KOH solution to dissolve soft tissues. Photos were made with a Cannon EOS70D digital camera mounted on an Olympus BX51 compound microscope. The digital images were taken and assembled using Helifocus 3.10 software package. The drawings were made using an Olympus drawing tube. Most of the hairs and macrosetae are not depicted in the palp and epigyne images.

All measurements were obtained using an Olympus SZX7 stereomicroscope and given in millimetres. Eye diameters are taken at widest point. The total body length does not include chelicerae or spinnerets length. Leg lengths are given as total length (femur, patella + tibia, metatarsus, tarsus). The type specimens of the new species are

deposited in College of Chemistry and Life Sciences, Guizhou Education University, Guiyang, Guizhou, China

Abbreviations used are:

A	epigynal atrium;	MOQL	length of MOQ;
AER	anterior eye row;	MOQA	MOQ anterior width;
ALE	anterior lateral eyes;	MOQP	MOQ posterior width;
AM	atrial margin;	PER	posterior eye row;
AME	anterior median eyes;	PLE	posterior lateral eyes;
AME–AME	distance between AMEs;	PME	posterior median eyes;
AME–ALE	distance between AME and ALE;	PME–PME	distance between PMEs;
BS	bursa;	PME–PLE	distance between PME and PLE;
C	conductor;	RTA	retrolateral tibial apophysis;
CD	copulatory duct;	SB	spermathecal bases;
CO	copulatory opening;	SH	spermathecal heads;
E	embolus;	SP	spermatheca;
FD	fertilization duct;	SS	spermathecal stalks;
MOQ	median ocular quadrangle;	TA	tegular apophysis.

The terminology used in text and figure legends follows Yu et al. (2012).

Taxonomy

Family Clubionidae Wanger, 1887

Genus *Clubiona* Latreille, 1804

The *japonica*-group

Diagnosis. In general, members of the *japonica*-group can be recognized by the following combination of characters (see also Dankittipakul and Singtripop 2008): dark colour pattern of carapace and dorsum of opisthosoma (Figs 1–3); the male retrolateral tibial apophysis small and not branched (Figs 5, 10), the sperm duct is sinuate and distinct (Figs 6–7), the embolus filiform or reduced (Figs 4–9, 11), the conductor sclerotized with variable shapes (e.g. a small tubercle in *C. picturata* Deeleman-Reinhold, 2001, long and filiform in *C. biembolata* Deeleman-Reinhold, 2001 and *C. filicata* O. Pickard-Cambridge, 1874, large and beak-shaped in *C. japonica* L. Koch, 1878 and *C. grucollaris* sp. n., Figs 4–12); the female epigyne has a relatively large atrium situated anteriorly, and the copulatory openings are located in rebordered groove of atrial margin (Fig 13). The *japonica*-group resembles the *corticalis*-group in having the similar simple palp bulb in male, the atrium and copulatory openings located anteriorly in female, however, the latter can be distinguished from the former by: (1)

the lack of a colour pattern on the opisthosoma; (2) the presence of a inflated tegulum with indistinct sperm duct; (3) the conductor membranous or absent; (4) the presence of a ventral tibial apophysis in many species; (5) the atrium is significantly smaller or absent; (6) copulatory openings are often located at anterior part of the epigynial plate, instead of close to the middle part in the *japonica*-group. All the provided *corticalis*-group characters are according to Deeleman-Reinhold (2001) and recent clubionid papers such as Wu and Zhang (2014) and Liu et al. (2016).

Taxonomic notes. Dankittipakul and Singtripop (2008) divided the Southeast Asia *japonica*-group into two lineages. It appears that this standard of division may also apply to the *japonica*-group from China. The species of the 1st lineage have a large sclerotized and beak-shaped conductor that aligned transversely on apical part of the bulb (Figs 4–6, 15–17), such as *C. circulata* Zhang & Yin, 1998, *C. calycina* Wu & Zhang, 2014 and *C. grucollaris* sp. n., etc. Members of the 2nd lineage share the following characters: the reduced embolus; a long and filiform conductor; and the embolus and conductor fused with each other, forming an apical appendage together and situated on the apical portion of the tegulum (Figs 7–12). The 2nd lineage includes *C. filicata* and *C. filoramula* Zhang & Yin, 1998.

In spite of the variable conductor in the male palp, the female genitalia of the two different lineages are very similar. The epigynial plate has a large atrium situated anteriorly, and the atrium is bounded by an atrial margin. The posterior atrial margins are often not rebordered. Copulatory openings relatively small, located in rebordered groove of basolateral atrial margin (Figs 13, 18). Vulva consisting of anterior spermathecae and posterior bursae. The bursae are membranous, larger than the spermathecae (Figs 14, 19).

Strictly based on the group characters, figures and text descriptions of 495 *Clubiona* species were checked one by one. In this work, we focused on ungrouped species, but also considered grouped species based on previous infrageneric revisions (Mikhailov 1990, 1991, 1995, 2002; Deeleman-Reinhold 2001). As a result, there are at least 31 *japonica*-group species all over the world (but mainly distributed in Asia) at present, among which 9 species were recorded from China, including a new species described here as *Clubiona grucollaris* sp. n. (see Table 1).

***Clubiona grucollaris* sp. n.**

<http://zoobank.org/25D9CD29-56E7-4D2E-9FBD-DB7C24DA5F1C>

Figs 1–2, 4–6, 13–20

Type material. Holotype ♂ (HUBU-GZ-IV-140057): China, Guizhou Province, Tongren City, Fanjing Mountain Nature Reserve (578 m; 21°51'12"N, 108°46'45"E), 3 August 2014, Jian Chen and Jianyong Li leg. **Paratypes:** 2 ♂ and 18 ♀, same data as holotype; 11 ♀, Tongren City, Mayanghe Nature Reserve (394 m; 28°46'53"N, 108°12'32"E), 15 August 2014, Mu Yan and Yaqian Fu leg; 1 ♂ and 1 ♀, Tongren City, Fanjing Mountain Nature Reserve (539 m; 27°50'42"N, 108°46'48"E), 6 April 2016, Hao Yu and Yang Zhong leg. 1 ♂, Hainan Province, Qiongzong County, Limu

Table 1. A list of current *Clubiona japonica*-group species in alphabetical order.

	Species name	Known sex	Distribution
1	<i>C. annuligera</i> Lessert, 1929	♂♀	Congo, Mozambique
2	<i>C. biembolata</i> Deeleman-Reinhold, 2001	♂♀	Borneo
3	<i>C. bilobata</i> Dhali, Roy, Saha & Raychaudhuri, 2016	♀	India
4	<i>C. calycina</i> Wu & Zhang, 2014	♂♀	China
5	<i>C. campylacantha</i> Dankittipakul, 2008	♂♀	Thailand
6	<i>C. charleneae</i> Barrion & Litsinger, 1995	♂♀	Philippines
7	<i>C. circulata</i> Zhang & Yin, 1998	♂♀	China
8	<i>C. coreana</i> Paik, 1990	♂♀	Russia, Korea, China
9	<i>C. digitata</i> Dankittipakul, 2012	♂♀	Thailand
10	<i>C. drassodes</i> O. Pickard-Cambridge, 1874	♂♀	India, Bangladesh, China
11	<i>C. flicata</i> O. Pickard-Cambridge, 1874	♂♀	India, Bangladesh, Pakistan, Thailand, Myanmar, Laos, China
12	<i>C. flifera</i> Dankittipakul, 2008	♂♀	Thailand
13	<i>C. floramula</i> Zhang & Yin, 1998	♂	China
14	<i>C. foliata</i> Keswani & Vankhede, 2014	♂♀	India
15	<i>C. gallagheri</i> Barrion & Litsinger, 1995	♀	Indonesia
16	<i>C. japonica</i> L. Koch, 1878	♂♀	Russia, China, Korea, Japan
17	<i>C. lala</i> Jäger & Dankittipakul, 2010	♀	Laos
18	<i>C. melanosticta</i> Thorell, 1890	♂♀	Thailand, Sumatra, Krakatau, New Guinea
19	<i>C. melanothele</i> Thorell, 1895	♀	Myanmar, Thailand, Laos, Sumatra
20	<i>C. munda</i> Thorell, 1887	♀	Myanmar
21	<i>C. nigromaculosa</i> Blackwall, 1877	♂♀	Seychelles, Réunion
22	<i>C. octoginta</i> Dankittipakul, 2008	♂♀	Thailand
23	<i>C. picturata</i> Deeleman-Reinhold, 2001	♂♀	Bali
24	<i>C. pila</i> Dhali, Roy, Saha & Raychaudhuri, 2016	♀	India
25	<i>C. pupula</i> Thorell, 1897	♂♀	Myanmar
26	<i>C. scandens</i> Deeleman-Reinhold, 2001	♂♀	Borneo
27	<i>C. submaculata</i> (Thorell, 1891)	♂♀	Nicobar Is.
28	<i>C. suthepica</i> Dankittipakul, 2008	♂♀	Thailand
29	<i>C. vigil</i> Karsch, 1879	♂♀	Russia, Korea, Japan, China
30	<i>C. vukomi</i> Jäger & Dankittipakul, 2010	♂	Thailand, Laos
31	<i>C. grucollaris</i> sp. n.	♂♀	China

Mountain Nature Reserve (417 m; 19°50'06"N, 109°47'52"E), 1 October 2009, Hao Yu and Zhenyu Jin leg.

Etymology. The specific name is an adjective and is derived from the combination of two Latin words: *gru* (crane) + *collaris* (with neck), referring to the long and cylindrical conductor base, which is like the neck of crane.

Diagnosis. *Clubiona grucollaris* sp. n. resembles the other *japonica*-group species by the similar habitus (Figs 1–3), but is consistently separable by its genitalia. Males of *Clubiona grucollaris* sp. n. appear to be closely related to *C. circulata* (Zhang and



Figures 1–3. Habitus of *Clubiona grucollaris* sp. n. and *C. filicata* O. Pickard-Cambridge, 1874, dorsal view. **1** *C. grucollaris* sp. n., male holotype **2** *C. grucollaris* sp. n., female paratype **3** *C. filicata* O. Pickard-Cambridge, 1874, male from Guangxi, China. Scale bars 5 mm (**1–2**); 2.5 mm (**3**).

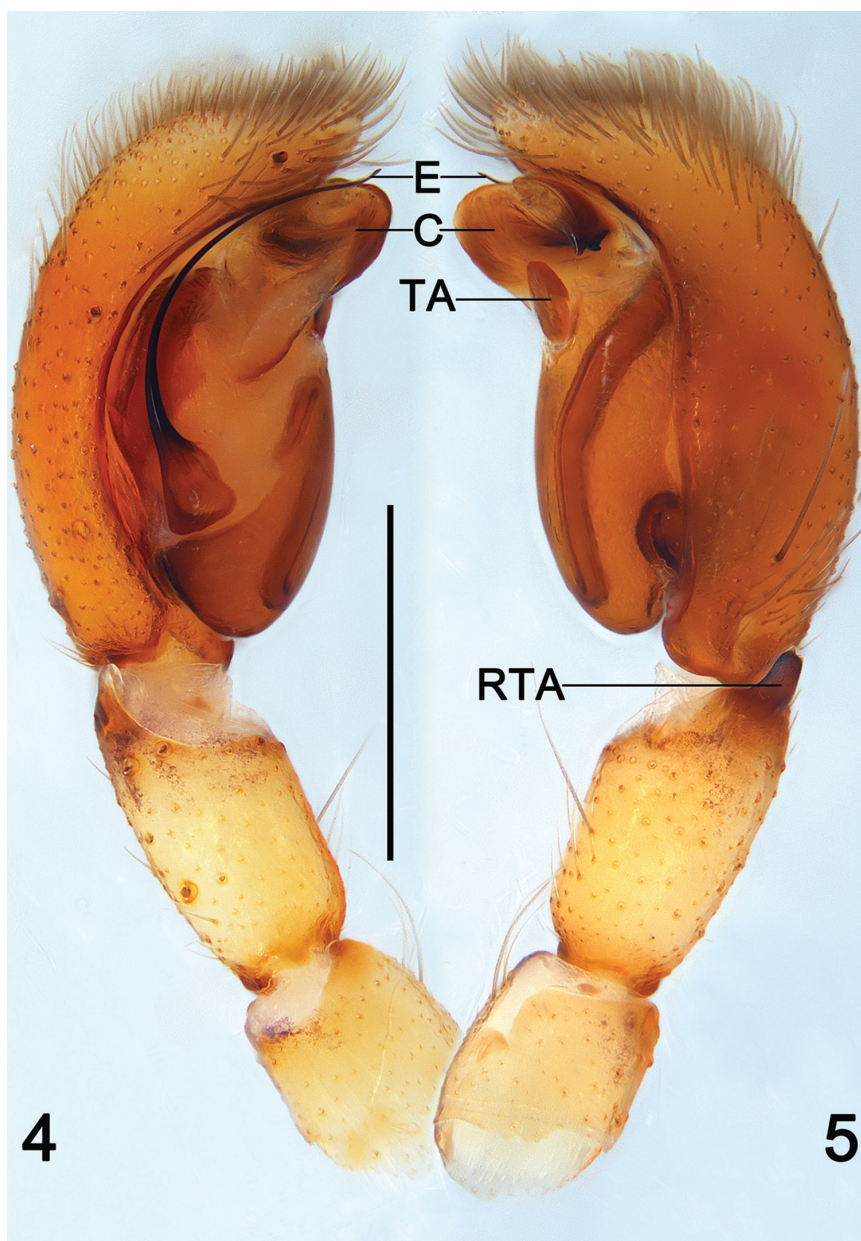
Yin 1998: 9, f. 1–3), *C. calycina* (Wu and Zhang 2014: 211, f. 1–12), and *C. suthepica* (Dankittipakul and Singtripop 2008: 42, f. 22–23, 56–58) in having the filiform embolus, and heavily sclerotized distal apex of beak-shaped conductor, but can be easily distinguished from these species by the crane's neck-shaped conductor base, and by the nearly U-shaped sperm ducts (Figs 4–6, 15–17). Females of *C. grucollaris* sp. n. are similar to *C. circulata* (Zhang and Yin 1998: 9, f. 4–5), *C. filifera* (Dankittipakul et al. 2012: 57, f. 18–19, 23–24) and *C. octoginta* (Dankittipakul and Singtripop 2008: 39, f. 17–19, 45–46) by the broad atrium situated anteriorly, and the membranous bursae situated posteriorly, but can be recognized by the more or less inverted trapezoidal atrium with M-shaped anterior margin, and by the spiral spermathecae (Figs 13–14, 18–19).

Description. Male. Total length 6.23–7.75. Holotype (Fig. 1): body 7.54 long; carapace 3.75 long, 2.42 wide; abdomen 3.96 long, 1.76 wide. Carapace brownish red, with a distinctive pattern on pars cephalica consisting of a pair of dark lateral bands and Ψ-shaped markings behind posterior eyes, markings starting from behind PME and PLE almost reaching dark fovea. Fovea longitudinal. In dorsal view, AER recurved and slightly narrowed than procurved PER. Eye diameters and interdistances: AME 0.16, ALE 0.18, PME 0.16, PLE 0.15; AME–AME 0.14, AME–ALE 0.19, PME–PME 0.38, PME–PLE 0.32. MOQL 0.51, MOQA 0.46, MOQP 0.72. Chelicerae protruding and coloured as carapace, three promarginal teeth and two retromarginal teeth. Endites brown, longer than wide. Labium dark brown, longer than wide. Sternum 2.10 long, 1.45 wide. Abdomen oval, brown, with conspicuous anterior tufts of hairs, dorsum with dense grey hairs and two pairs of muscle impression, and with broken dark median band, reaching half of opisthosoma length, posteriorly with paired dark markings consisting of numerous stripes and spots; venter brown. Legs brownish yellow, all legs with conspicuous dark brown annuli in the distal parts of femur, patella, tibia, metatarsus and tarsus. Measurements of legs: I 8.60 (2.52, 3.20, 1.70, 1.20), II 9.07 (2.64, 3.46, 2.00, 0.97), III 7.49 (2.20, 2.40, 2.06, 0.83), IV 10.43 (2.86, 3.57, 2.82, 1.19).

Palp (Figs 4–6, 15–17). RTA dark, small but strong, triangular; cymbium longer than wide, bulb nearly spherical and proapically membranous; sperm duct distinct and sinuate, U-shaped or reversed S-shaped; embolus slender and filiform, originated at 8–9 o' clock position in prolateral view, its tip slightly overpasses the genital bulb; conductor with a heavily sclerotized and beak-shaped apex, its base part membranous and crane's neck-shaped; tegular apophysis small and petal-shaped in retrolateral view.

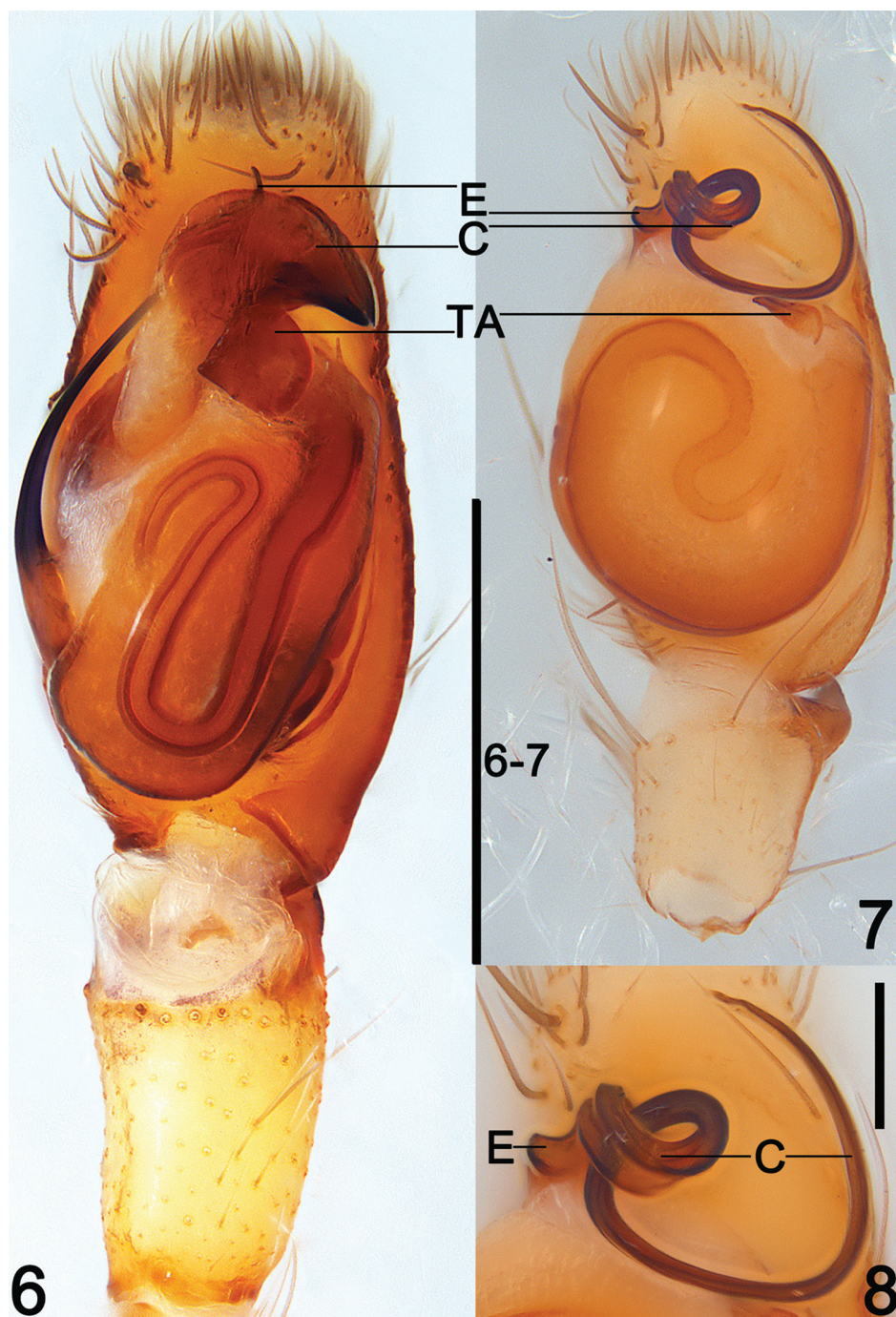
Female. Total length 6.53–7.83. One paratype (Fig. 2) measured, body 7.70 long; carapace 3.03 long, 2.08 wide; abdomen 4.55 long, 2.41 wide. Eye sizes and interdistances: AME 0.13, ALE 0.14, PME 0.15, PLE 0.12; AME–AME 0.14, AME–ALE 0.16, PME–PME 0.34, PME–PLE 0.27. MOQL 0.49, MOQL 0.42, MOQP 0.66. Sternum 1.71 long, 1.18 wide. Measurements of legs: I 6.40 (1.83, 2.36, 1.24, 0.97), II 7.04 (2.02, 2.71, 1.41, 0.89), III 5.02 (1.60, 1.83, 1.33, 0.27), IV 8.43 (2.32, 2.82, 2.44, 0.86). General characters as in male, but slightly larger in size and darker in colour.

Epigyne (Figs 13–14, 18–19). Atrium large and nearly inverted trapezoidal, with a shallow depression, located at anterior portion of epigynal plate, anterior atrial margin

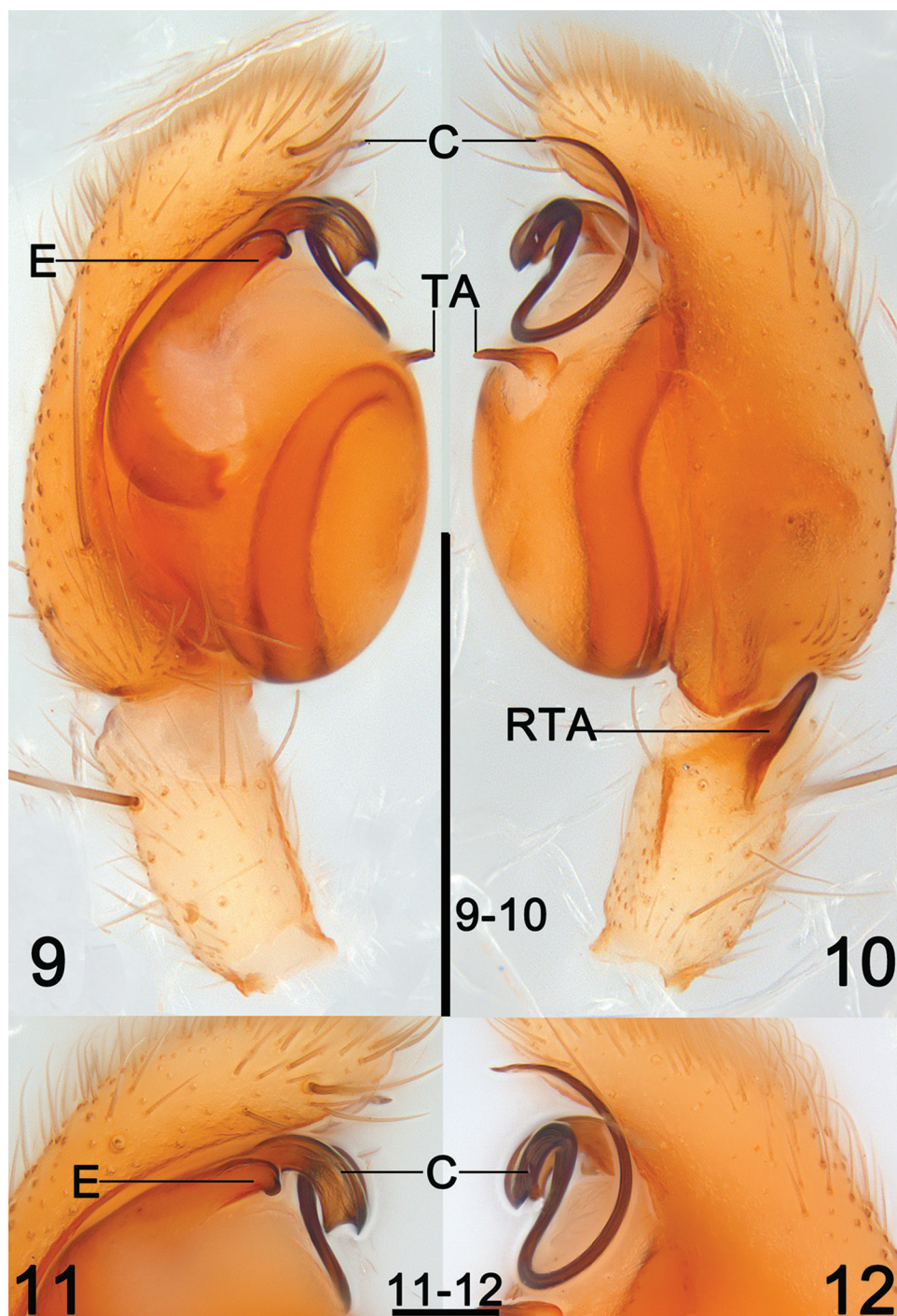


Figures 4–5. *Clubiona grucollaris* sp. n., male holotype. **4** left palp, prolateral view **5** same, retrolateral view. Scale bars 0.5 mm.

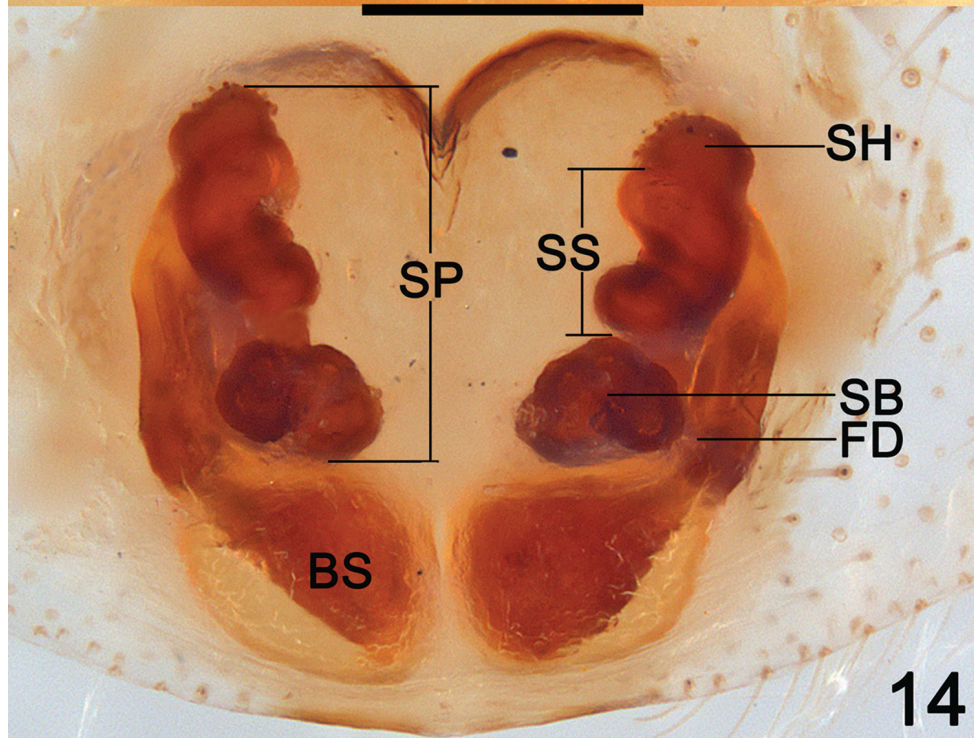
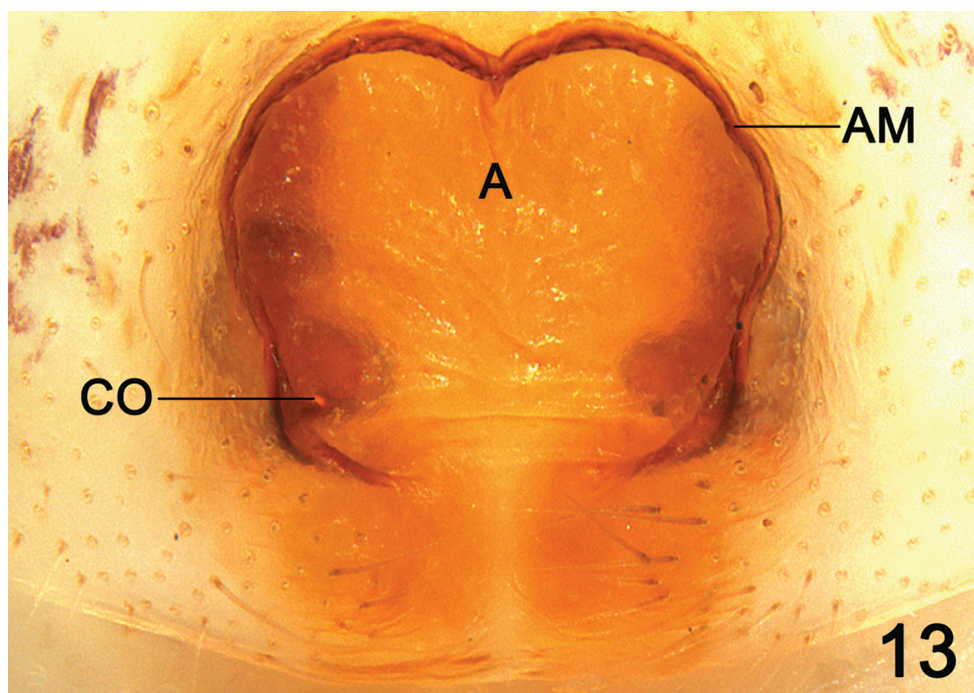
“M” shaped; spermathecae and burse are prominently through epigynal plate in ventral view; two copulatory openings located at basolateral atrial borders; spermathecae consisting of papilliform base, tubular stalk and ovoid head, ascend spirally; bursae globular and translucent; fertilization ducts short, acicular.



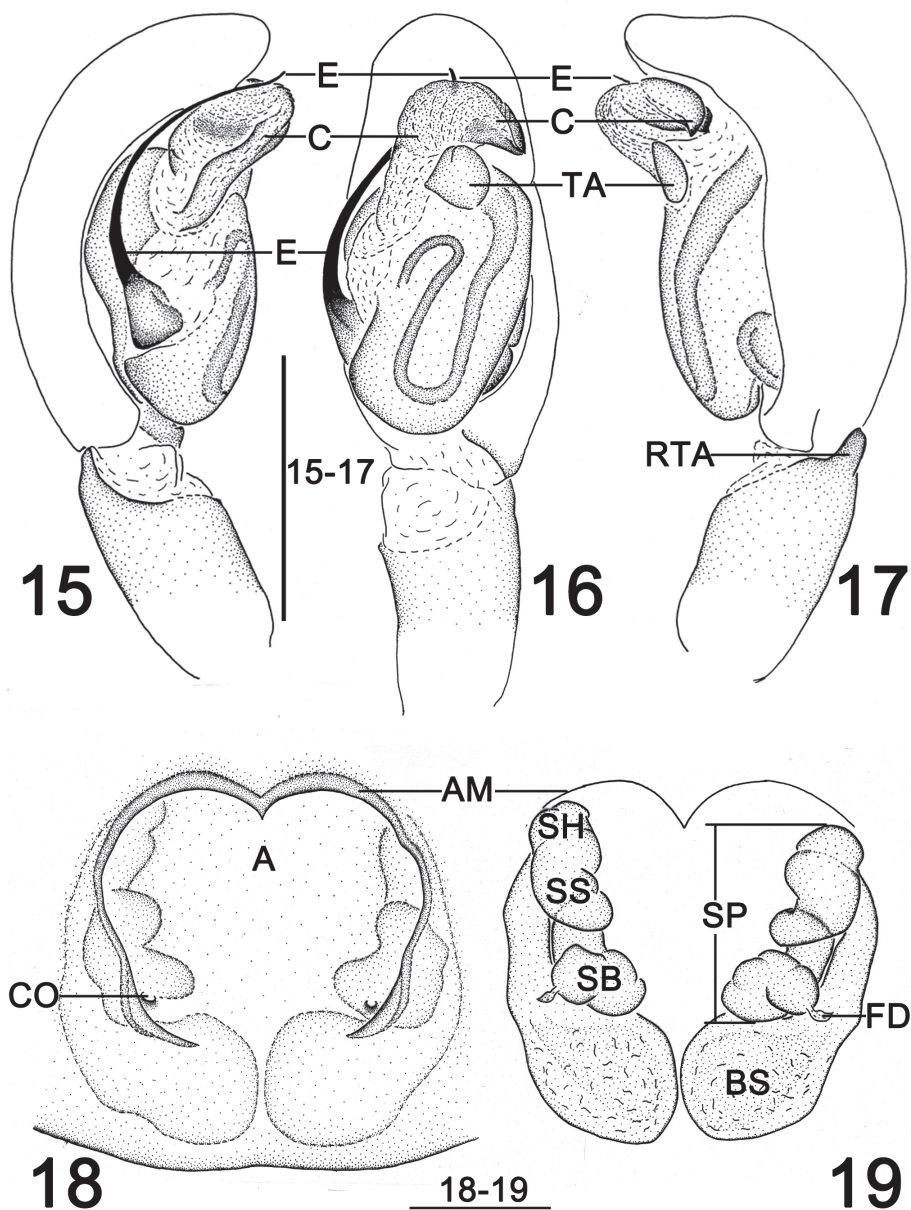
Figures 6–8. Left male palp of *Clubiona gracollaris* sp. n. and *C. filicata* O. Pickard-Cambridge, 1874, ventral view. **6** *C. gracollaris* sp. n., male holotype **7** *C. filicata* O. Pickard-Cambridge, 1874, male from Guangxi, China **8** *C. filicata* O. Pickard-Cambridge, 1874 from Guangxi, China, apical appendage of regulum, ventral. Scale bars 0.5 mm (**6–7**); 0.1 mm (**8**).



Figures 9–12. *Clubiona filicata* O. Pickard-Cambridge, 1874, male from Guangxi, China. **9** left palp, prolateral view **10** same, retrolateral view **11** apical appendage of tegulum, prolateral view **12** same, retrolateral view. Scale bars 0.5 mm (**9–10**); 0.1 mm (**11–12**).



Figures 13–14. *Clubiona grucollaris* sp. n., female paratype. **13** epigyne, ventral view **14** vulva, dorsal view. Scale bars 0.2 mm.



Figures 15–19. *Clubiona grucollaris* sp. n., male holotype and female paratype. **15** left palp, prolateral view **16** same, ventral view **17** same, retrolateral view **18** epigyne, ventral view **19** vulva, dorsal view. Scale bars 0.5 mm (**15–17**); 0.2 mm (**18–19**).

Natural history. *Clubiona grucollaris* sp. n. mainly inhabit the upper levels of the forest and most specimens were collected by canopy fogging, while a few spiders were obtained by beating twigs and branches of vegetation. The type locality, Fanjing Moun-

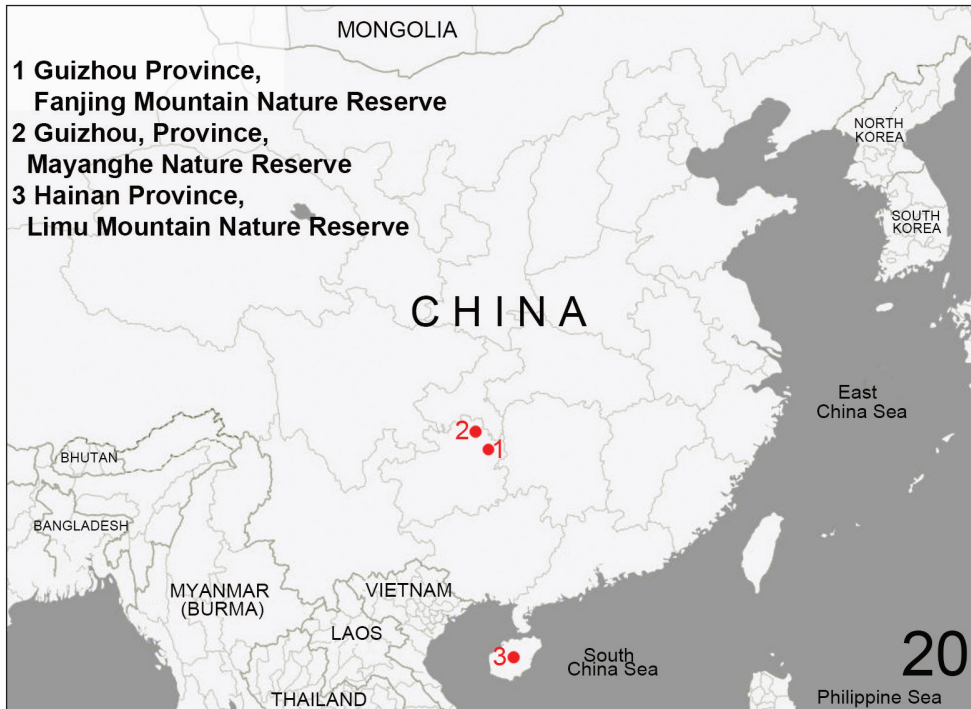


Figure 20. Distribution of *Clubiona grucollaris* sp. n. (red circles).

tain Nature Reserve, extending from 27°49'50" to 28°01'30"N and 108°49'30" to 108°18'30"E, is the core zone and the highest peak of the Wuling Mountains, and is known for its high floral biodiversity (Wang et al. 2015). The evergreen broad-leaved forests, where the holotype was obtained, are located in low elevation areas (alt. 300–600 m) of the Reserve.

Distribution. Guizhou Province (Mt. Fanjing, Mayanghe natural reserves) and Hainan Island (Mt. Limu), China (Fig. 20).

Clubiona flicata O. Pickard-Cambridge, 1874

Figs 3, 7–12

Clubiona flicata O. P.-Cambridge, 1874: 413, fig. 35 (description of ♂, ♀); Gravely 1931: 261, fig. 16d; Tikader and Biswas 1981: 69, figs 120–121; Gong 1989: 109, figs 1–13; Zhang and Hu 1989: 58, figs 7, 22; Majumder and Tikader 1991: 23, figs 30–35; Biswas and Raychaudhuri 1996: 199, figs 27–33; Song et al. 1999: 415, figs 245L–M, 248F–G; Dankittipakul and Singtripop 2008: 37, figs 5–7, 30–33; Dankittipakul et al. 2012: 59, figs 25–31; Yin et al. 2012: 1095, figs 575a–e.

Clubiona distincta Thorell, 1887: 48

Clubiona swatowensis Strand, 1907: 562 (Description of ♀); Strand 1909: 39, fig. 24.

Examined material. 1 ♂, China, Guangxi Province, Guilin City, Guilin Tea Science and Research Institute (150 m; 27°17'48"N, 110°21'34"E), 3 October 2010.

Description. Male (Figs 3, 7–12). For details see Dankittipakul and Singtripop (2008).

Natural history. The examined specimen was collected by a pitfall trap set in a tea plantation.

Distribution. India, Bangladesh, Pakistan, Thailand, Myanmar, Laos, China (see Table 1).

Acknowledgements

The manuscript benefited from comments by Dr. Cor J. Vink (Natural History Canterbury Museum, New Zealand), and two anonymous reviewers. This work was supported by the National Natural Sciences Foundation of China (NSFC-31702006/31272268/31172113), the Special Foundation of Ministry of Science and Technology of the People's Republic of China (MOST grant no. 2014FY110100), the Natural Science Foundation of Guizhou Province (J [2014] 2146) and PhD grant from Guizhou Normal University (11904/0517069). We thank the staff of the Centre for Behavioural Ecology and Evolution (CBEE, Hubei University) for all their help and support throughout this study.

References

- Barrion AT, Litsinger JA (1995) Riceland Spiders of South and Southeast Asia. CAB International, Wallingford, UK, 700 pp.
- Biswas V, Raychaudhuri D (1996) Clubionid spiders of Bangladesh – I: Genus *Clubiona* Latreille. Proceedings of Recent Advances in Life Sciences, Dibrugarh University 1: 191–210.
- Blackwall J (1877) A list of spiders captured in the Seychelle Islands by Professor E. Perceval Wright, M. D., F. L. S.; with descriptions of species supposed to be new to arachnologists. Notes and preface by the Rev. O. P.-Cambridge, M.A., C.M.Z.S., etc. Proceedings of the Royal Irish Academy (2)3: 1–22.
- Dankittipakul P, Singtripop T (2008) Five new species of the spider genus *Clubiona* Latreille (Araneae: Clubionidae) from Thailand. Zootaxa 1747: 34–60.
- Dankittipakul P, Tavano M, Chotwong W, Singtripop T (2012) New synonym and descriptions of two new species of the spider genus *Clubiona* Latreille, 1804 from Thailand (Araneae, Clubionidae). Zootaxa 3532: 51–63.
- Deeleman-Reinhold CL (2001) Forest spiders of South East Asia: with a revision of the sac and ground spiders (Araneae: Clubionidae, Corinnidae, Liocranidae, Gnaphosidae, Prodidomidae and Trochanterriidae). Brill, Leiden, 591 pp.
- Dhali DC, Roy TK, Saha S, Raychaudhuri D (2016) On the new sac spiders (Araneae: Clubionidae) of Dooars, West Bengal, India. World Scientific News 50: 278–305.

- Dondale CD, Redner JH (1976) A rearrangement of the North American species of *Clubiona*, with descriptions of two new species (Araneida: Clubionidae). Canadian Entomologist 108: 1155–1165. <https://doi.org/10.4039/Ent1081155-11>
- Dondale CD, Redner JH (1982) The insects and arachnids of Canada, Part 9. The sac spiders of Canada and Alaska, Araneae: Clubionidae and Anyphaenidae. Research Branch Agriculture Canada Publication 1724: 1–194.
- Edwards RJ (1958) The spider subfamily Clubioninae of the United States, Canada and Alaska (Araneae: Clubionidae). Bulletin of the Museum of Comparative Zoology, Harvard 118(6): 365–436.
- Gertsch WJ (1941) New American spiders of the family Clubionidae. I. American Museum Novitates 1147: 1–20.
- Gong JX (1989) First record of *Clubiona filicata* Cambridge for China (Araneae: Clubionidae). Wuyi Science Journal 7: 109–113.
- Gravely FH (1931) Some Indian spiders of the families Ctenidae, Sparassidae, Selenopidae and Clubionidae. Records of the Indian Museum, Calcutta 33: 211–282.
- Jäger P, Dankittipakul P (2010) Clubionidae from Laos and Thailand (Arachnida: Araneae). Zootaxa 2730: 23–43. <https://doi.org/10.11646/zootaxa.2730.1.2>
- Karsch F (1879) Baustoffe zu einer Spinnenfauna von Japan. Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens 36: 57–105.
- Keswani S, Vankhede G (2014) Description of one new species of the genus *Clubiona* (Araneae: Clubionidae) from India. Indian Journal of Arachnology 3(1): 35–40.
- Koch L (1878) Japanesische Arachniden und Myriapoden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 27: 735–798.
- Lessert R (1929) Araignées du Congo recueillies au cours de l'expédition organisée par l'American Museum (1909–1915). Troisième partie. Revue Suisse de Zoologie 36: 103–159. <https://doi.org/10.5962/bhl.part.117628>
- Liu P, Peng XJ, Yan HM (2016) Five new species of the *Clubiona corticalis* species group (Araneae, Clubionidae) from China. Zootaxa 4184(3): 561–575. <https://doi.org/10.11646/zootaxa.4184.3.10>
- Li SQ, Lin YC (2016) Species Catalogue of China. Volume 2. Animals. Invertebrates (I), Arachnida: Araneae. Science Press, Beijing, 549 pp.
- Lohmander H (1944) Vorläufige Spinnennotizen. Arkiv för zoologi 35(A, 16): 1–21.
- Majumder SC, Tikader BK (1991) Studies on some spiders of the family Clubionidae from India. Records of the Zoological Survey of India, Occasional Paper 102: 1175.
- Mikhailov KG (1990) The spider genus *Clubiona* Latreille 1804 in the Soviet Far East, 1 (Arachnida, Aranei, Clubionidae). Korean Arachnology 5(2): 139–175.
- Mikhailov KG (1991) The spider genus *Clubiona* Latreille 1804 in the Soviet Far East, 2 (Arachnida, Aranei, Clubionidae). Korean Arachnology 6(2): 207–235.
- Mikhailov KG (1995) Erection of infrageneric groupings within the spider genus *Clubiona* Latreille, 1804 (Aranei Clubionidae): a typological approach. Arthropoda Selecta 4(2): 33–48.
- Mikhailov KG (2002) The spider genus *Clubiona* Latreille, 1804 (Aranei: Clubionidae) in the fauna of the former USSR: 2003 update. Arthropoda Selecta 11: 283–317.

- Paik KY (1990) Korean spiders of the genus *Clubiona* (Araneae: Clubionidae) I. Description of eight new species and five unrecorded species from Korea. Korean Arachnology 5(2): 85–129.
- Pickard-Cambridge O (1874) On some new species of *Drassides*. Proceedings of the Zoological Society of London 42(3): 370–419, Pl. LI–LII. <https://doi.org/10.1111/j.1096-3642.1874.tb02495.x>
- Simon E (1932) Les arachnides de France. Tome VI. Synopsis générale et catalogue des espèces françaises de l'ordre des Araneae; 4^e partie. Paris, 6: 773–978.
- Song DX, Zhu MS, Chen J (1999) The Spiders of China. Hebei University of Science and Technology Publishing House, Shijiazhuang, 640 pp.
- Strand E (1907) Vorläufige Diagnosen süd- und ostasiatischer Clubioniden, Ageleniden, Pisauriden, Lycosiden, Oxyopiden und Salticiden. Zoologischer Anzeiger 31: 558–570.
- Strand E (1909) Süd- und ostasiatische Spinnen. II. Fam. Clubionidae. Fam. Salticidae. Abhandlungen der Naturforschenden Gesellschaft Görlitz 26: 1–128.
- Thorell T (1887) Viaggio di L. Fea in Birmania e regioni vicine. II. Primo saggio sui ragni birmani. Annali del Museo Civico di Storia Naturale di Genova 25: 5–417.
- Thorell T (1890) Studi sui ragni Malesi e Papuani. IV, 1. Annali del Museo Civico di Storia Naturale di Genova 28: 1–419.
- Thorell T (1891) Spindlar från Nikobarerna och andra delar af södra Asien. Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar 24(2): 1–149.
- Thorell T (1895) Descriptive catalogue of the spiders of Burma. London, 1–406.
- Thorell T (1897). Viaggio di Leonardo Fea in Birmania e regioni vicine. LXXIII. Secondo saggio sui Ragni birmani. I. Parallelodontes. Tubitelariae. Annali del Museo Civico di Storia Naturale di Genova (2): 161–267.
- Tikader BK, Biswas B (1981) Spider fauna of Calcutta and vicinity: Part-I. Records of the Zoological Survey of India, Occasional Paper 30: 1–149.
- World Spider Catalog (2017) World spider catalog. Natural History Museum Bern. <http://wsc.nmbe.ch>, version 18.0 [accessed on 1 November 2017]
- Wang LY, Chen HM, Zhou KX, Zhang F, Zhang ZS (2015) Diversity of spiders in Fanjing Mountain Nature Reserve, Guizhou, China, I: Six new species of Phrurolithidae (Araneae). Zootaxa 4012(3): 447–464. <https://doi.org/10.11646/zootaxa.4012.3.2>
- Wu PL, Zhang F (2014) A new species of the spider genus *Clubiona* from China, with description of the male of *Clubiona qiyunensis* (Araneae: Clubionidae). Acta Zoologica Academiae Scientiarum Hungaricae 60(3): 207–215.
- Wunderlich J (2011) Extant and fossil spiders (Araneae). Beiträge zur Araneologie 6: 1–640.
- Yin CM, Peng XJ, Yan HM, Bao YH, Xu X, Tang G, Zhou QS, Liu P (2012) Fauna Hunan: Araneae in Hunan, China. Hunan Science and Technology Press, Changsha, 1590 pp.
- Yu H, Sun ZX, Zhang GR (2012) New taxonomic data on the sac spiders (Arachnida: Araneae: Clubionidae) from China, with description of a new species. Zootaxa 3299: 44–60.
- Zhang GR, Hu YJ (1989) Arrangement of some Chinese species of *Clubiona* (Araneae: Clubionidae). Journal of Xiangtan Normal University 6: 53–61.
- Zhang YJ, Yin CM (1998) Six new species of the spiders of genus *Clubiona* from China (Araneae: Clubionidae). Acta Zootaxonomica Sinica 23(1): 9–17.

Descriptions of two new species and one new subspecies from the *Exocelina okbapensis*-group, and notes on the *E. aipo*-group (Coleoptera, Dytiscidae, Copelatinae)

Helena Shaverdo¹, Bob Sumoked², Michael Balke³

1 Naturhistorisches Museum, Burgring 7, 1010 Vienna, Austria **2** Walian 2, Tomohon Selatan, N Sulawesi 95439, Indonesia **3** SNSB-Zoologische Staatssammlung München, Münchhausenstraße 21, D-81247 Munich, Germany and GeoBioCenter, Ludwig-Maximilians-University, Munich, Germany

Corresponding author: Helena Shaverdo (shaverdo@mail.ru; helena.shaverdo@nhm-wien.ac.at)

Academic editor: M. Michat | Received 19 July 2017 | Accepted 21 September 2017 | Published 9 November 2017

<http://zoobank.org/3587B83B-D0D4-4943-93CA-09B16BBF231B>

Citation: Shaverdo H, Sumoked B, Balke M (2017) Descriptions of two new species and one new subspecies from the *Exocelina okbapensis*-group, and notes on the *E. aipo*-group (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 715: 17–37. <https://doi.org/10.3897/zookeys.715.15913>

Abstract

Two new species and one new subspecies of *Exocelina* Broun, 1886 from New Guinea are described: *E. okbapensis* Shaverdo & Balke, **sp. n.**, *E. okbapensis hajeki* Shaverdo & Balke, **ssp. n.**, and *E. may* Shaverdo & Balke, **sp. n.** These and two already described species are assigned to the *E. okbapensis*-group, which is morphologically (based on setation of the paramere) and phylogenetically close to the *E. aipo*-group. On the latter, morphological and taxonomic notes are provided. An identification key to all known species of the groups is presented, and important diagnostic characters are illustrated. Data on the species distributions are mapped and show that the species occur only in the central mountain part of the island restricted by Wamena in the west and Sandaun Province in the east.

Keywords

Exocelina aipo-group, *Exocelina okbapensis*-group, Copelatinae, Dytiscidae, new species, New Guinea

Introduction

Here, we continue to build up the infrageneric structure of the genus that was started in our previous taxonomic studies on the New Guinea species of the diving beetle genus *Exocelina* Broun, 1886 (Balke 1998, Shaverdo et al. 2005, 2012, 2016b, c,

2017). A new species group, *E. okbapensis*-group, is proposed for two new species and two already described ones: *E. ketembang* (Balke, 1998) and *E. talaki* (Balke, 1998) based on the shape and setation of the paramere as well as on results of a phylogenetic analysis of molecular data (Toussaint et al. 2014). It is shown that representatives of another species group, namely *E. aipo*-group, share the same shape and setation of the paramere with the new species group and, therefore, both are most likely closely related. This is also supported by a preliminary molecular analysis of the new species and old material of the *E. aipo*-group species and *E. talaki*, which suggests that they form a monophyletic clade.

As in most of our previous papers on the genus, all species data will be presented on the species-id.net portal automatically created by ZooKeys with the publication of this paper (Shaverdo et al. 2012, 2013, 2014, 2016a, b, c, 2017).

Materials and methods

The present work is based on material from the following collections:

CGW	Collection of Günther We-walka, Vienna, Austria	NMPC	Národní museum, Prague, Czechia
MZB	Museum Zoologicum Bogoriense, Cibinong, Indonesia	ZSM	Zoologische Staatssammlung München, Munich, Germany
NHMW	Naturhistorisches Museum Wien, Vienna, Austria		

All methods follow those described in detail in previous articles (Shaverdo and Balke 2014, Shaverdo et al. 2012, 2014). All specimen data are quoted as they appear on the labels attached to the specimens. Label text is cited using quotation marks. Comments in square brackets are ours. The following abbreviations were used:

TL	total body length	MW	maximum body width
TL-H	total body length without head	hw	handwritten

Notes on diagnostic characters of the groups

As already mentioned above, both groups build a monophyletic clade according to the results of molecular analyses (Toussaint et al. 2014; unpublished results). This monophyly is also supported morphologically by the structure and setation of the male genitalia, especially of the paramere. The paramere of all representatives of the groups have a distinct notch on its dorsal side and a small, evidently separated subdistal part with a tuft of very dense, strong setae; proximal setae of the paramere are sparse and fine, inconspicuous (e.g., Fig. 5C; figs 32–35 in Balke (1998)). Other diagnostic characters of the clade comprising these two groups are:

- beetles small or middle-sized (TL-H 3.25–4.65 mm);
- habitus oblong-oval (broadest approximately at elytral midlength), with rounded pronotal and elytral sides, body outline continuous;
- pronotum short, trapezoidal, with posterior angles not drawn backwards;
- coloration brown to piceous, mainly uniform, sometimes with paler head and pronotum and darker elytra;
- microreticulation and punctation of dorsal surface very fine to strongly impressed, beetles shiny to matt dorsally;
- metacoxae and abdominal ventrites 1–5 (and 6 in males) with thin, almost longitudinal striae/strioles;
- pronotum and elytra without striae or strioles;
- pronotum with lateral bead;
- antennomeres not modified or modified: mainly, antennomeres 3–6 strongly or slightly enlarged in male and stout in female; antennomere 2 elongate;
- male protarsomeres 1–3 not expanded laterally;
- male protarsomere 4 cylindrical, narrow, with large or small anterolateral hook-like seta;
- median lobe of aedeagus with continuous outline in ventral and lateral view;
- ventral sclerite of median lobe more or less deeply divided apically;
- median lobe without setation.

Representatives of the two groups can be distinguished by the shape and setation of the male protarsomere 5. The species of the *E. aipo*-group have distinctly modified male protarsomere 5: concave ventrally, usually with some ventral setae enlarged and shifted to base (Fig. 1; figs 25–28 in Balke (1998)), whereas the species of the *E. okbapensis*-group have the male protarsomere 5 long and narrow, without concavity, ventrally with two rows of relatively short setae (e.g., Fig. 5D).

Checklist and distribution of the species of the *Exocelina aipo*- and *okbapensis*-groups

Abbreviations: IN – Indonesia, PNG – Papua New Guinea.

	<i>Exocelina aipo</i> -group	
1.	<i>Exocelina aipo</i> (Balke, 1998)	IN: Papua: Yahukimo
2.	<i>Exocelina karmurensis</i> (Balke, 1998)	IN: Papua: Yahukimo
3.	<i>Exocelina manfredi</i> (Balke, 1998)	IN: Papua: Pegunungan Bintang
4.	<i>Exocelina me</i> (Balke, 1998)	IN: Papua: Pegunungan Bintang
	<i>Exocelina okbapensis</i> -group	
1.	<i>Exocelina okbapensis</i> sp. n.	IN: Papua: Pegunungan Bintang; PNG: Sandaun
1a.	<i>Exocelina okbapensis hajeki</i> ssp. n.	IN: Papua: Jayawijaya
2.	<i>Exocelina may</i> sp. n.	PNG: Sandaun
3.	<i>Exocelina ketembang</i> (Balke, 1998)	IN: Papua: Yahukimo, Pegunungan Bintang
4.	<i>Exocelina talaki</i> (Balke, 1998)	IN: Papua: Pegunungan Bintang

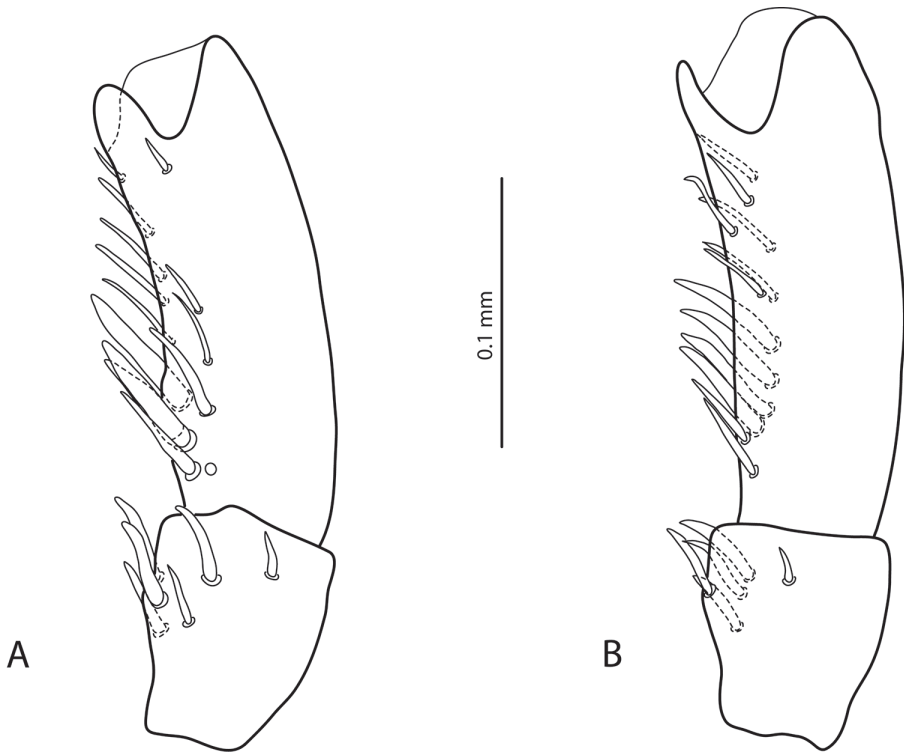


Figure 1. *Exocelina manfredi* (Balke, 1998), male protarsomeres 4–5 in lateral view **A** paratype, Borme **B** Aipomek-Takime.

Species descriptions

Exocelina aipo-group

The representatives of the group have male protarsomere 5 distinctly modified: it is concave ventrally, with some ventral setae enlarged and shifted to base, except those in *E. karmurensis*. They also have very similar shape of the median lobe of the aedeagus: in lateral view, it is curved, with apex curved downwards and slightly rounded; in ventral view, it is evenly tapering to the broadly pointed apex (fig. 40 in Balke 1998). The most evident difference is its size: the shortest median lobe is in *E. manfredi* and the longest and most robust one is in *E. karmurensis*. Shape of the paramere is also very similar: it has a distinct notch on dorsal side and a small, evidently separated subdistal part with a tuft of very dense, strong setae; proximal setae inconspicuous (figs 32–35 in Balke 1998).

To date, only four species of the group are described and no new species have been discovered. The only possible exception is one male from Aipomek-Tanime area (“IR 92#17a: West New Guinea, Aipomek-Tanime, 2000 m, 20.viii.1993, Balke” (NHMW)), which was mentioned in Balke (1998) under sp.5. Most likely, it belongs to *E. manfredi*, which was described from Borme area. The only morphological difference is less modified male protarsomere 5: concavity very shallow and basal enlarged setae

smaller than in the type specimens from Borne (Fig. 1). Additional material is required for a conclusion whether it is a form of *E. manfredi* or a new species of the *E. aipo*-group.

The differences between the species of this group are given in the key. For their descriptions, see Balke (1998).

***Exocelina okbapensis*-group**

1. *Exocelina okbapensis* Shaverdo & Balke, sp. n.

<http://zoobank.org/FD15BCDA-16A7-4961-B4A7-E44F2AEB0DAF>

Figs 2, 5

Sp. 4: Balke 1998: 338.

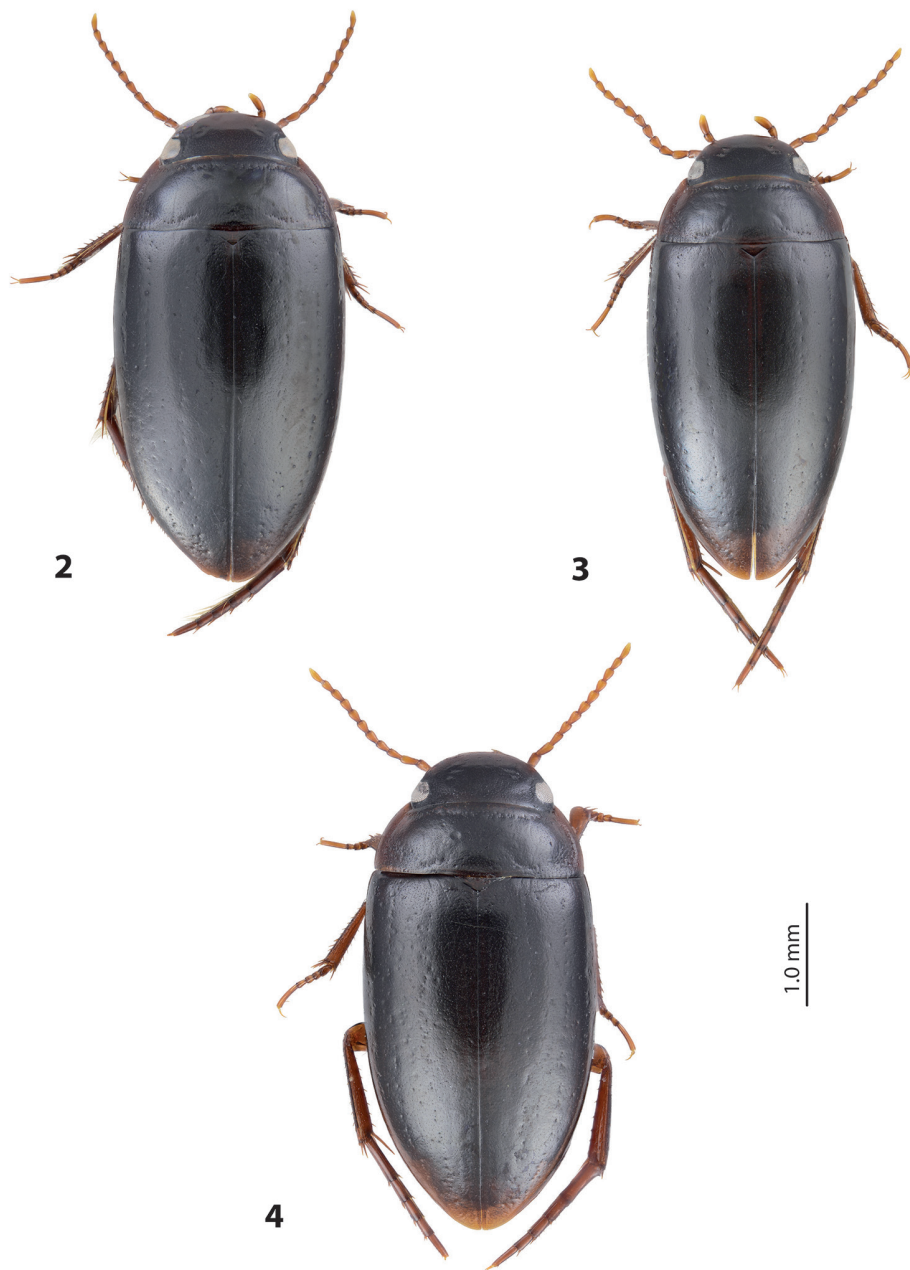
Type locality. Papua: Pegunungan Bintang Regency, Ok Bab, 4°49'28.6"S; 140°24'47.0"E, 1961 m a.s.l.

Type material. *Holotype*: male "Indonesia: Papua, nr Ok Bab [sic!], 1961m, 8.vi.2015, -4,82460033148527 140.413050251081, Sumoked (Pap049)" (MZB).

Paratypes: **Indonesia: Papua**: 10 males and 6 females with the same label as the holotype (MZB, NHMW, ZSM). 3 males, 3 females "Indonesia: Papua, nr Ok Bab, 2121 m, 8.vi.2015, -4,84880341216921 140,367602147161, Sumoked (Pap050)", one male and one female with additional labels with green text "M. Balke 7002" and "M. Balke 7003" (NHMW, ZSM). 3 males, 2 females "Indonesia: Papua, N Ok Sibil, 1564m, 10.vi.2015, -4,87003368 140,64401, Sumoked (Pap052)", two males with additional labels with green text "M. Balke 7000" and "M. Balke 6999" (NHMW, ZSM). **PNG: Sandaun**: 1 male "PAPUA, Selminumtem [Selminum Tem, 45 km SWS Telefomin, ca. 5°S; 141°15'E], W.Sepik d. P.Beron leg.", "Copelatus nomax J.B.Br. det.V. Guéorguiev 1917" [partly hw] (NHMW). 1 male "PAPUA N.G.: Sandaun Prov. Telefomin, 16.-17.5.1998 trail to Eliptamin 1700–1800 m; leg. Riedel" (NHMW).

Diagnosis. Beetle medium-sized; usually piceous, with brown pronotal sides; more or less shiny to submatt; pronotum with distinct lateral bead; antennomeres simple or stout; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 long and narrow, without concavity, with anterior row of 18–27 and posterior row of eight relatively short setae; median lobe curved, with apex curved downwards and slightly rounded in lateral view. The species is similar to *E. me* but its protarsomere 5 is not modified. From *E. may* sp. n., it differs in a large, strongly curved anterolateral hook-like seta of the male protarsomere 4.

Description. *Size and shape*: Beetle small to medium-sized (TL-H 3.35–4.5 mm, TL 3.7–4.9 mm, MW 1.75–2.4 mm for Papua populations), with oblong-oval habitus, broadest at elytral middle. Medium-sized specimens more common. *Coloration*: Head, disc of pronotum and elytra dark brown to piceous, pronotal sides broadly reddish brown, some specimens with narrow reddish sutural lines; head appendages and legs reddish brown, distally darker (Fig. 2). Teneral specimens paler.



Figures 2–4. Habitus and coloration **2** *Exocelina okbapensis* sp. n. **3** *E. okbapensis hajeki* ssp. n. **4** *E. may* sp. n.

Surface sculpture: Head with dense punctation (spaces between punctures 1–2 times size of punctures), finer and sparser anteriorly; diameter of punctures equal to diameter of cells of microreticulation. Pronotum and elytra with distinct punctation, sparser and finer than on head. Elytral punctation slightly sparser than pronotal one. Pronotum

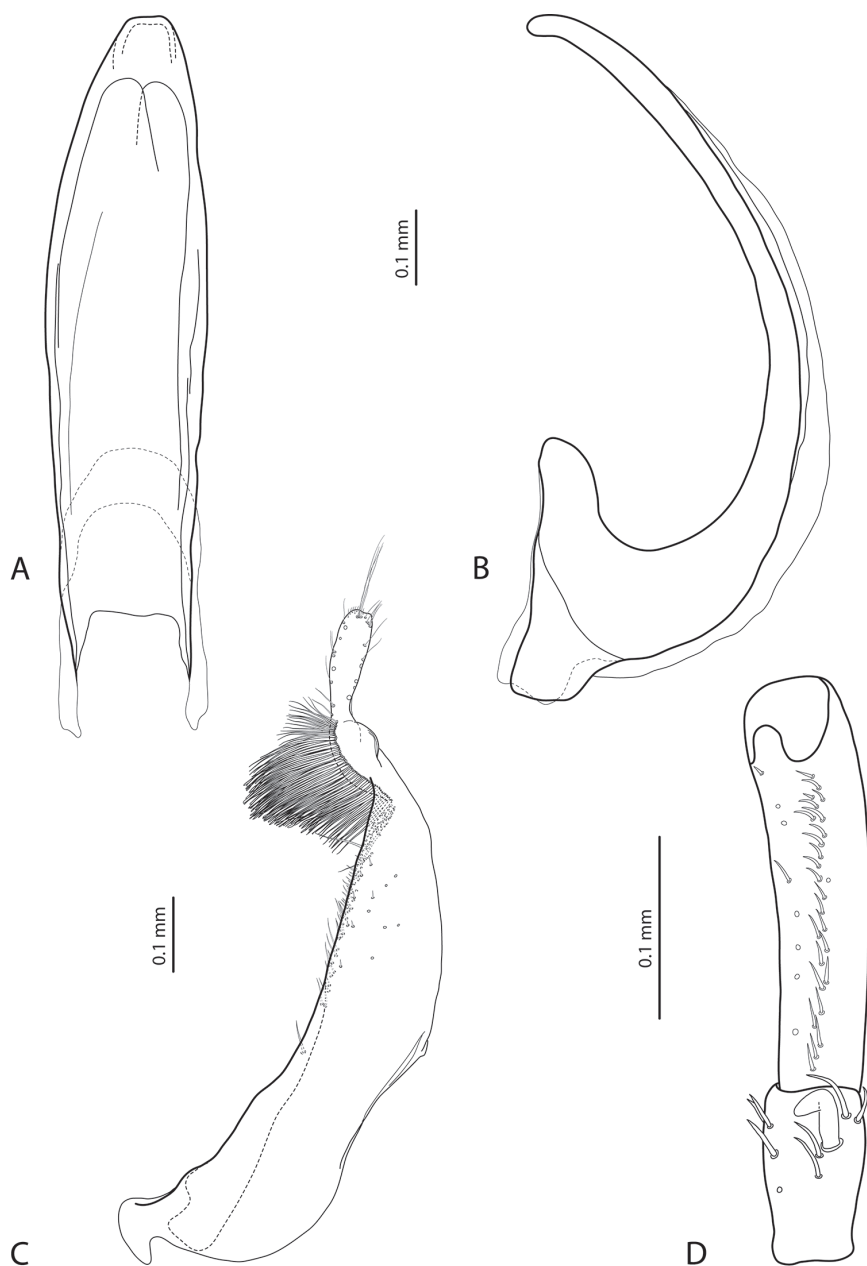


Figure 5. *Exocelina okbapensis* sp. n. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

and elytra with evident microreticulation, dorsal surface more or less shiny to submatt. Head with microreticulation stronger. Metaventricle and metacoxa distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and very fine sparse punctation.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly joined. Abdominal ventrite 6 broadly rounded.

Male: Antennae simple or stout (Fig. 2). Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 18–27 and posterior row of 8 relatively short setae (Fig. 5D). Median lobe curved, with apex curved downwards and slightly rounded in lateral view and evenly tapering to the broadly pointed apex in ventral view. Paramere with distinct notch on its dorsal side and small, evidently separated subdistal part with a tuft of very dense, strong setae; proximal setae inconspicuous, strongly reduced in some specimens (Fig. 5A–C). Abdominal ventrite 6 with 5–16 long lateral striae on each side.

Holotype: TL-H 4.2 mm, TL 4.6 mm, MW 2.25 mm.

Female: Antennae simple. Pro- and mesotarsi not modified. Abdominal ventrite 6 without striae.

Variability. In some males, antennomeres 2–6 slightly thicker, stout. Some specimens have the dorsal microreticulation more strongly impressed. Two specimens from Sandaun are smaller than most of the Papua specimens (TL-H 3.3–3.65 mm, TL 3.7–4.1 mm, MW 1.75–1.95 mm) and have less dense subdistal setae on the paramere.

Distribution. Papua: Pegunungan Bintang Regency and Papua New Guinea: Sandaun Province (Fig. 12).

Habitat. Near Ok Bap, the species was collected in small creeks as well as in slowly flowing, sun exposed irrigation ditches along road.

Etymology. The species is named after Ok Bap, where most of the specimens were collected. The name is an adjective in the nominative singular.

1a. *Exocelina okbapensis hajeki* Shaverdo & Balke, ssp. n.

<http://zoobank.org/56F86E0C-984E-4066-92FB-4739CD8DD7EC>

Figs 3, 6

Exocelina undescribed sp. MB0066: Toussaint et al. 2014: Supplementary figs 1–4, tab. 2.

Type locality. Papua: Jayawijaya Regency, Wamena, 04°03.6'S; 139°01.9'E, 2050 m a.s.l.

Type material. *Holotype:* male “IN, PA: Jayawijaya Regen., Baliem vall., 10km NE Wamena, forest above ‘Baliem vall. Resort’, 2050 m, 2–3.II.2015, 04°03.6'S, 139°01.9'E; J.Hájek & J.Šumpich leg” (NMPC). *Paratypes:* 2 males and 7 females with the same label as the holotype, one female with an additional label “M. Balke 7372” (MZB, NHMW, NMPC, ZSM). 6 males, 11 females “INDONESIA, Papua: Jayawijaya Distr., Ballem valley, 10km NE of Wamena, forest above “Baliem valley resort”, 04°03.6'S, 139°01.9'E, 2050 m; 2-3.ii.2015 J.Hájek & J.Šumpich leg.” (NHMW, NMPC, ZSM). 1 male “66 M. Balke” [green], “measured J. Parkin 43”, “Indonesia: Irian Jaya, N Wamena, Cerny, M. Balke: MB 66” (ZSM).

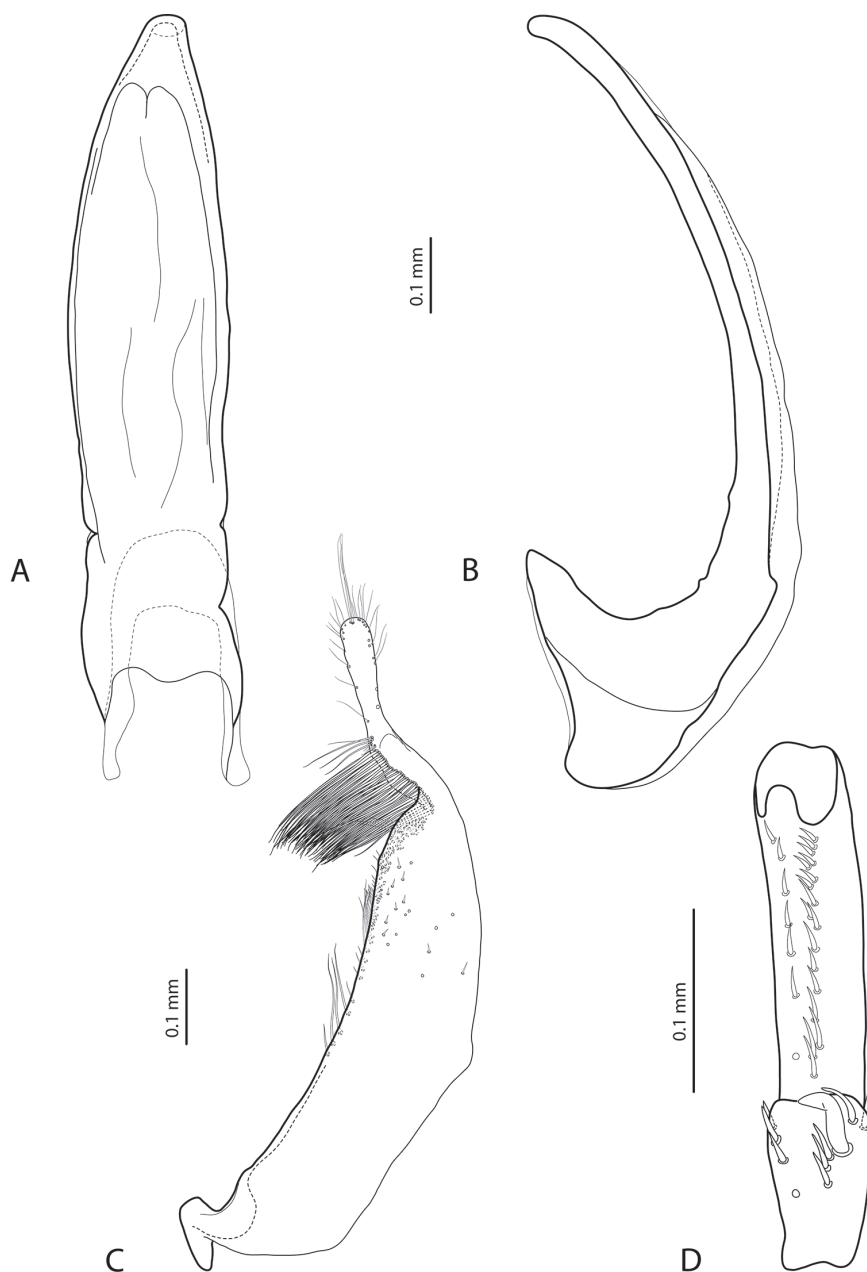


Figure 6. *Exocelina okbapensis hajeki* ssp. n. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

Diagnosis. Beetle medium-sized; dark brown to piceous, with reddish brown pronotal sides; submatt; pronotum with distinct lateral bead; male antennomeres 2–6 slightly, but evidently enlarged, female antennomeres 2–6 stout; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 long and narrow, without

concavity, with anterior row of 26 and posterior row of eight relatively short setae; median lobe curved, with apex curved downwards and slightly rounded in lateral view. The subspecies differs from the nominative subspecies in the modified antennae, in the shape and setation of the paramere, and in the more striated abdominal ventrite 6; some beetles are also somehow slightly more matt due to more strongly impressed dorsal microreticulation.

Description. *Size and shape:* Beetle medium-sized (TL-H 3.75–4.5 mm, TL 4.1–4.9 mm, MW 2.0–2.3 mm), with oblong-oval habitus, broadest at elytral middle (Fig. 3). *Coloration:* As in nominative subspecies.

Surface sculpture: As in nominative subspecies apart from pronotum and elytra with evident, rather strongly impressed microreticulation, dorsal surface submatt.

Structures: As in nominative subspecies.

Male: Antennomeres 2–6 slightly, but evidently enlarged, antennomere 2 with slightly extended external upper angle (Fig. 3). Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 26 and posterior row of eight relatively short setae (Fig. 6D). Median lobe curved, with apex curved downwards and slightly rounded in lateral view and evenly tapering to the slightly truncate apex in ventral view. Paramere with distinct notch on dorsal side and small, evidently separated subdistal part with a tuft of very dense, strong setae; proximal setae inconspicuous (Fig. 6A–C). Abdominal ventrite 6 with numerous (16–22) long lateral striae on each side.

Holotype: TL-H 4.0 mm, TL 4.4 mm, MW 2.05 mm.

Female: Antennomeres 2–6 stout, in some specimens only slightly more slender than in males, antennomere 2 with slightly extended external upper angle; pro- and mesotarsi not modified and abdominal ventrite 6 without striae.

Variability. In some males, antennomeres 2–6 more strongly enlarged, in some others less strongly enlarged, similar to those of females.

Distribution. Papua: Jayawijaya Regency. The subspecies is known only from the type locality (Fig. 12).

Habitat. Near Wamena, the species was collected from wet ground with weak water flow and forest puddles, which turn to a small creek during rain (Figs 13–14).

Etymology. The subspecies is named after our friend and colleague Jirí Hájek who collected almost all the specimens. The name is a noun in the genitive case.

2. *Exocelina may Shaverdo & Balke*, sp. n.

<http://zoobank.org/C403A69C-67D8-49AB-A65B-1A4D3BD166B9>

Figs 4, 7

Exocelina undescribed sp. MB0662: Toussaint et al. 2014: Supplementary figs 1–4, tab. 2.

Exocelina undescribed sp. MB0671: Toussaint et al. 2014: Supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Sandaun Province, May River, 04°49.80'S; 141°38.17'E, above 2000 m a.s.l.

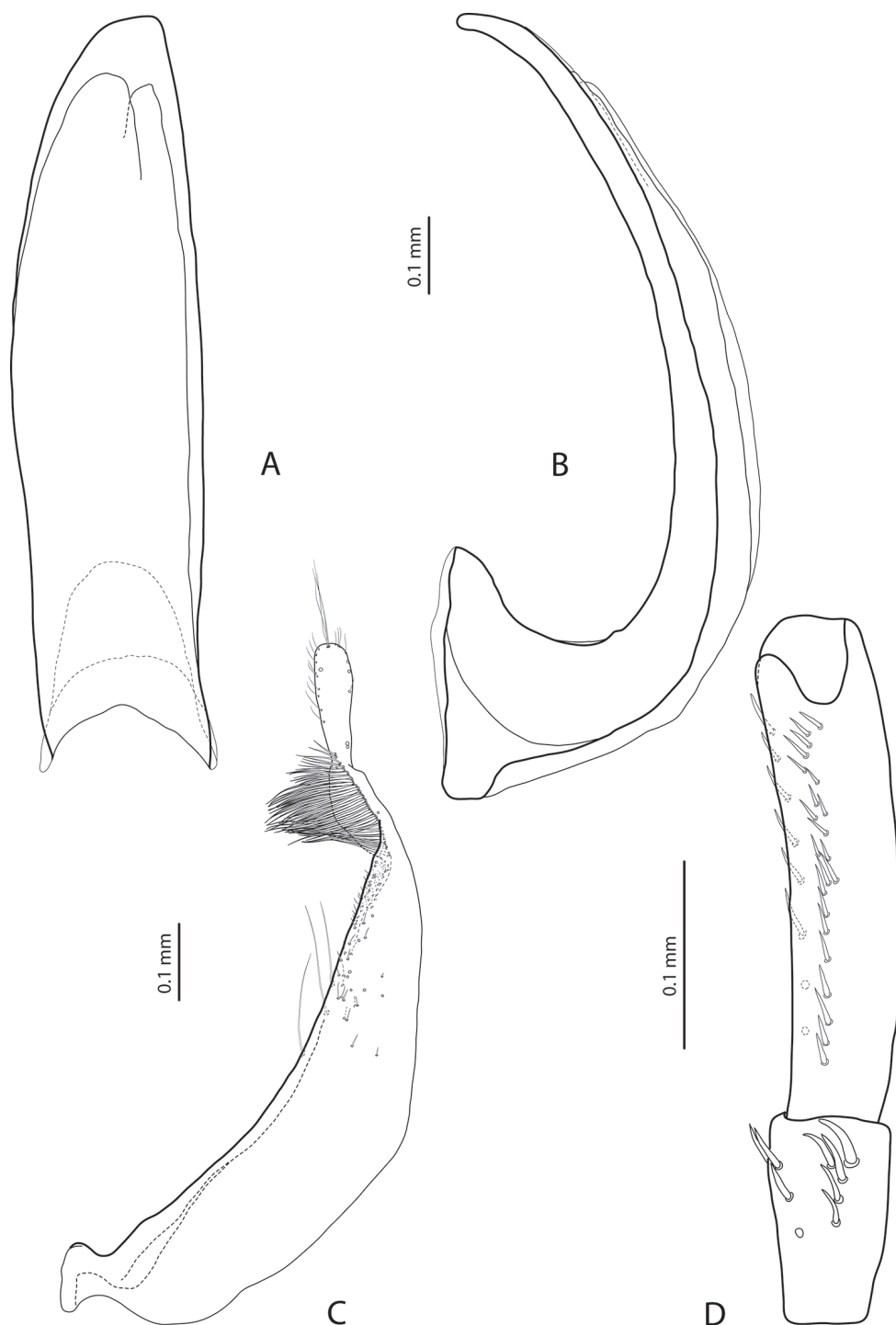


Figure 7. *Exocelina may* sp. n. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

Type material. *Holotype*: male “M. Balke 662”, “Papua New Guinea: Sandaun, May River (WB47), 15.x.2003, K. Sagata, M. Balke: MB 662” (ZSM). *Paratypes*: 1 male, 2 females “Papua New Guinea: Sandaun, May River, 8.x.2003, 2627m, 4 49.779S 141 38.174E K. Sagata (WB47)”, male with an additional label “M. Balke 663” (ZSM). 1 male “M. Balke 664”, “Papua New Guinea: Sandaun: Sandaun, May River (WB47), 15.x.2003, K. Sagata, M. Balke: MB 664” (ZSM).

Additional material. 1 male “M. Balke 671”, “Papua New Guinea: Sandaun, Mekil (WB106), 14.x.2003, K. Sagata, M. Balke: MB 671” (ZSM). 1 male “M. Balke 679”, “Papua New Guinea: Sandaun, Mekil (WB106), 14.x.2003, K. Sagata, M. Balke: MB 679” (ZSM).

Diagnosis. Beetle medium-sized; piceous, with brown head and sides of pronotum; submatt, with distinct punctation and microreticulation; male antennae simple; male protarsomere 4 with small (smaller than more laterally situated large seta), weakly curved anterolateral “hook-like” seta; male protarsomere 5 long and narrow, without concavity, with anterior and posterior rows of relatively short setae; median lobe curved, with apex curved downwards and slightly rounded in lateral view. The species is similar to the submatt representatives of the *E. aipo*-group with non-modified antennae but differs from them in non-modified male protarsomere 5. From *E. okbapensis* sp. n., it differs in the small and weakly curved anterolateral “hook-like” seta of the male protarsomere 4.

Description. *Size and shape*: Beetle medium-sized (TL-H 3.6–4.65 mm, TL 3.75–5.1 mm, MW 1.9–2.4 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head, pronotum and elytra dark brown to piceous, pronotal sides sometimes reddish brown; head appendages and legs reddish brown, distally darker (Fig. 4).

Surface sculpture: Head with relatively dense and coarse punctation (spaces between punctures 1–2 times size of punctures); diameter of punctures equal to diameter of cells of microreticulation. Pronotum with finer, sparser punctation, and more evenly distributed punctation than on head. Elytra with sparser punctation than on pronotum. Pronotum and elytra with distinct microreticulation, dorsal surface submatt. Head with microreticulation slightly stronger. Metaventricle, metacoxa, and abdominal ventrites distinctly microreticulate. Metacoxal plates with longitudinal striae and transverse wrinkles; abdominal ventrites with striae. Ventricle with inconspicuous punctation, more evident on metacoxal plates and two last abdominal ventrites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively broad, slightly convex and smooth, with distinct lateral bead and few lateral setae; neck and blade of prosternal process evenly joined. Abdominal ventrite 6 broadly rounded.

Male: Antennae simple (Fig. 4). Protarsomere 4 with small (smaller than more laterally situated large seta), weakly curved anterolateral “hook-like” seta. Protarsomere 5 long and narrow, without concavity, ventrally with anterior row of 14–22 and posterior row of 4–9 relatively short setae (Fig. 7D). Median lobe curved, with apex

curved downwards and slightly rounded in lateral view. Paramere with distinct notch on its dorsal side and small, evidently separated subdistal part with a tuft of very dense, strong setae; proximal setae inconspicuous (Fig. 7A–C). Abdominal ventrite 6 with 4–9 lateral striae on each side.

Holotype: TL-H 4.25 mm, TL 4.7 mm, MW 2.15 mm.

Female: Without evident differences in external morphology from males, except for non-modified pro- and mesotarsi and abdominal ventrite 6 without striae.

Variability. Two males from Mekil have dorsal punctation finer and microreticulation less strongly impressed, therefore, they are shinier. Shape and setation of the genitals are very similar to those of the May specimens but also difficult to estimate precisely since both beetles are teneral. For these reasons, they are considered to belong to the species but are not included into the type series.

Distribution. Papua New Guinea: Sandaun Province. The species is known from two localities in the southern part of the province (Fig. 12).

Etymology. The species is named after May River. The name is a noun in the nominative singular standing in apposition.

3. *Exocelina ketembang* (Balke, 1998)

Figs 8, 10

Copelatus (Papuadytes) ketembang Balke, 1998: 332; Nilsson 2001: 77 (catalogue).

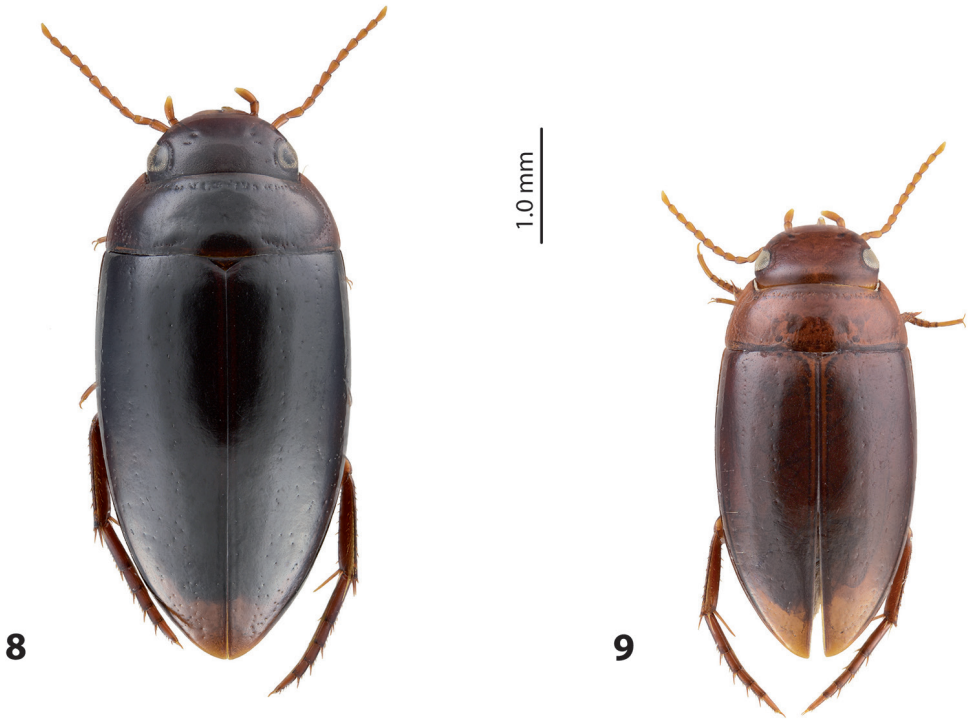
Papuadytes ketembang (Balke, 1998): Nilsson and Fery 2006: 56 (comb.n.).

Exocelina ketembang (Balke, 1998): Nilsson 2007: 34 (comb.n.).

Exocelina ketembang (Balke, 1998): MB0680: Toussaint et al. 2014: Supplementary figs 1–4, tab. 2.

Type locality. Papua: Pegunungan Bintang Regency, Borme, according to the original description.

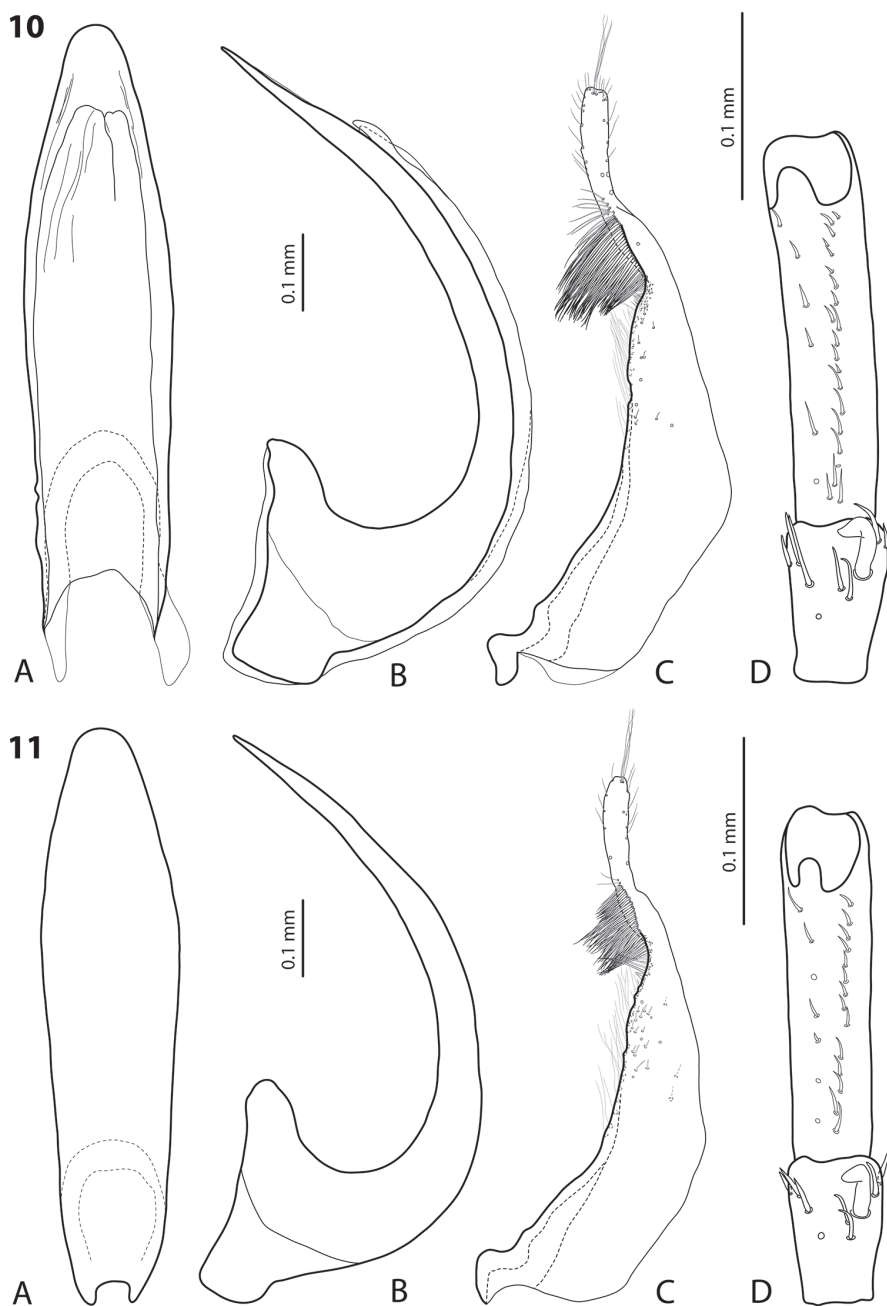
Type material studied. *Holotype*: The holotype and 46 paratypes from the same locality have not been found. According to the original description (Balke 1998), they were deposited at the NHMW and had labels with the following data: Irian Jaya, Jayawijaya Province, Borme, 900 m, 18.viii.1992, IR 92#17, M. Balke leg. No beetles with such label data have been found in the collections of NHMW, ZSM, CGW, or in London. Moreover, the label data of this locality (17 from 1992) are wrongly given in the original descriptions not only for this species but also for *Copelatus takime* Balke, 1998: locality 17 is not Borme but Kali Takime, as the labels of the type specimens of *C. takime* state. There are four males (three in NHMW and one in CGW) with the geographical labels “IRIAN JAYA Zentralmassive 140°25'E, 04°24'S” and “14./17. viii.1992 Borme, 1900 m leg. Balke (11)”, one of which has a red holotype label. Therefore, perhaps, the holotype label was simply misquoted in the original description. However, since the type series, indicated in the original description, is very large (47 specimens), investigations on this subject are ongoing.



Figures 8–9. Habitus and coloration **8** *Exocelina ketembang* (Balke, 1998) **9** *E. talaki* (Balke, 1998).

Paratypes: 2 males “IRIAN JAYA: Borme, Tarmlu, 1500 m 6.9.1993”, “ca. 140°25'E, 04°24'S leg. M. Balke (4)”, “Paratypus Copelatus ketembang Balke des. 1997” [red], one of them with an additional green label “M. Balke 3284” (NHMW). 3 males “IRIAN JAYA: Borme, Tarmlu, 1500 m, 6.ix.1993”, “ca. 140°25'E, 04°24'S leg. M. Balke (4-6)”, “Paratypus Copelatus ketembang Balke des. 1997” [red], one of them with two additional labels “M. Balke 3285” [green] and “M. Balke 6410” [green text] (NHMW). 4 males “IRIAN JAYA Zentralmassive 140°25'E, 04°24'S”, “14./17.8.1992 Borme, 1900 m leg. Balke (11)”, “Paratypus Copelatus ketembang Balke des. 1997” [red] (CGW, NHMW). 1 male “IRIAN JAYA: 1.x.1993 Eme Gebiet Okloma, 1500 m”, “ca. 139°55'E, 04°14'S leg. M. Balke (28)”, “Paratypus Copelatus ketembang Balke des. 1997” [red] (NHMW). 5 males, 4 females “IRIAN JAYA, 7.9.1992 Kono, 1800 m 139°47'E, 04°21'S, leg. Balke (41)” (CGW, NHMW); the females might belong to two species, *Exocelina ketembang* and *E. damantiensis* (Balke, 1998).

Additional material. Indonesia: Papua Province: Pegunungan Bintang Regency: 1 female “IRIAN JAYA Zentralmassive 140°25'E, 04°24'S”, “14./17.8.1992 Borme, 1900 m leg. Balke (11)” (NHMW). 1 male, 1 female “IRIAN JAYA Zentralmassive 140°25'E, 04°24'S”, “Borme, 1800 m 16.8.1992 leg. Balke (12, 12 A)” (NHMW). **Papua New Guinea: Sandaun Province**: 1 male “M. Balke 670”, “Papua New Guinea: Sandaun, Mekil (WB106), 14.x.2003, K.Sagata, M. Balke: MB 670” (ZSM). 1 male “M. Balke 680”, “Papua New Guinea: Sandaun, Mekil (WB106),



Figures 10–11. 10 *Exocelina ketembang* (Balke, 1998) 11 *E. talaki* (Balke, 1998) **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

14.x.2003, K. Sagata, M. Balke: MB 680" [04°48.742S 141.39.075E] (ZSM). 1 male "M. Balke 3727" [green], "Papua New Guinea: Sandaun, Ofektaman, 820 m, 17.x.2008, 5.04.113S 141.35.841E, Ibalim (PNG 190)" (ZSM).

Females of doubtful identity. Indonesia: Papua Province: Pegunungan Bintang Regency: 1 female “IR 92#17B: West New Guinea, Tanime, 1600 m, 20.viii.1992, Balke” (NHMW); this female might belong to three species: *Exocelina ketembang*, *E. danae* (Balke, 1998) and *E. damantiensis*. 1 female “IRIAN JAYA, 7.ix.1992 Kono, 1800m 139°47'E, 04°21'S, leg. Balke (41) (CGW), the female might belong to two species: *Exocelina ketembang* and *E. damantiensis*. **Papua New Guinea: Sandaun Province:** 3 females “Papua New Guinea: Sandaun, MekilK [sic!], 1718 m, 14.x.2003, 4 48.742S 141 39.075E, K. Sagata (WB 106)” (ZSM); these females might belong to two species: *E. sandaunensis* Shaverdo & Balke, 2014 and *E. ketembang*. 7 females “Papua New Guinea: Sandaun, Ofektaman, 820 m, 17.x.2008, 5.04.113S 141.35.841E, Ibalim (PNG 190)” (ZSM); these females might belong to three species: *E. sandaunensis*, *E. aipomek* (Balke, 1998), and *E. ketembang*.

Diagnosis. Beetle medium-sized (TL-H 3.9–4.35 mm); oblong-oval; dark brown to piceous, sometimes with reddish brown pronotal sites and head anteriorly; shiny, with very fine punctation and weakly impressed microreticulation; pronotum with distinct lateral bead; male antennae simple (Fig. 8); male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male protarsomere 5 long and narrow, without concavity, with anterior row of 21 and posterior row of six relatively short setae; median lobe strongly curved, sharply pointed in lateral view, evenly tapering, with narrowly rounded apex in ventral view; paramere with notch on its dorsal side and small, less evidently separated subdistal part with a tuft of dense setae; proximal setae inconspicuous (Fig. 10A–D). For complete description, see Balke (1998).

Distribution. Papua: Pegunungan Bintang Regency and PNG: Sandaun Province (Fig. 12).

4. *Exocelina talaki* (Balke, 1998)

Figs 9, 11

Copelatus (Papuadytes) talaki Balke, 1998: 337; Nilsson 2001: 77 (catalogue).

Papuadytes talaki (Balke, 1998): Nilsson and Fery 2006: 56 (comb.n.).

Exocelina talaki (Balke, 1998): Nilsson 2007: 34 (comb.n.).

Type locality. Papua: Pegunungan Bintang Regency, Borme, ca. 04°24'S; 140°25'E, 1200 m a.s.l.

Type material studied. *Holotype*: male “IRIAN JAYA: Borme ca. 140°25'E, 04°24'S 1200 m, 2.9.1993 leg. M. Balke (1)”, “HOLOTYPUS” [red], “*Copelatus talaki* Balke des. 1997” [red] (NHMW). *Paratypes*: Three females with the same label as the holotype and additionally with red labels “*Paratypus Copelatus talaki* Balke des. 1997”, one of them with two additional labels “M. Balke 3294” [green] and “M. Balke 6415” [green text] (NHMW).

Diagnosis. Beetle small (TL-H 3.25–3.4 mm); oblong-oval; reddish brown to brown, with paler head and pronotum, with fine punctation and weakly impressed microreticulation, shiny; pronotum with distinct lateral bead; male antennae simple (Fig. 9); male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; male

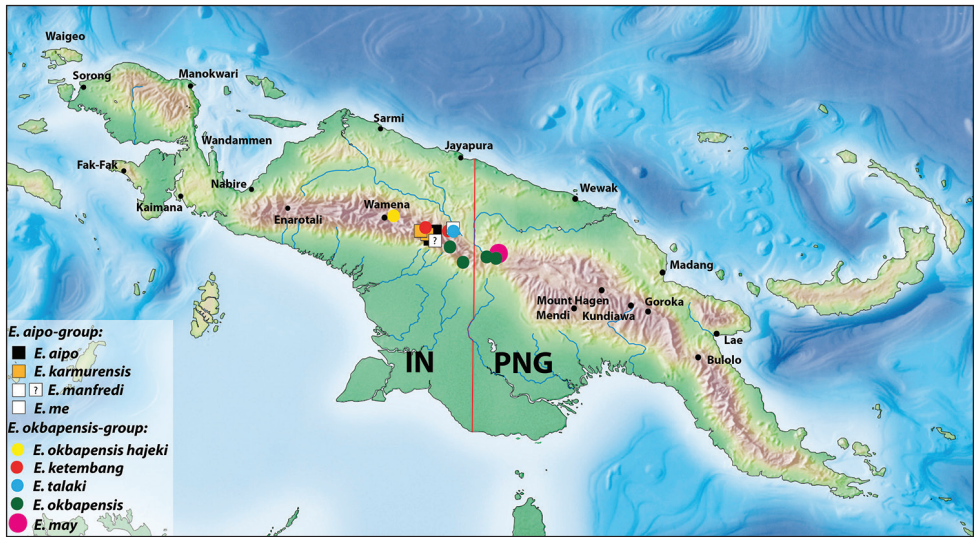


Figure 12. Map of New Guinea showing distribution of the species of both groups. The white square with a question mark indicates the male from Aipomek-Tanime area, which most likely belongs to *E. manfredi* (Balke, 1998).

protarsomere 5 long and narrow, without concavity, with anterior row of 14 and posterior row of seven relatively short setae; median lobe strongly curved, sharply pointed in lateral view, evenly tapering, with broadly pointed apex in ventral view; paramere with notch on its dorsal side and small, less evidently separated subdistal part with a tuft of dense setae; proximal setae inconspicuous (Fig. 11A–D). For complete description, see Balke (1998).

Distribution. Papua: Pegunungan Bintang Regency (Fig. 12). The species is known only from the type material.

Key to species of the *Exocelina aipo*- and *E. okbapensis*-groups

Since the representatives of the groups occur on the same geographic area (the central part of New Guinea), we treat them in the same key to simplify identification.

The key is based mostly on male characters. In many cases females cannot be assigned to species due to similarity of their external and internal structures (for female genitalia see figs 17a and 17b in Shaverdo et al. (2005)). Some species are rather similar in external morphology; therefore, in most cases male genitalia need to be studied for reliable species identification. Numbers in parentheses refer to the arrangement of species descriptions above.

- 1 Male protarsomere 5 concave ventrally, shorter, usually with some ventral setae enlarged and shifted to base (Fig. 1; figs 25–28 in Balke 1998)....**2 (*aipo*-group)**
- Male protarsomere 5 long and narrow, without concavity, setae not modified**5 (*okbapensis*-group)**

- 2 Beetle distinctly larger, TL-H: 4.4–5.4 mm. Male protarsomere 5 with concavity deep but small and rounded, without enlarged ventral setae (fig. 26 in Balke 1998). Male antennae distinctly modified (fig. 9 in Balke 1998)***karmurensis***
- Beetle distinctly smaller, TL-H: 3.5–4.55 mm. Male protarsomere 5 with concavity large, with some ventral setae enlarged and shifted to base (as in fig. 25 in Balke 1998). Male antennomeres distinctly modified or just stout.....**3**
- 3 Male antennomeres stout (fig. 10 in Balke 1998). Dorsal punctuation stronger and denser ***manfredi***
- Male antennae distinctly modified (figs 8, 11 in Balke 1998). Dorsal punctuation weaker **4**
- 4 Male antennomeres 3–6 strongly enlarged, 3–5 largest, 4 and 5 slightly rounded, 2 and 7–9 slightly enlarged (fig. 8 in Balke 1998). Male protarsomere 5 with concavity deeper (fig. 25 in Balke 1998). Dorsal punctuation distinct but weak ***aipo***
- Male antennomeres 3–7 distinctly enlarged, 3–5 largest, not rounded, 2 and 8–9 slightly enlarged (fig. 11 in Balke (1998)). Male protarsomere 5 with concavity shallower (fig. 27 in Balke (1998)). Dorsal punctuation stronger and denser.....***me***
- 5 Male protarsomere 4 with weakly curved anterolateral “hook-like” seta, which is smaller or equal to more laterally situated large seta (Fig. 7D)..... **(2) *may* sp. n.**
- Male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta, evidently larger than more laterally situated large seta (e.g., Fig. 5D) **6**
- 6 Median lobe with straight, sharply pointed apex in lateral view.....**7**
- Median lobe with apex slightly to strongly curved downwards, rounded in lateral view..... **8**
- 7 Beetle larger, TL-H: 3.9–4.35 mm, dark brown to piceous (Fig. 8)..... **(3) *ketembang***
- Beetle smaller, TL-H: 3.25–3.4 mm, reddish brown to brown (Fig. 9)..... **(4) *talaki***
- 8 Antennomeres 2–6 simple, in some males slightly stout (Fig. 3). Abdominal ventrite 6 with 5–16 long lateral striae on each side. Median lobe and paramere as in Fig. 5A–C **(1) *okbapensis* sp. n.**
- Antennomeres 2–6 slightly, but evidently enlarged in males and stout in females (Fig. 2). Abdominal ventrite 6 with 16–22 long lateral striae on each side. Median lobe and paramere as in Fig. 6A–C..... **(1a) *okbapensis hajeki* ssp. n.**

Habitats

The studied species have the same habitat preferences as those described in Shaverdo et al. (2012). They are associated with running water, but avoid the current, i.e., their preferred microhabitats are small creeks, small and quiet backflows, puddles at the edge of streams and creeks, and other similar situations (e.g., Figs 13–14). Habitats can be shadowed (in the forest) or sun exposed.



Figure 13. Forest puddle, habitat of *Exocelina okbapensis hajeki* ssp. n. 10 km NE Wamena, forest above 'Baliem vall. Resort'. Photo by Jiří Hájek.



Figure 14. Wet forest ground, habitat of *Exocelina okbapensis hajeki* ssp. n. 10 km NE Wamena, forest above 'Baliem vall. Resort'. Photo by Jiří Hájek.

Acknowledgements

We are grateful Jiří Hájek (Prague) for providing material and habitat photos for this study, Dr. H. Schillhammer (Vienna) for habitus photos and Prof. D. Bilton (Plymouth) for a linguistic review of the manuscript. Financial support for the study was provided by the FWF (Fonds zur Förderung der wissenschaftlichen Forschung – the Austrian Science Fund) through project P 24312-B17 to Helena Shaverdo. Michael Balke was supported by the German Science Foundation (DFG BA2152/11-1, 11-2, 19-1).

References

- Balke M (1998) Revision of New Guinea *Copelatus* Erichson, 1832 (Insecta: Coleoptera: Dytiscidae): The running water species, Part I. *Annalen des Naturhistorischen Museum Wien* 100B: 301–341.
- Broun T (1886) *Manual of the New Zealand Coleoptera*. Parts III and IV. Wellington, Government Printer, 817–973.
- Nilsson AN (2001) Dytiscidae. *World catalogue of insects*. Vol. 3. Stenstrup, Apollo Books, 395 pp.
- Nilsson AN (2007) *Exocelina* Broun, 1886, is the valid name of *Papuadytes* Balke, 1998. *Laticsimus* 23: 33–34.
- Nilsson AN, Fery H (2006) *World Catalogue of Dytiscidae – corrections and additions*, 3 (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* 76: 55–74.

- Shaverdo HV, Balke M (2014) *Exocelina kinibeli* sp.n. from Papua New Guinea, a new species of the *E. ullrichi*-group (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* 84: 31–40.
- Shaverdo HV, Sagata K, Balke M (2005) Five new species of the genus *Papuadytes* Balke, 1998 from New Guinea (Coleoptera: Dytiscidae). *Aquatic Insects* 27(4): 269–280. <https://doi.org/10.1080/01650420500290169>
- Shaverdo HV, Surbakti S, Hendrich L, Balke M (2012) Introduction of the *Exocelina ekari*-group with descriptions of 22 new species from New Guinea (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 250: 1–76. <https://doi.org/10.3897/zookeys.250.3715>
- Shaverdo HV, Hendrich L, Balke M (2013) *Exocelina baliem* sp. n., the only known pond species of New Guinea *Exocelina* Broun, 1886 (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 304: 83–99. <https://doi.org/10.3897/zookeys.304.4852>
- Shaverdo H, Sagata K, Panjaitan R, Menufandu H, Balke M (2014) Description of 23 new species of the *Exocelina ekari*-group from New Guinea, with a key to all representatives of the group (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 468: 1–83. <https://doi.org/10.3897/zookeys.468.8506>
- Shaverdo H, Panjaitan R, Balke M (2016a) A new, widely distributed species of the *Exocelina ekari*-group from West Papua (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 554: 69–85. <https://doi.org/10.3897/zookeys.554.6065>
- Shaverdo H, Sagata K, Balke M (2016b) Description of two new species of the *Exocelina broschii*-group from Papua New Guinea, with revision and key to all representatives of this species group (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 577: 125–148. <https://doi.org/10.3897/zookeys.577.7254>
- Shaverdo H, Sagata K, Balke M (2016c) Taxonomic revision of New Guinea diving beetles of the *Exocelina danae* group, with description of ten new species (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 619: 45–102. <https://doi.org/10.3897/zookeys.619.9951>
- Shaverdo H, Wild M, Sumoked B, Balke M (2017) Six new species of the genus *Exocelina* Broun, 1886 from Wano Land, New Guinea (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 665: 93–120. <https://doi.org/10.3897/zookeys.665.11792>
- Toussaint EFA, Hall R, Monaghan MT, Sagata K, Ibalim S, Shaverdo HV, Vogler AP, Pons J, Balke M (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nature Communications* 5, 4001: 1–10 [10 supplements] <https://doi.org/10.1038/ncomms5001>

Ichthyofauna of Ceará-Mirim River basin, Rio Grande do Norte State, northeastern Brazil

Nathalia Kaluana Rodrigues da Costa¹, Roney Emanuel Costa de Paiva^{1,2},
Márcio Joaquim da Silva^{1,2}, Telton Pedro Anselmo Ramos¹, Sergio Maia Queiroz Lima¹

1 Universidade Federal do Rio Grande do Norte, Centro de Biociências, Departamento de Botânica e Zoologia, Laboratório de Ictiologia Sistemática e Evolutiva, Campus Central, Lagoa Nova, CEP 59078-900, Natal, RN, Brazil **2** Programa de Pós-Graduação em Sistemática e Evolução

Corresponding author: Telton Pedro Anselmo Ramos (telton@gmail.com)

Academic editor: D. Bloom | Received 27 May 2017 | Accepted 24 September 2017 | Published 13 November 2017

<http://zoobank.org/0DBBB3C6-239E-4492-B36A-30DCE1FB4996>

Citation: Costa NKR, Paiva REC, Silva MJ, Ramos TPA, Lima SMQ (2017) Ichthyofauna of Ceará-Mirim River basin, Rio Grande do Norte State, northeastern Brazil. ZooKeys 715: 39–51. <https://doi.org/10.3897/zookeys.715.13865>

Abstract

Ichthyological studies in coastal basins of the Mid-Northeastern Caatinga ecoregion were first conducted in the early 20th century, including collections from the Ceará-Mirim River basin, in northeastern Brazil. Besides a few systematics and ecological studies, the knowledge on fishes from this watershed is still considered partial and restricted to the freshwater portion. Thus, the objective of this paper was to conduct a comprehensive ichthyological survey of the entire Ceará-Mirim River basin, from the headwaters to the estuarine area. Fish surveys were conducted from 2011 to 2016 using varied fishing gear, resulting in the record of 63 native species (24 freshwater, 15 estuarine, and 24 marine species) and two introduced species. Four species are putatively endemic to the ecoregion, and 48 consist of new records for the basin. According to the Brazilian's threatened fish list, three species are currently classified as 'vulnerable' (*Megalops atlanticus*, *Hippocampus reidi* and *Mycteroperca bonaci*), four as 'near threatened' (*Kryptolebias hermaphroditus*, *Dormitator maculatus*, *Lutjanus synagris* and *L. jocu*) and three as 'data deficient' (*Cheirodon jaguaribensis*, *Mugil curema* and *Sphoeroides testudineus*). The Ceará-Mirim River basin does not have any protected areas and has been suffering multiple anthropogenic impacts, however the "Centro Tecnológico de Aquicultura" (Aquaculture Technological Center) of the Universidade Federal do Rio Grande do Norte (CTA/UFRN) at the lower portion of the basin may help in the conservation of the estuarine and estuarine fish species.

Keywords

Mid-Northeastern Caatinga Ecoregion, coastal basin, fishes of Caatinga and Atlantic Forest, estuarine ichthyofauna, inventory

Introduction

The Mid-Northeastern Caatinga freshwater ecoregion (MNCE) located in the extreme northeast Brazil comprises the drainages between the largest perennial rivers of the region, the São Francisco and Parnaíba (Albert et al. 2011, Rosa et al. 2003). When compared to adjacent ecoregions, its hydrographical network is simpler and composed of small to medium size basins. In addition, most of its rivers are intermittent due to the predominance of the semi-arid climate (Rosa et al. 2003). Their margins usually present xeric shrublands and thorny forests of the Caatinga vegetation, except for the humid highland enclaves (Rosa and Groth 2004), and for a narrow strip of land running along the eastern coast of Brazil that harbors fragmented remnants of Atlantic Forest. This strip extends from the State of Rio Grande do Norte to Alagoas in the MNCE (Rosa 2004).

One of the basins draining into the eastern coast of the MNCE is the Ceará-Mirim River basin, in the Rio Grande do Norte State, and presents an intermittent hydrological regimen in the upper and medium portions, while the lower stretch, located in the Atlantic Forest area, is perennial. This particular basin is of historic importance due to the "Stanford Expedition" specimen collection conducted in 1911. This expedition, led by the naturalist Edwin Chapin Starks, visited locations in northern and northeastern Brazil, and cataloged 11 fish species in the Ceará-Mirim River basin, including the original description of the armored catfish *Hypostomus pusarum* (Starks, 1913). Samples from this basin were also taken in 1933 by the "Departamento Nacional de Obras Contra Secas – DNOCS", in an effort by the "Comissão Técnica de Piscicultura do Nordeste do Brasil", institution managed by Rodolpho von Ihering, to study the region's ichthyofauna (Canan 2011).

Rosa (2004) recorded 11 freshwater fish species at the Ceará-Mirim River basin, without providing a list, and this same number were presented by Nascimento et al. (2014) in an ichthyofauna inventory of the basins of the Rio Grande do Norte State, also based on secondary data. In addition, studies on trophic ecology of freshwater fishes (Andrade et al. 2000, Gurgel et al. 2005, Dias and Fialho 2009) were also conducted in the basin. Recently, a new species was described (*Serrapinnus potiguar*, Jerep and Malabarba 2014), and the record of a self-fertilizing mangrove killifish (*Kryptolebias hermaphroditus*) was reported (Lira et al. 2015). Such occurrences corroborate the need for a broad ichthyofaunal inventory at this particular basin.

The lower portion of this basin is included within the northern limits of the Atlantic Forest domain and presents a mangrove forest area of approximately 3.15 km² (0.12% of the basin) (Maia et al. 2006) that might serve as feeding, breeding and refuge grounds for both marine and estuarine fish (Osório et al. 2011). This mangrove forest also comprises the "Centro Tecnológico de Aquicultura – CTA" (Aquaculture Technological Center) of the Universidade Federal do Rio Grande do Norte – UFRN, an area of approximately 7.7 km² that was previously used for shrimp farming. This area was incorporated to the UFRN facilities in 2007, to develop research, teaching and training courses on Biological Sciences. Although part of the lower portion of the

basin is somewhat protected by the CTA/UFRN, the Ceará-Mirim River basin suffers the impact of anthropogenic activities. Among such activities are the intake of domestic sewage, fertilizers and agrochemicals, as well as siltation and the deforestation of riparian forests or mangroves that compromise, especially, the aquatic biota (Soares et al. 2010).

Considering that knowledge on the ichthyofauna of a basin is paramount to monitoring anthropic impacts, as well as to encourage the development of further fish studies and other academic activities, the objective of this paper was to inventory the ichthyofauna of the Ceará-Mirim River basin. One important goal of this list is to provide data on the status of commercially significant and introduced species (Leão et al. 2011, Nóbrega et al. 2015) relevant to management and conservation actions, and compare this data with previous studies on the basin (Starks 1913, Nascimento et al. 2014).

Material and methods

Study area

The Ceará-Mirim River basin is approximately 2,770 km², which corresponds roughly to 4.9% of the Rio Grande do Norte State territory (Dias and Fialho 2009) (Figure 1). The main course of the Ceará-Mirim River begins in the municipality of Lajes (05°42'18.4"S, 036°14'49.6"W) and flows for about 120 km in the east direction through the municipalities of Bento Fernandes, Caiçara do Rio do Vento, Ceará-Mirim, Fernando Pedrosa, Jardim de Angicos, João Camara, Pedra Preta, Pedro Avelino, Poço Branco, Riachuelo and Taipu, draining into the ocean at the Extremoz municipality (05°40'33.2"S, 035°13'04.8"W) (Ipea 2016).

Eleven sites (S01-S11) from five municipalities (Lajes, Jardim dos Angicos, Taipu, Ceará-Mirim and Extremoz) were sampled from the headwaters to the estuary of the Ceará-Mirim drainage, including streams, rivers, mangroves and estuary, both at Caatinga (S01-S08) and Atlantic Forest (S09-S11) areas, in order to cover variable microhabitats (Table 1). Two sampling sites (S09-S10) are located at the CTA/UFRN area lower Ceará-Mirim River basin.

Data Collection

Specimen collections were conducted from June 2011 to September 2016 under permits 30532-1/2011 and 51341-1/2015 provided by ICMBio/SISBIO (Instituto Chico Mendes de Conservação da Biodiversidade/Sistema de Autorização e Informação em Biodiversidade). Fishes were captured using sieves, dip nets, trawl nets, cast nets, and traps. The specimens collected were anesthetized using eugenol, fixed in an aqueous solution of 10% formalin (approximately 8 days) and then preserved in 70% alcohol (Malabarba and Reis 1987). Voucher specimens were deposited at the ichthyologic collection of UFRN.

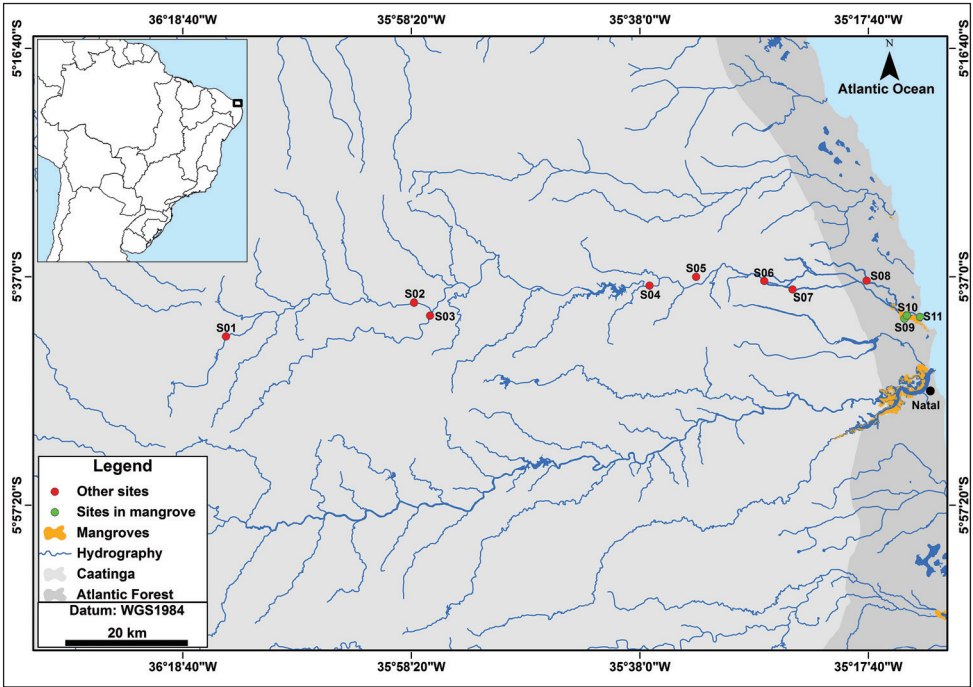


Figure 1. Map of the Ceará-Mirim River basin in Rio Grande do Norte State, northeastern Brazil, showing the sampling sites. Natal, the largest urban center of the state and location of the Potengi River estuary, is indicated by a black dot. Numbers are in accordance to Table 1.

Table 1. Sampling sites in Ceará-Mirim River basin, Rio Grande do Norte State, northeastern Brazil. CTA/UFRN = "Centro Tecnológico de Aquicultura" (Aquaculture Technological Center) of the Universidade Federal do Rio Grande do Norte.

ID	Municipality	Sampling sites	Biome	Latitude	Longitude
S01	Lajes	River	Caatinga	05°42'18.4"S	36°14'49.5"W
S02	Jardim de Angicos	River	Caatinga	05°39'17.1"S	35°58'05.2"W
S03	Jardim de Angicos	Stream	Caatinga	05°40'26.4"S	35°56'39.6"W
S04	Taipu	River	Caatinga	05°37'46.9"S	35°37'08.8"W
S05	Taipu	River	Caatinga	05°37'00.0"S	35°33'00.0"W
S06	Ceará-Mirim	River	Caatinga	05°37'21.6"S	35°26'56.2"W
S07	Ceará-Mirim	River	Caatinga	05°38'07.4"S	35°24'24.8"W
S08	Ceará-Mirim	Stream	Caatinga	05°37'20.3"S	35°17'49.6"W
S09	Extremoz	Mangrove (CTA/UFRN)	Atlantic Forest	05°40'42.6"S	35°14'27.1"W
S10	Extremoz	Mangrove (CTA/UFRN)	Atlantic Forest	05°40'27.5"S	35°14'22.9"W
S11	Extremoz	Estuary	Atlantic Forest	05°40'33.5"S	35°03'05.0"W

Data from the ichthyologic collections of the California Academy of Sciences which include the Stanford University collections (CAS-SU), and the Universidade Federal da Paraíba (UFPB) were also used in order to qualitatively supplement the species list.

The collected specimens were identified to the lowest taxonomic level possible according to available keys for respective groups (Araújo et al. 2004, Figueiredo and Menezes 1978, 1980, 2000, Jerep and Malabarba 2014, Marceniuk 2005, Menezes and Figueiredo 1980, 1985, Ploeg 1991, Buckup et al. 2007). Some individuals were photographed alive to provide a registry of their live coloration.

Data obtained was compared with the studies of Starks (1913) and Nascimento et al. (2014). The terminology and systematic classification follows Eschmeyer et al. (2016). Habitat details for each species were obtained from *Fishbase* (Froese and Pauly 2016) and *Catalog of Fishes* (Eschmeyer et al. 2016). The conservation status was classified according to the Brazilian lists of endangered species (MMA 2014), and 'near threatened' and 'data deficiency' species lists (ICMBio 2016). Endemism was defined as species restricted to a single ecoregion according Albert et al. (2011), in this case, the MNCE. Species relevant to artisanal fisheries in coast of Rio Grande do Norte State followed Nóbrega et al. (2015). The classification of introduced species followed Leão et al. (2011).

Results

Specimen collections were conducted along 11 sampling sites (S01-S11) (Table 1, Figure 1) from the upper to the lower Ceará-Mirim River basin, and resulted in the record of 62 fish species, including two non-native (*Oreochromis niloticus* and *Poecilia reticulata*) (Table 2, Figure 2). Based on records for the basin from all the sources consulted (Starks 1913, Nascimento et al. 2014), the species richness is 65, however, *Hoplosternum littorale* probably represents a misidentification (possibly *Megalechis thoracata* Valenciennes) (Table 1).

The 63 native species belong to 54 genera, 32 families and 11 orders. From those species, four (6.3%) are endemic to the MNCE (*Characidium bimaculatum*, *Cheirodon jaguaribensis*, *Hypostomus puarum* (Figure 2E) and *Serrapinnus potiguar*). Freshwater species represented 38.1% (24 species, excluding two non-native species), estuarine 23.8% (15 species), and marine 38.1% (24 of the total registered species) (Table 2). Among the 39 estuarine and marine species, 17 are important for artisanal fisheries (Nóbrega et al. 2015). Considering only the two sampling sites in the CTA/UFRN (S09-S10) 28 species were caught, including both introduced species, which represents almost half of the species recorded in the basin and 66.6% of the estuarine and marine species (Table 2).

Regarding the conservation status, *Megalops atlanticus* (recorded at S10 location), *Hippocampus reidi* and *Mycteroperca bonaci* (S11) are classified as 'vulnerable' (MMA 2014), *Kryptolebias hermaphroditus* (Figure 2F) (S09), *Dormitator maculatus* (S08), *Lutjanus sygnagris* and *L. jocu* (S11) as 'near threatened', while *Cheirodon jaguaribensis* (S05, S07 and S08), *Mugil curema* (S09 and 10) and *Sphoeroides testudineus* (S11) are listed as 'data deficient' (ICMBio 2016). Among those species, only *C. jaguaribensis* is a freshwater species. The remaining species are currently classified as 'least concern' or were not evaluated (Table 2).

Table 2. Systematic list of fish species of the Ceará-Mirim River basin. Abbreviations: F = freshwater, E = estuarine, M = marine, S = Starks (1913), N = Nascimento et al. (2014), T = this study, DD = deficient data, LC = least concern, NE = not evaluated, NT = near threatened, VU = vulnerable, END = endemic, MIS = misidentification, NNA = non-native, CAS(SU) = Stanford University collections in California Academy of Sciences, UFPB = Universidade Federal da Paraíba, UFRN = Universidade Federal do Rio Grande do Norte. * Importance for artisanal fisheries activities according to Nóbrega et al. (2015), + recorded in the "Centro Tecnológico de Aquicultura" (Aquaculture Technological Center) of the UFRN.

Order/Family/Species	Habitat	Status	Voucher	S	N	T
ELOPIFORMES						
Elopidae						
<i>Elops saurus</i> Linnaeus, 1766*	M	NE	UFRN 4189			X*
Megalopidae						
<i>Megalops atlanticus</i> Valenciennes, 1847*	M	VU	UFRN 4182			X*
CLUPEIFORMES						
Engraulidae						
<i>Anchovia clupeioides</i> (Swainson, 1839)*	M	LC	UFRN 0138			X*
<i>Anchoa januaria</i> (Steindachner, 1879)	M	LC	UFRN 2661			X*
CHARACIFORMES						
Crenuchidae						
<i>Characidium bimaculatum</i> Fowler, 1941	F	LC, END	UFRN 0841			X
Erythrinidae						
<i>Erythrinus erythrinus</i> (Bloch & Schneider, 1801)	F	LC	UFRN 0082			X
<i>Hoplias malabaricus</i> (Bloch, 1794)	F	LC	UFRN 0181	X	X	X
Anostomidae						
<i>Leporinus piau</i> Fowler, 1941	F	LC	UFRN 0839			X
Curimatidae						
<i>Steindachnerina notonota</i> (Miranda-Ribeiro, 1937)	F	LC	UFRN 4283	X		X
Prochilodontidae						
<i>Prochilodus brevis</i> Steindachner, 1875	F	LC	UFPB 9160		X	X
Serrasalmididae						
<i>Metynnis lippincottianus</i> (Cope, 1870)	F	LC	-		X	
Characidae						
<i>Astyanax</i> aff. <i>bimaculatus</i> (Linnaeus, 1758)	F	-	UFRN 0837	X	X	X
<i>Astyanax</i> aff. <i>fasciatus</i> (Cuvier, 1819)	F	-	UFRN 0835		X	X
<i>Compsura heterura</i> Eigenmann, 1915	F	LC	UFRN 0846			X
<i>Cheirodon jaguaribensis</i> Fowler, 1941	F	DD, END	UFRN 0851			X
<i>Hemigrammus marginatus</i> (Ellis, 1911)	F	LC	UFRN 0830		X	X
<i>Hemigrammus rodwayi</i> Durbin, 1909	F	NE	UFRN 0843			X
<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	F	LC	UFRN 0871		X	X
<i>Serrapinnus piaba</i> (Lütken, 1875)	F	LC	UFRN 0829	X	X	X
<i>Serrapinnus potiguar</i> Jerep & Malabarba, 2014	F	NE, END	UFRN 0870			X
SILURIFORMES						
Auchenipteridae						
<i>Trachehopterus galeatus</i> (Linnaeus, 1766)	F	LC	-	X	X	X
Heptapteridae						
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	F	LC	CAS(SU) 22446	X		

Order/Family/Species	Habitat	Status	Voucher	S	N	T
Ariidae						
<i>Cathorops arenatus</i> (Valenciennes, 1840)	E	LC	UFRN 4297			X*
<i>Sciades herzegbergii</i> (Bloch, 1794)*	E	LC	UFRN 4289			X*
Callichthyidae						
<i>Hoplosternum littorale</i> (Hancock, 1828)	F	LC, MIS			X	
Loricariidae						
<i>Hypostomus pusaarum</i> (Starks, 1913)	F	LC, END	UFRN 0842	X		X
ATHERINIFORMES						
Atherinopsidae						
<i>Atherinella brasiliensis</i> (Quoy & Gaimard, 1825)*	M	LC	UFRN 4161			X*
CYPRINODONTIFORMES						
Poeciliidae						
<i>Poecilia vivipara</i> Bloch & Schneider, 1801	F	LC	UFRN 0073	X	X	X*
<i>Poecilia reticulata</i> Peters, 1859	F	NNA	UFPB 9162			X
Cynolebiidae						
<i>Kryptolebias hermaphroditus</i> Costa, 2011	E	NT	UFRN 2475			X*
SYNGNATHIFORMES						
Syngnathidae						
<i>Hippocampus reidi</i> Ginsburg, 1933	M	VU	UFRN 2314			X
<i>Microphis lineatus</i> (Kaup, 1856)	E	NE	UFRN 4418			X
SYNBRANCHIFORMES						
Synbranchidae						
<i>Synbranchus</i> aff. <i>marmoratus</i> Bloch, 1795	F	-	UFRN 0186	X		X
PERCIFORMES						
Centropomidae						
<i>Centropomus undecimalis</i> (Bloch, 1792)*	M	LC	UFRN 0132			X*
Serranidae						
<i>Mycteroperca bonaci</i> (Poey, 1860)*	M	VU	UFRN 2313			X
<i>Rypiticus</i> sp.	M	-	UFRN 2310			X
Lutjanidae						
<i>Lutjanus jocu</i> (Bloch & Schneider, 1801)*	M	NT	UFRN 4409			X
<i>Lutjanus synagris</i> (Linnaeus, 1758)*	M	NT	UFRN 4408			X
Gerreidae						
<i>Eucinostomus argenteus</i> Baird & Girard, 1855*	M	NE	UFRN 0127			X*
<i>Eugerres brasilianus</i> (Cuvier, 1830)	M	NE	UFRN 0128			X*
<i>Ulaema lefroyi</i> (Goode, 1874)*	M	NE	UFRN 4135			X*
Mugilidae						
<i>Mugil curema</i> Valenciennes, 1836*	M	DD	UFRN 0129			X*
Cichlidae						
<i>Cichlasoma orientale</i> Kullander, 1983	F	LC	UFRN 0188	X		X
<i>Crenicichla menezesi</i> Ploeg, 1991	F	LC	UFRN 0555	X		X
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	F	NNA	UFPB 9165			X*
Scaridae						
<i>Sparisoma</i> sp.	M	-	UFRN 4414			X
<i>Sparisoma radians</i> (Valenciennes, 1840)	M	LC	UFRN 2312			X
Eleotridae						
<i>Dormitator maculatus</i> (Bloch, 1792)	E	NT	UFRN 0081			X

Order/Family/Species	Habitat	Status	Voucher	S	N	T
<i>Eleotris pisonis</i> (Gmelin, 1789)	E	LC	UFRN 4291			X*
<i>Erotelis smaragdus</i> (Valenciennes, 1837)	E	LC	UFRN 0131			X*
<i>Guavina guavina</i> (Valenciennes, 1837)	E	LC	UFRN 0088			X*
Gobiidae						
<i>Awaous tajasica</i> (Lichtenstein, 1822)	E	LC	UFRN 0183			X
<i>Bathygobius soporator</i> (Valenciennes, 1837)	M	LC	UFRN 4186			X*
<i>Ctenogobius boleosoma</i> (Jordan & Gilbert, 1882)	E	LC	UFRN 3195			X*
<i>Ctenogobius smaragdus</i> (Valenciennes, 1837)	E	LC	UFRN 3193			X*
<i>Ctenogobius shufeldti</i> (Jordan & Eigenmann, 1887)	E	LC	UFRN 3194			X*
<i>Gobionellus oceanicus</i> (Pallas, 1770)	M	LC	UFRN 0135			X*
<i>Gobioides broussonnetii</i> Lacépède, 1800.	E	LC	UFRN 3843			X*
Acanthuridae						
<i>Acanthurus chirurgus</i> (Bloch, 1787)*	M	LC	UFRN 4411			X
Sphyracnidae						
<i>Sphyracna</i> sp.	M	-	UFRN 4417			X
PLEURONECTIFORMES						
Achiridae						
<i>Achirus declivis</i> Chabanaud, 1940	M	LC	UFRN 0868			X*
<i>Achirus lineatus</i> (Linnaeus, 1758)*	M	LC	UFRN 0191			X*
<i>Trinectes paulistanus</i> (Miranda Ribeiro, 1915)*	M	LC	UFRN 4298			X*
TETRAODONTIFORMES						
Tetraodontidae						
<i>Sphoeroides greeleyi</i> Gilbert, 1900*	E	LC	UFRN 0137			X*
<i>Sphoeroides testudineus</i> (Linnaeus, 1758)*	E	DD	UFRN 4407			X
TOTAL				11	11	62

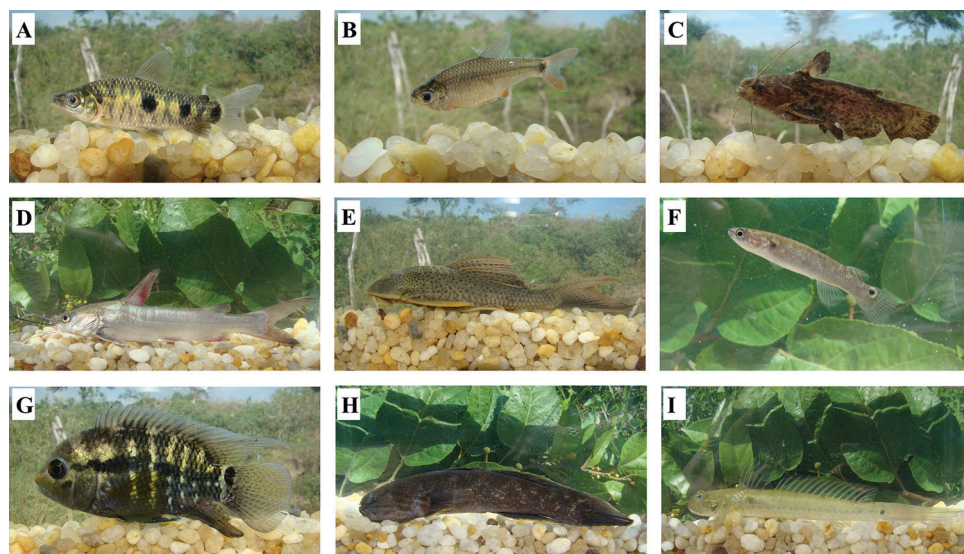


Figure 2. Subset of the ichthyofauna of the Ceará-Mirim River basin, Rio Grande do Norte State, Brazil. **A** *Leporinus piau* **B** *Serrapinnus piaba* **C** *Trachelyopterus galeatus* **D** *Sciades herzbergii* **E** *Hypostomus pusaerum* **F** *Kryptolebias hermaphroditus* **G** *Cichlasoma orientale* **H** *Guavina guavina* **I** *Gobionellus oceanicus*.

Discussion

This study reports 63 native and two introduced species in the Ceará-Mirim River basin, adding 48 species to the previous lists provided by Starks (1913) and Nascimento et al. (2014). Both studies mentioned only 11 species, all freshwater species, even though only five were common to both lists (*Astyanax* aff. *bimaculatus*, *Hoplias malabaricus*, *Poecilia vivipara*, *Serrapinnus piaba*, and *Trachelyopterus galeatus*). We recorded 26 freshwater species, nine of which are new records, including two non-native species (*Oreochromis niloticus* and *Poecilia reticulata*). The discrepancy between our species count data and those from previous studies may be due to the use of selective fishing gear in the earlier studies, or the small number of microhabitats explored. Starks (1913) and Nascimento et al. (2014) did not identify the same taxa in their work. Starks (1913) collected specimens of *Cichlasoma orientale* (Figure 2G), *Crenicichla menezesi*, *Hypostomus pusalum*, *Rhamdia quelen*, *Steindachnerina notonota* and *Synbranchus* aff. *marmoratus*. In turn, Nascimento et al. (2014) listed *Astyanax* aff. *fasciatus*, *Hemigrammus marginatus*, *Hoplosternum littorale*, *Metynnis lippincottianus*, *Prochilodus brevis* and *Serrapinnus heterodon*, all not mentioned by Starks (1913), even when updating the taxonomic identification (Eschmeyer et al. 2016).

Among the species listed by Starks (1913), *Rhamdia quelen* was not found in our field surveys, and *Hoplosternum littorale* and *Metynnis lippincottianus*, present in both lists (Starks 1913, Nascimento et al. 2014) were also not collected. With the exception of *H. littorale*, that is not known in the MNCE, and could actually represent a misidentification (the species might actually be *Megalechis thoracata*, the callichthyid known to occur in MNCE), all species not listed in our collections were recently recorded in a nearby coastal basin (Paiva et al. 2014) and may occur in the Ceará-Mirim drainage.

Although Starks (1913) did not mention any marine or estuarine fish among the Ceará-Mirim River basin material, he listed 79 marine and ten estuarine species at the municipality of Natal, some probably obtained in the Potengi River estuary, but also in intertidal rock pools and local markets. Among those, seven marine (*Achirus lineatus*, *Eugerres brasiliensis*, *Eretelis smaragdus*, *Lutjanus jocu*, *L. synagris*, *Mugil curema* and *Ulaema lefroyi*), and two estuarine species (*Ctenogobius boleosoma* and *Spheroides testudineus*) were also recorded at Ceará-Mirim River basin. Due to the proximity of the above-mentioned estuaries (about 9 km), the presence of the other species in Ceará-Mirim River cannot be ruled out. In this study, the collections in the estuary were carried out in flooded areas of the mangrove forest, an area that is usually poorly sampled in ichthyological surveys, while in other studies, especially Starks (1913), they were probably performed on the main channel of the estuary resulting in the collection of larger species. In addition, the species collected in the present study are small, as well as juveniles of other marine fish species, emphasizing the role of the mangroves in fish recruitment and reproduction (Osório et al. 2011).

Sales et al. (2016) stressed the importance of hypersaline estuaries at the north coast of Rio Grande do Norte State as nurseries for reef fish, and listed 45 estuarine and

33 marine, respectively. Although putatively widely distributed along Brazilian estuaries, the following species found in our surveys were not registered by Sales et al. (2016): estuarine, *Awaous tajasica*, *Cathorops arenatus*, *Ctenogobius shufeldti*, *Eleotris pisonis*, *Erotelis smaragdus*, *Gobioides broussonnetii*, *Guavina guavina*, *Kryptolebias hermaphroditus*, *Microphis lineatus* and *Sciades herzbergii*; marine, *Achirus declivis*, *Anchovia clupeoides*, *Anchoviella lepidentostole*, *Atherinella brasiliensis*, *Elops saurus*, *Gobionellus oceanicus*, *Megalops atlanticus*, *Rypticus* sp., *Sparisoma* sp., *Sphyræna* sp., *Sparisoma radians* and *Trinectes paulistanus*. Among the marine species recorded in the Ceará-Mirim River basin, *Megalops atlanticus* and *Mycteroperca bonaci* are classified as 'vulnerable'. However they are also considered important for artisanal fisheries in Rio Grande do Norte State (Nóbrega et al. 2015). In both cases only juvenile individuals were registered, corroborating Araújo et al. (2002) in the importance of coastal basins, even the small ones, for the maintenance of fish stocks and life cycles of several marine species that use estuaries as nurseries.

According to Blaber and Barletta (2016), it was only over the last 40 years that more detailed studies involving estuarine fish started to be conducted. This data deficiency may be linked to logistical difficulties (e.g. use of inappropriate fishing gear, access and dislocation in the muddy substrate and through its complex structure), taxonomic difficulties, financing sources and research infrastructure. The Ceará-Mirim River estuary has a small area when compared to the whole extent of the basin (0.12%, Lira et al. 2015), but it harbors 38 (60.3%) of the 63 native fish species of the drainage. Among those species, only *Poecilia vivipara* is considered as freshwater, although it shows tolerance to saline environments (Gomes 2008).

At the Ceará-Mirim River basin, environmental impacts caused by inadequate use of soil, irregular human occupation of sand dunes and mangrove areas, deficiencies in wastewater treatment systems, as well as marginal deforestation have been reported by Soares et al. (2010). Such impacts may negatively affect the most sensitive species such as the endangered seahorse *Hippocampus reidi* (MMA 2014) and the 'piaba' *Serrapinnus potiguar*, a species recently described for the Ceará-Mirim River basin (Jerep and Malabarba 2014). Blaber and Barletta (2016) mentioned the pollution caused by industrialization, intensive agriculture and climate change as major anthropogenic effects affecting estuaries. Due to climatic changes some introduced freshwater species with high tolerance to salinity, such as the tilapia *Oreochromis niloticus* recorded in the lower reaches of the Ceará-Mirim River basin, might increase their chances of dispersion and establishment in neighboring basins by dislocation among estuaries (Guttiere et al. 2014).

This survey of the Ceará-Mirim River basin's ichthyofauna can be an useful tool contributing to further academic activities and environmental education, including making local inhabitants aware of the need to preserve the diversity of fish in the coastal basins of Brazil, highly modified by the irregular occupation and unregulated tourism in northeastern Brazil. The CTA/UFRN, although not a conservation unit, may represent an important area for the recovering of the mangrove vegetation and maintenance of estuarine and marine fish species, some of them endangered and commercially exploited.

Acknowledgements

The authors would like to thank Cleto Freire, Flávia Petean, Luciano Barros-Neto, Mateus Germano, Miguel Fernandes, Rafael Frigo, Silvia Yasmin, Thais Araújo, Waldir Berbel-Filho and the GEEFAA (Grupo de Estudos em Ecologia e Fisiologia de Animais Aquáticos) team at the UFRN for their help in the collection of specimens. We are also grateful to Fernando R. Carvalho for confirming the identity of the Characidae family specimens, and to Graco Viana and Beethoven Brandão for logistic support at CTA/UFRN. TPAR acknowledges the post doctorate scholarship granted by CNPq/FAPERN (Fundação de Apoio à Pesquisa do Estado do Rio Grande do Norte, proc. 350674/2012-4). MJS thanks CAPES (Comissão de Aperfeiçoamento de Pessoal do Nível Superior) for granting the doctorate scholarship, and RECP the PRH-ANP (Programa de Recursos Humanos da Agência Nacional do Petróleo, Gás natural e Biocombustíveis) for the masters scholarship.

References

- Albert JS, Petry P, Reis RE (2011) Major Biogeographic and Phylogenetic Patterns. In: Albert JS, Reis RE (Eds) Historical biogeographical of neotropical freshwater fishes. University of California Press, Berkeley and Los Angeles, California, 21–58. <https://doi.org/10.1525/california/9780520268685.003.0002>
- Andrade HTA, Nascimento RSS, Gurgel HCB, Medeiros JF (2000) Simuliidae (Diptera) integrantes da dieta de *Poecilia vivipara* Bloch & Schneider, 1801 (Atheriniformes; Poeciliidae) no Rio Ceará Mirim, Estado do Rio Grande do Norte, Brasil. *Entomologia y Vectores* 27 (2): 119–122. <https://www.cabdirect.org/cabdirect/abstract/20000507419>
- Araújo FG, Azevedo MCC, Silva MA, Pessanha ALM, Gomes ID, Cruz-Filho AG (2002) Environmental Influences on the Demersal Fish Assemblages in the Sepetiba Bay, Brazil. *Estuaries* 25(3): 441–450. <https://doi.org/10.1007/BF02695986>
- Araújo ME, Teixeira JMC, Oliveira AME (2004) Peixes estuarinos marinhos do Nordeste brasileiro: guia Ilustrado. Edições UFC, Fortaleza, 260 pp.
- Canan B, (2011) Primeira contribuição à história da ictiologia no estado do Rio Grande do Norte. *CARPE DIEM: Revista Cultural e Científica da FACEX* 9(9): 1–17. <https://periodicos.unifacex.com.br/Revista/article/download/107/31>
- Blaber SJM, Barletta M (2016) A review of estuarine fish research in South America: what has been achieved and what is the future for sustainability and conservation? *Journal of Fish Biology* 89(1): 386–402. <http://dx.doi.org/10.1111/jfb.12875>
- Buckup PA, Menezes NA, Ghazii MS (2007) Catálogo das Espécies de Peixes de Água Doce do Brasil. Museu Nacional, Rio de Janeiro, 195 pp.
- Dias TS, Fialho CB (2009) Biologia alimentar de quatro espécies simpátricas de Cheirodontinae (Characiformes, Characidae) do Rio Ceará Mirim, Rio Grande do Norte. *Iheringia, Serie Zoologia*. Porto Alegre 99(3): 242–248. <http://dx.doi.org/10.1590/S0073-472120090-00300003>

- Eschmeyer WN, Fricke R, van der Laan R (2016) Catalog of fishes: genera, species, references. <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp> [Electronic version accessed 20 Dec 2016]
- Figueiredo JL, Menezes NA (1978) Manual de Peixes Marinhos do Sudeste do Brasil. II. Teleostei (1). Museu de Zoologia, Universidade de São Paulo, São Paulo, 110 pp.
- Figueiredo JL, Menezes NA (1980) Manual de Peixes Marinhos do Sudeste do Brasil. III. Teleostei (2). Museu de Zoologia, Universidade de São Paulo, São Paulo, 90 pp.
- Figueiredo JL, Menezes NA (2000) Manual de Peixes Marinhos do Sudeste do Brasil. VI. Teleostei (5). Museu de Zoologia, Universidade de São Paulo, São Paulo, 116 pp.
- Froese R, Pauly D (2016) FishBase. World Wide Web electronic publication. <http://www.fishbase.org/> [Electronic version accessed 20 Dec 2016]
- Gomes JL, Monteiro LR (2008) Morphological divergence patterns among populations of *Poecilia vivipara* (Teleostei Poeciliidae): test of an ecomorphological paradigm. *Biological Journal of the Linnean Society* 93(4): 799–812. <https://doi.org/10.1111/j.1095-8312.20-07.00945.x>
- Gurgel HCB, Silva NB, Lucas FD, Souza LLG (2005) Alimentação da comunidade de peixes de um trecho do rio Ceará Mirim, em Umari, Taipu, Estado do Rio Grande do Norte, Brasil. *Acta Scientiarum. Animal Sciences* 27(2): 229–233. <https://doi.org/10.4025/act-ascianimsci.v27i2.1226>
- Guttiere SMM, Vitule JRS, Freire CA, Prodócimo V (2014) Physiological tools to predict invasiveness and spread via estuarine bridges: tolerance of Brazilian native and worldwide introduced freshwater fishes to increased salinity. *Marine and Freshwater Research* 65(5): 425–436. <http://dx.doi.org/10.1071/MF13161>
- IPEA, Instituto de Pesquisa Econômica Aplicada (2016) Região Metropolitana de Natal. http://www.ipea.gov.br/agencia/imagens/stories/PDFs/livros/livros/141125_atlas_natal
- ICMBio (2016) Lista de espécies quase ameaçadas e com dados insuficientes. <http://www.icmbio.gov.br/porta/fanabrasileira/lista-de-especies-dados-insuficientes>
- Jerep CF, Malabarba LR (2014) A new species of *Serrapinnus* Malabarba, 1998 (Characidae: Cheirodontinae) from Rio Grande do Norte State, northeastern Brazil. *Neotropical Ichthyology* 12(2): 301–308. doi: <http://dx.doi.org/10.1590/1982-0224-20130218>.
- Leão TCC, Almeida WR, Deuchoum MS, Ziller SR (2011) Espécies Exóticas Invasoras no Nordeste do Brasil: Contextualização. Manejo e Políticas públicas. Recife, Estado de Pernambuco, 33 pp.
- Lira MGS, Paiva REC, Ramos TPA, Lima SMQ (2015) First record of *Kryptolebias hermaphroditus* Costa, 2011 (Cyprinodontiformes: Rivulidae) in the extreme north Atlantic Forest mangroves, Rio Grande do Norte state, Brazil. *Check List* 11(3): 1656. <http://dx.doi.org/10.15560/11.3.1656>
- Maia LP, Lacerda LD, Monteiro LHU, Souza GM (2006) Atlas dos Manguezais do Nordeste do Brasil. SEMACE, Fortaleza, 125 pp.
- Malabarba LR, Reis RE (1987) Manual de técnicas para a preparação de coleções zoológicas. Peixes. Sociedade Brasileira de Zoologia. Campinas, 14 pp.
- Marceniuk AP (2005) Chave para identificação das espécies de bagres marinhos (Siluriformes, Ariidae) da costa brasileira. *Boletim do Instituto de Pesca* 31(2): 89–101.

- Menezes NA, Figueiredo JL (1980) Manual de Peixes Marinhos do Sudeste do Brasil. IV. Teleostei (3). Museu de Zoologia, Universidade de São Paulo, São Paulo, 96 pp.
- Menezes NA, Figueiredo JL (1985) Manual de Peixes Marinhos do Sudeste do Brasil. V. Teleostei (4). Museu de Zoologia, Universidade de São Paulo, São Paulo, 105 pp.
- MMA, Ministério do Meio Ambiente (2014) Portaria nº 445, de 17 de Dezembro de 2014. Lista Nacional Oficial de Espécies da Fauna Ameaçadas de Extinção - Peixes e Invertebrados Aquáticos. Diário Oficial da União, Brasília, 126–130.
- Nascimento WS, Barros NHC, Araújo AS, Gurgel LL, Canan B, Molina WF, Rosa RS, Chellappa S (2014) Composição da ictiofauna das bacias hidrográficas do Rio Grande do Norte, Brasil. *Biota Amazônia Open Journal System* 4(1): 126–131. <https://doi.org/10.18561/2179-5746/biotaamazonia.v4n1p126-131>
- Nóbrega MF, Garcia-Júnior J, Oliveira JEL (2015) Biodiversidade marinha da Bacia Potiguar/RN: Peixes da Pesca Artesanal. Museu Nacional, Rio de Janeiro, 53–293.
- Osório FM, Godinho WO, Lotufo TMC (2011) Fish fauna associated to mangrove roots at the Pacoti River estuary. *Biota Neotropica* 11(1). <http://www.biotaneotropica.org.br/v11n1/en/abstract?short-communication+bn00711012011>
- Paiva REC, Lima SMQ, Ramos TPA, Mendes LF (2014) Fish fauna of Pratagi River coastal microbasin, extreme north Atlantic Forest, Rio Grande do Norte State, northeastern Brazil. *Check List* 10(5): 968–975. <https://doi.org/10.15560/10.5.968>
- Ploeg A (1991) Revision of the South American cichlid genus *Crenicichla* Heckel, 1840, with descriptions of fifteen new species and considerations on species groups, phylogeny and biogeography. *Academisch Proefschrift, Universiteit van Amsterdam*, Amsterdam, 153 pp.
- Rosa RS, Menezes NA, Britski HA, Costa WJEM, Groth F (2003) Diversidade, padrões de distribuição e conservação dos peixes da caatinga. In: Leal I.R, Silva JMC, Tabarelli M (Eds) *Ecologia e Conservação da Caatinga*. Editora Universitária da Universidade Federal de Pernambuco, Recife, 135–180.
- Rosa RS (2004) Diversidade e conservação dos peixes da caatinga. In: Silva JMC, Tabarelli M, Fonseca MT, Lins LV (Eds) *Biodiversidade da Caatinga: Áreas e Ações Prioritárias para a Conservação*. Ministério do Meio Ambiente, Brasília, 149–161.
- Rosa RS, Groth F (2004) Ictiofauna dos Ecossistemas de Brejos de Altitude de Pernambuco e Paraíba. In: Pôrto KC, Cabral JJP, Tabarelli M (Eds) *Brejos de Altitude em Pernambuco e Paraíba: História Natural, Ecologia e Conservação*. Série Biodiversidade, 9. Ministério do Meio Ambiente, Brasília, 201–210.
- Sales NS, Dias TLP, Baeta A, Pessanha LM (2016) Dependence of juvenile reef fishes on semi-arid hypersaline estuary microhabitats as nurseries. *Journal of Fish Biology*. <https://doi.org/10.1111/jfb.13006>
- Soares IA, Oliveira JEL, Candido GA (2010) Utilização de indicadores ambientais para análise da degradação ambiental em áreas de preservação permanente: caso do estuário do Rio Ceará-Mirim/RN. In: Cândido GA (Eds.). *Desenvolvimento Sustentável e Sistemas de Indicadores de Sustentabilidade: formas de aplicações em contextos geográficos diversos e contingências específicas*. Editora da Universidade Federal de Campina Grande. Campina Grande, 470 pp.
- Starks ED (1913) *The fishes of the Stanford Expedition to Brazil*. Standford University, California published by the university, 126 pp.

A new species of *Leodice* from Korean waters (Annelida, Polychaeta, Eunicidae)

Hyun Ki Choi¹, Jong Guk Kim², Dong Won Kang¹, Seong Myeong Yoon³

1 National Marine Biodiversity Institute of Korea, Seochon, Chungcheongnam-do 33662, Korea **2** Marine Ecosystem and Biological Research Center, Korea Institute of Ocean Science and Technology, Busan 49111, Korea **3** Department of Biology, College of Natural Sciences, Chosun University, Gwangju 61452, Korea

Corresponding author: Seong Myeong Yoon (smyun@chosun.ac.kr)

Academic editor: Greg Rouse | Received 19 August 2017 | Accepted 21 September 2017 | Published 14 November 2017

<http://zoobank.org/4834E66F-E151-4F8A-8765-8BC14DB050E3>

Citation: Choi HK, Kim JG, Kang DW, Yoon SM (2017) A new species of *Leodice* from Korean waters (Annelida, Polychaeta, Eunicidae). ZooKeys 715: 53–67. <https://doi.org/10.3897/zookeys.715.20448>

Abstract

A new eunicid species, *Leodice duplexa* **sp. n.**, from intertidal and subtidal habitats in the eastern coast of South Korea is described. The new species is assigned to the C-2 group, and is similar to *Leodice antennata*, the type species of the genus, in having the following combination of characteristics: moniliform antennae and palps, bidentate compound falcigers, articulated peristomial and notopodial cirri, pectinate branchiae showing bimodal distribution of branchial filaments, and yellow aciculae. However, *L. duplexa* **sp. n.** is readily distinguished from *L. antennata* by the following features: the aciculae are 2–4 in number, with blunt or pointed tips and hammer-headed or bifid tips, and the subacicular hooks are paired in some chaetigers. A detailed description and illustrations are provided for the new species. The validity of the new species is also supported by a genetic comparison using sequences of the mitochondrial cytochrome c oxidase subunit I (COI). A revised key to known *Leodice* species is provided with a comparison of their morphological characteristics.

Keywords

COI, eunicid, Korea, polychaete, taxonomy

Introduction

The genus *Leodice* Savigny in Lamarck, 1818, a member of genera belonging to family Eunicidae Berthold, 1827, had been previously considered an invalid taxon (Hsueh and Li 2014, Zanol et al. 2014). However, Zanol et al. (2014) proposed the validity of this

genus based upon molecular and morphological data, and reinstituted the genus with 13 species previously reported as *Eunice* species: *Leodice americana* (Hartman, 1944), *L. antarctica* (Baird, 1869), *L. antennata* Savigny in Lamarck, 1818, *L. antillensis* (Ehlers, 1887), *L. gracilicirrata* Treadwell, 1922, *L. harassii* (Audouin & Milne Edwards, 1933), *L. limosa* (Ehlers, 1868), *L. lucei* (Grube, 1856), *L. marcusii* (Zanol et al., 2000), *L. miurai* (Carrera-Parra & Salazar-Vallejo, 1998), *L. rubra* (Grube, 1856), *L. thomasi* (Augener, 1922), *L. torquata* (Quatrefages, 1866), and *L. valens* Chamberlin, 1919. Subsequently, *Eunice laurillardii* Quatrefages, 1866 was additionally treated as a species belonging to *Leodice* by Arias et al. (2015). The fauna of this group generally show a cosmopolitan distribution (Zanol et al. 2014); two *Leodice* species, *L. antennata* and *L. gracilicirrata*, have been reported as *Eunice* species in East Asia (Imajima and Hartman 1964, Imajima 1967, Miura 1977, 1986, Wu et al. 2013b; Hsueh and Li 2014).

Zanol et al. (2014) suggested that this genus has at least one of the following diagnostics: regularly articulated antennae and palps, light aciculae, light and bi- or tridentate subacicular hooks, and lateral black dots between posterior parapodia. Almost all species assigned to the A and C groups of Fauchald (1970) in *Eunice* species are expected to be *Leodice* species (Zanol et al. 2014). Here, the morphological diagnosis of *Leodice* described by Zanol et al. (2014) is followed.

While studying the polychaetes from Korean waters as a part of the ‘Securement, Analysis and Evaluation of Marine Invertebrate Bioresources’, a new species of the genus *Leodice* was found. In the present paper, detailed description and illustrations of the new species are provided with a genetic comparison between the new species and other *Leodice* species in the barcode region of the mitochondrial cytochrome c oxidase subunit I (COI). A taxonomic comparison of known *Leodice* species is also presented, with a revised taxonomic key based on the previous literature (Miura 1977, 1986, Fauchald 1992, Carrera-Parra and Salazar-Vallejo 1998, Zanol et al. 2000, Steiner et al. 2002, Zanol et al. 2007, Wu et al. 2013b, Zanol et al. 2014, Arias et al. 2015).

Materials and methods

Sampling and morphological observation

Samples were collected from rocky bottoms of the intertidal and subtidal zone. Specimens were sorted using sieves with pore size of 0.5 mm, fixed initially with 5% formaldehyde-seawater solution, and transferred to 85% ethyl alcohol. The characteristics of the whole body were observed with appendages dissected in a petri dish using dissection forceps or surgical knives and needles under stereomicroscope (SMZ1500; Olympus, Tokyo, Japan). Dissected specimens were mounted onto temporary slides using glycerol or permanent slides using polyvinyl lactophenol solution. Drawings were made under the stereomicroscope and light microscope (LABOPHOT-2; Nikon, Tokyo, Japan) with the aid of drawing tubes. Photographs were taken of the appendages in a permanent slide. Images of appendages were captured using an image system

(i-SOLUTION/LITE, iMTechnology*, Vancouver, Canada). Specimens for scanning electron microscopy (SEM) were dehydrated by t-BuOH freeze dryer (VFD-21S; Vacuum Device, Ibaraki, Japan). They were mounted on stubs and coated with gold-palladium. SEM observations were carried out using a scanning electron microscope (SU3500; Hitachi, Tokyo, Japan). Type material and additional material examined were deposited in the National Marine Biodiversity Institute of Korea (MABIK).

Molecular analysis

Genomic DNA was extracted from the posterior segments of three specimens selected among additional materials using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacture's protocol. Amplifications of partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) from gDNA were carried out by polymerase chain reaction (PCR) method using a set of primers: ACOIAF 5'-CWAATCAYA AAGATATTGGAAC-3' and ACOIAR 5'-AATATAWACTTCW-GGGTGACC-3' (Zonal et al. 2010). PCR amplification was conducted in a total volume of 20 µL: 10 µL of 2x DyeMIX-Tenuto (Enzynomics), 0.5 µL of each primer, 1 µL of gDNA, and 8 µL of sterile water. PCR condition was determined based on the work of Zonal et al. (2010) as follows: 5 min at 94°C, followed by 35 cycles of 1 min at 94°C, 1 min at 45°C, and 2 min at 72°C, with a final extension of 7 min at 72°C. PCR products were purified with a QIAquick® PCR Purification Kit (Qiagen, Chatsworth, CA, USA). Sequences for the new species were obtained by an Applied Biosystems 3730 DNA sequencer, and deposited in GenBank under accession number MF669544–MF669546. These sequences were aligned with those of other *Leodice* species and outgroup taxa using Geneios Pro v.9.1.8 (Biomatters, Auckland, New Zealand). The genetic distances of the new species from other species and the phylogenetic tree of them were produced by MEGA v.6.06 (Tamura et al., 2013).

Systematic accounts

Family Eunicidae Berthold, 1827

Genus *Leodice* Savigny in Lamarck, 1818

***Leodice duplexa* sp. n.**

<http://zoobank.org/64134EF0-FFE9-4FB3-8C64-4030C310ED09>

Figs 1–2

Type locality. South Korea, Gyeongsangbuk-do Province: Gyeongju-si County, Gampo-eup, Oryu 1-ri, 35°48'13"N, 129°32'21"E, intertidal rocky bottom.

Material examined. *Holotype.* complete specimen (53.0 mm long, 4.8 mm width), cat no. MABIKNA00146045. *Paratypes.* one complete specimen (24.0 mm

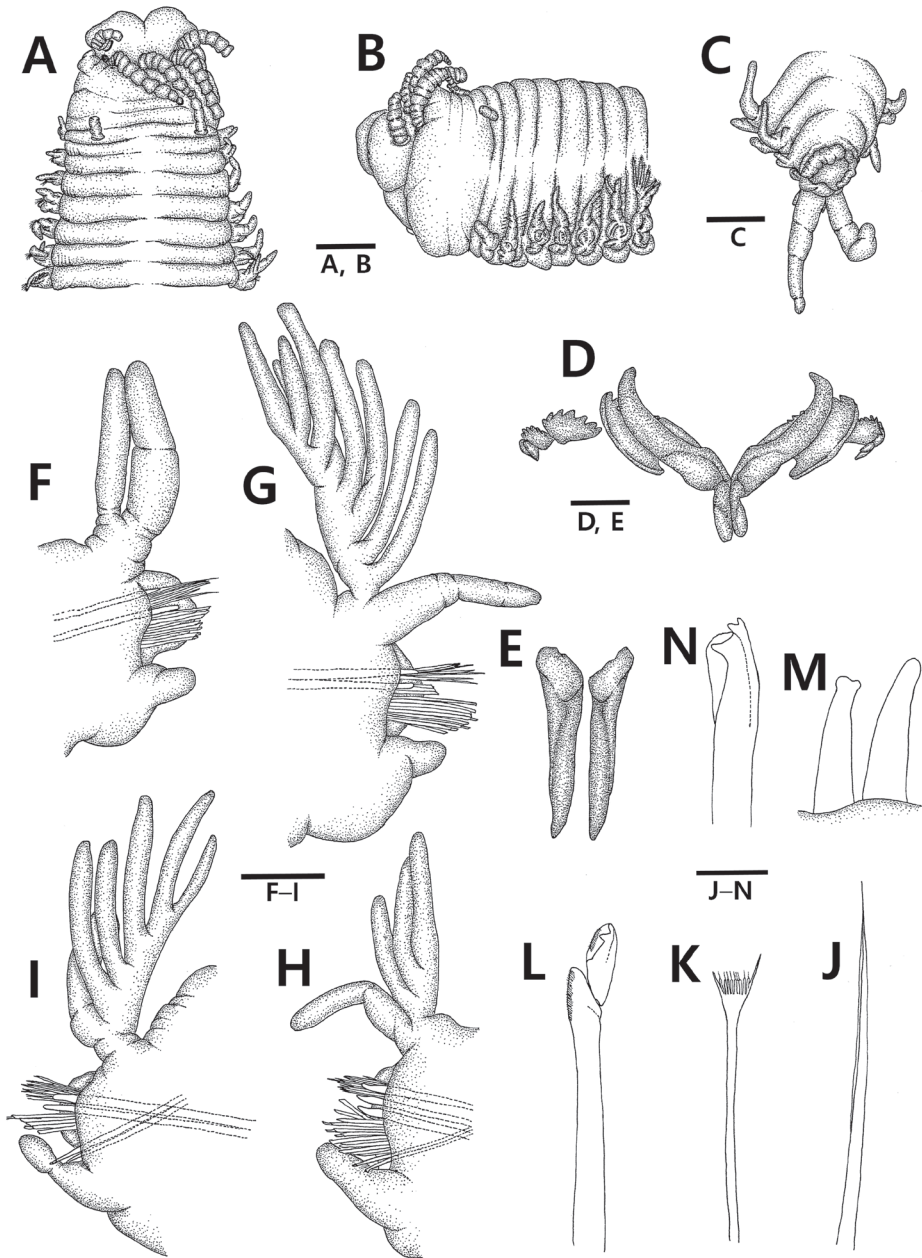


Figure 1. *Leodice duplexa* sp. n., **A–C, F–N** holotype (MABIKNA00146045) **D, F** paratype (MABIKNA00146046) **A** anterior end, dorsal view **B** anterior end, lateral view **C** posterior end, dorsal view **D** maxillae **E** mandible **F** left parapodium VI, anterior view **G** left parapodium XX, anterior view **H** right parapodium XXXVIII, anterior view **I** right parapodium LX, anterior view **J** limbate chaeta on parapodium XLVII **K** pectinate chaeta on parapodium XLVII **L** compound falciger on parapodium XLVII **M** subacicular hook on parapodium XXXVIII **N** aciculae with blunt and hammer-headed tips on parapodium LXXXV. Scale bars: 1.0 mm (**A, B**), 0.5 mm (**C–E**), 0.4 mm (**F–I**), 0.05 mm (**J–N**).

long, 4.9 mm width), cat no. MABIKNA00146046; one incomplete specimen (15.0 mm long, 3.3 mm width), cat no. MABIKNA00146047. All type material was collected from intertidal rocky bottom at the type locality on 9 April 2014.

Additional material. South Korea, Gyeongsangbuk-do Province: 5 specimens, Ulleung-gun County, Ulleung-eup, Dokdo-ri, 37°14'31"N, 131°52'06"E, 05 Sep. 2016, subtidal rocky bottom at 10–15 m depth; 5 specimens, Pohang-si County, Homigot-myeon, Guman-ri, 36°04'35"N, 129°34'31"E, 19 May 2015; 2 specimens, Yeongdeok-gun County, Chuksan-myeon, Gyeongjeong-ri, 36°27'40"N, 129°32'34"E, 17 Sep. 2014., intertidal rocky bottom.

Diagnosis. Prostomium with three antennae and one pair of lateral palps arranged in crescent pattern; palpostyles and ceratostyles regularly articulated and moniliform, and with ring-shaped palpo- and ceratophores. Peristomial cirri with four weak articulations, not extending middle part of first peristomial ring. Pectinate branchiae from chaetiger VI to near posterior end, with maximum of 7–8 branchial filaments. Limbate chaetae slender, with narrow wings. Heterodont pectinate chaetae with 5–10 teeth. Compound falcigers bidentate, with hoods marginally serrated. Aciculae yellow, with both blunt and hammer-headed or bifid tip, and 2–4 per parapodium. Subacicular hooks yellow, tridentate, present from chaetiger XXIII to last chaetiger, and 1–2 per parapodium. Pygidium with two pairs of anal cirri with four articulations.

Description. Holotype: complete specimen with cylindrical body, slightly flattened dorsoventrally in posterior segments, and with approximately 94 segments.

Prostomium bilobed, distinctly shorter and narrower than peristomium, and about as deep as 1/2 of peristomium; prostomial lobes anteriorly rounded, dorsally flattened, separated by shallow and narrow notch. Prostomial appendages consisted of three antennae and two lateral palps, arranged in shallow semicircle, evenly spaced, similar in thickness; palpophores and ceratophores ring-shaped without articulation; palpostyles and ceratostyles tapering, regularly articulated, with up to 12 moniliform articulations in A-I extending to anterior edge of chaetiger I, but incomplete distally with 8–11 moniliform articulations in others except A-I (Fig. 1A, B).

Eyes black, spherical, and located between bases of palps and lateral antennae (Fig. 1A).

Peristomium cylindrical, divided into first and second ring; first ring 3–4 times longer than second one; peristomial cirri with four weak articulations, not extending middle part of first peristomial ring (Fig. 1A, B).

Maxillary formula (in paratype): Mx I 1+1; Mx II 6+6; Mx III 7+0; Mx IV 6+7; Mx V 1+1; Mx III located at frontal end of distal arc with left Mx IV. Mandibles flat (Fig. 1D, E).

Branchiae pectinate, slightly longer than dorsal cirri, and present on more than 65% of total number of chaetigers from chaetiger VI to near posterior end. Branchial filaments bimodal distribution, single at first branchial chaetiger, reaching maximum of eight in number between chaetigers IX to XXIII, reduced to 3–4 in number on chaetigers XXXI to XLVIII, increasing to 5–6 in number on chaetigers XLIX to LXIV, and thereafter decreasing to 2–4 in number on posterior chaetigers. Last six chaetigers without branchiae (Fig. 1F–I).

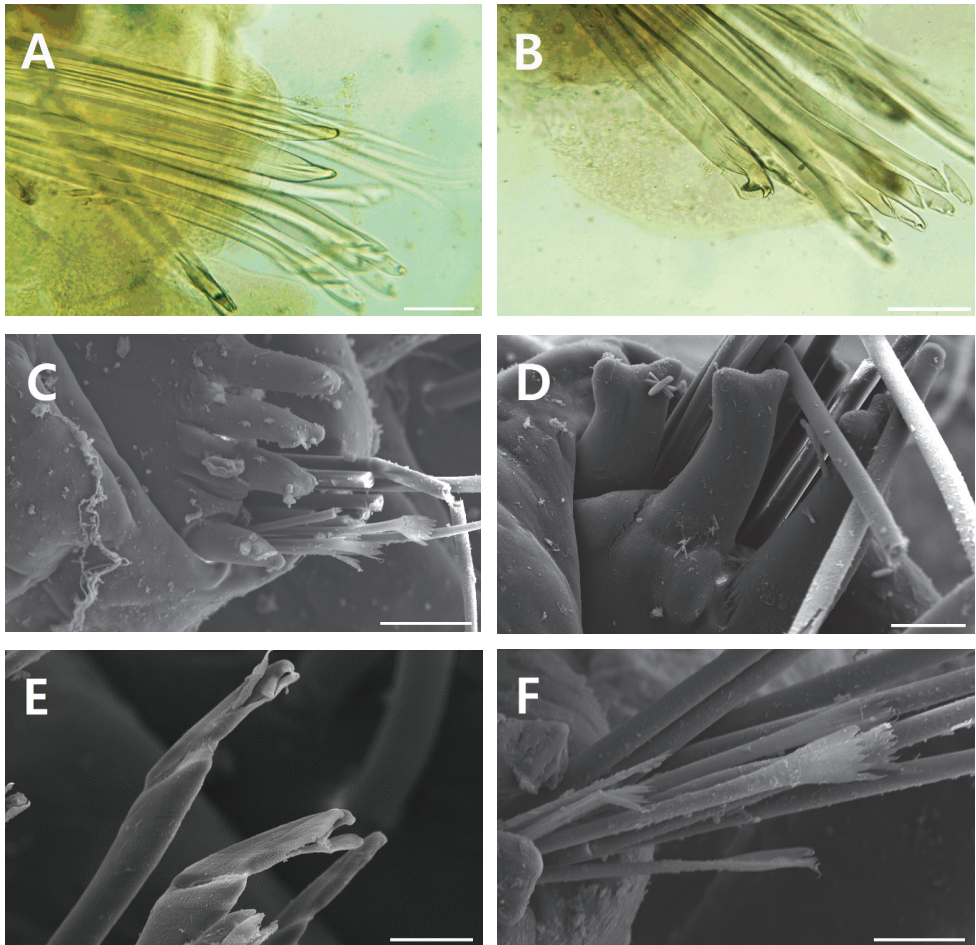


Figure 2. *Leodice duplexa* sp. n., **A–D** paratype (MABIKNA00146047) **A** yellow aciculae with pointed tips **B** yellow and paired subacicular hooks **C** parapodium with four aciculae **D** aciculae with hammer-headed or bifid tips **E** compound falcigers with bidentate appendages **F** pectinate chaeta. Scale bars: 0.05 mm (**A–C**), 0.025 mm (**D–F**).

Dorsal cirri tapering and digitiform, with 2–3 weak articulations (Fig. 1F–I).

Anterior neuropodial lobes truncate and distally rounded with aciculae emerging near midline; pre- and postchaetal lobes low, transverse folds. Ventral cirri on anterior chaetigers thick and ovoid-shaped, with slightly inflated base; median ones with inflated base more than anterior ones; posterior ones slightly elongated with smaller base than median ones (Fig. 1F–I).

Limbate chaetae slender and elongate, longer than other chaetae, and with narrow wings (Fig. 1J). Pectinate chaetae flaring and with marginal teeth and 4–9 inner teeth (Figs 1K, 2F). Compound falcigers with distally inflated shafts and bidentate appendage; shafts marginally serrated on inflated region; appendages tapering, slender, with both proximal tooth directed laterally and distal tooth gently curved and directed upwardly, and proximal tooth slightly smaller than distal tooth on anterior chaetigers,

but larger than distal tooth on posterior chaetigers; guards marginally serrated, without mucros (Figs 1L, 2E). Pseudocompound falcigers and compound spinigers absent. Aciculae yellow, straight, tapering with both blunt or pointed tips and hammer-headed or bifid tips, rounded in cross-section, and 2–3 in number per parapodium (maximum of four in paratype and more than two aciculae usually appeared in posterior parapodia); separation between core and sheath indistinct in aciculae and subacicular hooks (Figs 1M, 2A, C, D). Subacicular hooks yellow, tridentate, present from chaetiger XXIII to last chaetiger, and 1–2 in number per parapodium; shaft straight, subdistally tapering; proximal tooth triangle, distally blunt, directed laterally, larger than distal teeth; guards covering only proximal tooth (Figs 1N, 2B).

Pygidium with two pairs of anal cirri; dorsal pair as long as last five chaetigers with up to four cylindrical articulations, ventral pair reduced to small bump (Fig. 1C).

Etymology. The epithet of the specific name, *duplexa*, is derived from the Latin *duplex*, meaning ‘double’. This name refers to the presence of paired subacicular hooks.

Distribution. The East Sea (or the Sea of Japan) of South Korea.

Remarks. *Leodice* species were redefined by Zanol et al. (2014), but their specific characteristics were insufficiently dealt in that work. However, diagnostic features of many *Leodice* species have been well studied under the names of *Eunice* species by the previous works (Hartman 1944, Day 1967, Miura 1977, 1986, Fauchald 1992, Carrera-Parra and Salazar-Vallejo 1998, Zanol et al. 2000, Steiner et al. 2002, Zanol et al. 2007, Wu et al. 2013b). The new species of the present study can be discriminated from its relatives by the distinguishing morphological features provided by these previous works. *Leodice duplexa* sp. n. could be classified into the C-2 group of Fauchald (1970, 1992), because it has translucent and tridentate subacicular hooks and the branchiae are arising from the chaetigers more than 65% of a total number of them. Among the species assigned to this group, *L. duplexa* sp. n. is closely related to *L. antennata*, the type specie of *Leodice*, in the following morphological features: the antennae and palps are regularly articulated and moniliform; the compound falcigers are bidentate; the peristomial and notopodial cirri are articulated; the branchiae are pectinate and show the bimodal distribution of branchial filaments; the aciculae are yellow (Hartman 1944, Day 1967, Imajima 1967, Miura 1977, 1986, Fauchald 1970, 1992, Zanol et al. 2007, Wu et al. 2013b). Nonetheless, the new species is distinguishable from *L. antennata* in two points as follows: the new species has 2–4 aciculae, while *L. antennata* bears one pair; the subacicular hooks are paired in some chaetigers in the new species, but always single in each chaetiger in *L. antennata* (Day 1967, Imajima 1967, Miura 1977, Fauchald 1992, Zanol et al. 2007, Wu et al. 2013b).

The distal shape of aciculae has been considered as a useful character for distinguishing eunicid species (Miura 1986, Fauchald 1992, León-González et al. 2004, Zanol et al. 2007, Wu et al. 2013a, Hsueh and Li 2014). The new species shows aciculae with blunt or pointed tips and hammer-headed or bifid tips, which are clearly differentiated from the aciculae with blunt or pointed tips of *L. antennata* described from the Gulf of Suez, its type locality (Fauchald 1992, Zanol et al. 2007). However, the appearance of the aciculae with hammer-headed or bifid tips, which is found in the new species, has been frequently mentioned in the previous descriptions of *L. antennata* (Hartman 1944, Day 1967, Imajima, 1967, Miura 1977, 1986). Despite the discrepancy among the previous descriptions of

L. antennata, we accepted that the difference in terms of the distal shape of aciculae between *L. duplexa* sp. n. and *L. antennata* is valid, based on the description of *L. antennata* from the type locality by Fauchald (1992) and Zanol et al. (2007). We think that the taxonomic validity of the previous descriptions of *L. antennata*, including the presence of aciculae with hammer-headed or bifid tips, is questionable (Hartman 1944, Day 1967, Imajima 1967, Miura 1977, 1986) and they could be assigned to another species or subspecies through further study and detailed comparison with the materials from the type locality.

The aciculae with both blunt or pointed and hammer-headed or bifid tips, which appear in the new species, have been often described in the eunicid species. In the species of the C-2 group of the eunicids (Fauchald 1970, 1992), this feature is known from three *Eunice* species (which might be *Leodice* species), *E. aedificatrix* Monro, 1933, *E. ornata* Andrews, 1891, *E. uschakovi* Wu, Sun & Liu, 2013, and from two *Leodice* species, *L. rubra* (Grube, 1856) and *L. lucei* (Grube, 1856) (Fauchald 1992, Wu et al. 2013a). Among them, *L. rubra* is especially similar to *L. duplexa* sp. n. in the presence of paired subacicular hooks in some chaetigers (Fauchald 1992, Steiner et al. 2002). However, these two species differ from each other by the number of branchial filaments and aciculae: *L. duplexa* sp. n. is with a maximum of eight branchial filaments and 2–4 aciculae per parapodium, whereas *L. rubra* displays a maximum of 21 filaments and single paired aciculae (Fauchald 1992, Steiner et al. 2002). Meanwhile, *L. duplexa* sp. n. resembles *L. valens* in the number of aciculae and subacicular hooks. However, these two species are distinguishable from each other because *L. valens*, which is regarded as the member of the A-1 group by Fauchald (1970, 1992), has translucent and bidentate subacicular hooks (Fauchald 1992), while *L. duplexa* sp. n. has translucent but tridentate subacicular hooks. Additionally, the branchiae are present on less than 55% of chaetigers in *L. valens* (Fauchald 1992), but on more than 65% in the new species.

Genetic comparison. We obtained three partial COI sequences of a total 664 bp size from three individuals of *Leodice duplexa* sp. n., respectively. All COI sequences obtained are identical. For the genetic comparison on the new species, we sort out the sequences of 14 eunicid species including 12 *Leodice* species, which were originally registered as *Eunice* species, and two non-*Leodice* species as outgroup taxa, *Eunice norvegica* (Linnaeus, 1767) and *Marphysa sanguinea* (Montagu, 1813), from GenBank (Schulze 2006, Zanol et al. 2010). The genetic distances between the new species and these 14 eunicid species measured by Kimura-2-parameter model are represented in Table 2. *Leodice duplexa* sp. n. is distinguishable from previously described 12 *Leodice* species in that the inter-specific distances between the new species and other *Leodice* species are distinct with the ranges from 8.2 to 14.4%. Among *Leodice* species, *L. duplexa* sp. n. is turned out to be closely related to *L. lucei* and mostly distinguished from *L. cf. antillensis* (Table 2). In Maximum likelihood (ML) tree based on these genetic data (Fig. 3), the new species is contained within *Leodice* species. Especially, *L. duplexa* sp. n. belongs to a clade with *L. antennata*, *L. rubra*, *L. lucei*, and *L. miurai*, and they share several significant morphological characteristics such that the antennae and palps are regularly moniliform and the subacicular hooks are yellow and tridentate (Fauchald 1992, Carrera-Parra and Salazar-Vallejo 1998, Steiner et al. 2002, Zanol et al. 2007).

Table 1. Comparison of morphological characteristics among known *Leodice* species.

Species	Eyes	Articulations of antennae and palpal styles	Peristomial cirri	Branchiae				Notopodial cirri	Subacicular hooks			Compound falcigers	Aciculae		Data source
				Shape	Starting chaetiger	Distribution	Number of filaments		Shape	Starting chaetiger	Number per parapodium		shape	Number per parapodium	
<i>L. americana</i> (Hartman 1944)	present	regularly cylindrical	smooth	pectinate	3	less than 55% of body	2–20	articulated	yellow, tridentate	25	single	bidentate, with mucros	yellow, bently blunt tips	paired	Fauchald 1992
<i>L. antarctica</i> (Baird, 1869)	absent	irregularly cylindrical	smooth	pectinate	3	less than 55% of body	1–5	articulated	yellow, bidentate	31–44	single	bidentate	yellow, blunt tips	paired	Fauchald 1992
<i>L. antennata</i> Lamarck, 1818	present	moniliform	with articulations	pectinate	5–7	more than 65% of body	2–7	articulated	yellow, tridentate	24–26	single	bidentate	yellow, blunt or pointed tips	paired	Fauchald 1992, Zanol et al. 2007
<i>L. anitlensis</i> (Ehlers, 1887)	present	irregularly cylindrical	with articulations	pectinate	4	less than 55% of body	1–6	articulated	yellow, bidentate	33	1–2	bidentate	yellow, flattened and expanded tips	paired	Fauchald 1992
<i>L. duplex</i> sp. n.	present	moniliform	with articulations	pectinate	5–6	more than 65% of body	1–8	articulated	yellow, tridentate	24–26	1–2	bidentate	yellow, both blunt and hammer-headed or bifid tips	2–4	Present study
<i>L. gracilicirrata</i> Treadwell, 1922	unknown	irregularly cylindrical	with articulations	pectinate	3	less than 55% of body	1–7	articulated	yellow, bidentate	63	single	bidentate	yellow, both pointed with mucros and bluntly rounded tips	paired	Fauchald 1992, Miura 1986
<i>L. harasii</i> (Audouin & Milne Edwards, 1933)	faintly present	regularly cylindrical	smooth	pectinate	4	more than 65% of body	1–10	smooth	light brown, bidentate	28	single	bidentate	yellow, turned dark brown, pointed tips	paired	Fauchald, 1992, Zanol et al. 2007
<i>L. laurillardii</i> (Quatrefages, 1866)	present	regularly cylindrical	with articulations	pectinate	2–3	more than 65% of body	1–10	articulated	dark brown, bidentate	29–32	single	bidentate	dark brown, blunt tips	paired	Fauchald, 1992, Arias et al. 2015

Table 1. (Continued).

Species	Eyes	Articulations of antennae and palpal styles	Peristomial cirri	Branchiae				Notopodial cirri	Subacicular hooks			Compound falcigers	Aciculae		Data source
				Shape	Starting chaetiger	Distribution	Number of filaments		Shape	Starting chaetiger	Number per parapodium		shape	Number per parapodium	
<i>L. limosa</i> (Ehlers 1868)	unknown	regularly cylindrical	smooth	pectinate	3	less than 55% of body	1–12	smooth	yellow, tridentate	before 30	unknown	bidentate, with mucros	yellow, blunt tips	unknown	Fauchald 1992
<i>L. lupei</i> (Grube, 1856)	present	moniliform	with articulations	pectinate	5	more than 65% of body	1–8	articulated	yellow, tridentate	24–34	single	bidentate, with mucros	yellow, distinctly hammer-headed or bifid tips	paired	Fauchald 1992
<i>L. murusi</i> (Zanol et al., 2000)	present	moniliform	with articulations	palmate	4	more than 65% of body	1–4	articulated	black, bidentate	19–26	single	bidentate	black, pointed tips	paired	Zanol et al. 2000
<i>L. miniui</i> (Carrera-Parra & Salazar-Vallejo, 1998)	present	moniliform	with articulations	pectinate	5–6	less than 55% of body	1–3	articulated	yellow, tridentate	18–23	single	bidentate to tridentate	black, bifid tips	unknown	Carrera-Parra & Salazar-Vallejo 1998, Zanol et al. 2007
<i>L. rubra</i> (Grube, 1856)	present	moniliform	with articulations	pectinate	4–6	more than 65% of body	1–21	articulated	yellow, tridentate	27	1–2	bidentate	yellow, both pointed or blunt and bifid tips	paired	Fauchald 1992, Steiner et al. 2002, Zanol et al. 2007
<i>L. thomasi</i> (Augener, 1922)	present	basally cylindrical and distally ovate	with articulations	palmate	4	more than 65% of body	1–3	articulated	brown, bidentate	22–24	1–2	bidentate	brown, blunt tips	paired	Fauchald 1992, Zanol et al. 2007
<i>L. torquata</i> (Quatrefages, 1866)	present	moniliform	with articulations	pectinate	3	more than 65% of body	2–7	articulated	brown, bidentate	22	1–2	bidentate	brown, blunt tips	paired	Fauchald 1992, Zanol et al. 2007
<i>L. valens</i> Chamberlin, 1919	present	regularly cylindrical	with articulations	pectinate	3	less than 55% of body	1–11	articulated	yellow, bidentate	43	1–2	bidentate	yellow, blunt tips	2–4	Fauchald 1992

Table 2. Genetic distance (K2P) based on 664 bp size of COI sequence among 13 *Leodice* species with two outgroup taxa (*Eunice norvegica* and *Marphysa sanguinea*).

No.	Species	Accession No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Data source
1	<i>Leodice duplexa</i> sp. n.	MF669544																	Present study
2	<i>Leodice duplexa</i> sp. n.	MF669545	0.000																"
3	<i>Leodice duplexa</i> sp. n.	MF669546	0.000	0.000															"
4	<i>L. americana</i>	GQ497561	0.095	0.095	0.095														Zanol et al. 2010
5	<i>L. antarctica</i>	GQ497532	0.088	0.088	0.088	0.043													"
6	<i>L. antennata</i>	DQ317858	0.097	0.097	0.097	0.103	0.124												Schulze 2006
7	<i>L. cf. antillensis</i>	GQ497533	0.144	0.144	0.144	0.102	0.088	0.159											Zanol et al. 2010
8	<i>L. harassii</i>	GQ497535	0.108	0.108	0.108	0.062	0.043	0.115	0.095										"
9	<i>L. cf. limosa</i>	GQ497531	0.124	0.124	0.124	0.104	0.110	0.102	0.153	0.116									"
10	<i>L. lucei</i>	GQ497529	0.082	0.082	0.082	0.088	0.095	0.062	0.115	0.088	0.102								"
11	<i>L. minutai</i>	GQ497530	0.104	0.104	0.104	0.109	0.116	0.096	0.145	0.123	0.153	0.083							"
12	<i>L. rubra</i>	GQ497528	0.083	0.083	0.083	0.089	0.109	0.012	0.144	0.101	0.102	0.062	0.111						"
13	<i>L. thomasi</i>	GQ497563	0.143	0.143	0.143	0.094	0.081	0.136	0.108	0.068	0.129	0.128	0.150	0.121					"
14	<i>L. torquata</i>	GQ497539	0.114	0.114	0.114	0.094	0.068	0.121	0.094	0.055	0.144	0.128	0.135	0.107	0.024				"
15	<i>L. valens</i>	GQ497534	0.116	0.116	0.116	0.089	0.069	0.139	0.075	0.075	0.103	0.095	0.132	0.124	0.129	0.115			"
16	<i>Eunice norvegica</i> (outgroup)	GQ497541	0.188	0.188	0.188	0.143	0.121	0.165	0.150	0.129	0.157	0.180	0.180	0.165	0.144	0.129	0.143		"
17	<i>Marphysa sanguinea</i> (outgroup)	GQ497547	0.172	0.172	0.172	0.135	0.101	0.157	0.115	0.101	0.150	0.121	0.157	0.142	0.136	0.121	0.114	0.101	"

1	Antennae and palps regularly articulated	2
–	Antennae and palps irregularly articulated	13
2	Subacicular hooks bidentate	3
–	Subacicular hooks tridentate	7
3	Peristomial cirri and notopodial cirri articulated	4
–	Peristomial cirri and notopodial cirri smooth	
 <i>L. harassii</i> (Audouin & Milne Edwards, 1933)	
4	Branchiae present on more than 65% of body	5
–	Branchiae present on less than 55% of body <i>L. valens</i> Chamberlin, 1919	
5	Parapodia with pectinate branchiae	6
–	Parapodia with palmate branchiae	<i>L. marcusii</i> (Zanol et al., 2000)
6	Subacicular hooks usually paired	<i>L. torquata</i> (Quatrefages, 1866)
–	Subacicular hooks always single	<i>L. laurillardii</i> (Quatrefages, 1866)
7	Branchiae with up to 20–21 filaments	8
–	Branchiae with less than 12 filaments	9
8	Aciculae with bifid or hammer-headed tips absent	
 <i>L. americana</i> (Hartman, 1944)	
–	Aciculae with bifid or hammer-headed tips present <i>L. rubra</i> (Grube, 1856)	
9	Guards of compound falcigers with mucros	10
–	Guards of compound falcigers without mucros	11
10	Palpostyles and ceratostyles cylindrical; peristomial cirri smooth	
 <i>L. limosa</i> (Ehlers 1868)	
–	Palpostyles and ceratostyles moniliform; peristomial cirri articulated	
 <i>L. lucei</i> (Grube, 1856)	
11	Compound falcigers tridentate in posterior chaetigers	
 <i>L. miurai</i> (Carrera-Parra & Salazar-Vallejo, 1998)	
	Compound falcigers only bidentate	12
12	Subacicular hooks always single; aciculae paired ... <i>L. antennata</i> Lamarck, 1818	
–	Subacicular hooks paired in some chaetigers; aciculae 2–4 in number	
 <i>L. duplexa</i> sp. n.	
13	Subacicular hooks and acicular light; branchiae pectinate	14
–	Subacicular hooks and acicular dark; branchiae palmate	
 <i>L. thomasiana</i> (Augener, 1922)	
14	Subacicular hooks paired in some chaetigers <i>L. antillensis</i> (Ehlers, 1887)	
–	Subacicular hooks always single	15
15	With finely hooded aciculae	<i>L. gracilicirrata</i> Treadwell, 1922
–	Without finely hooded aciculae	<i>L. antarctica</i> (Baird, 1869)

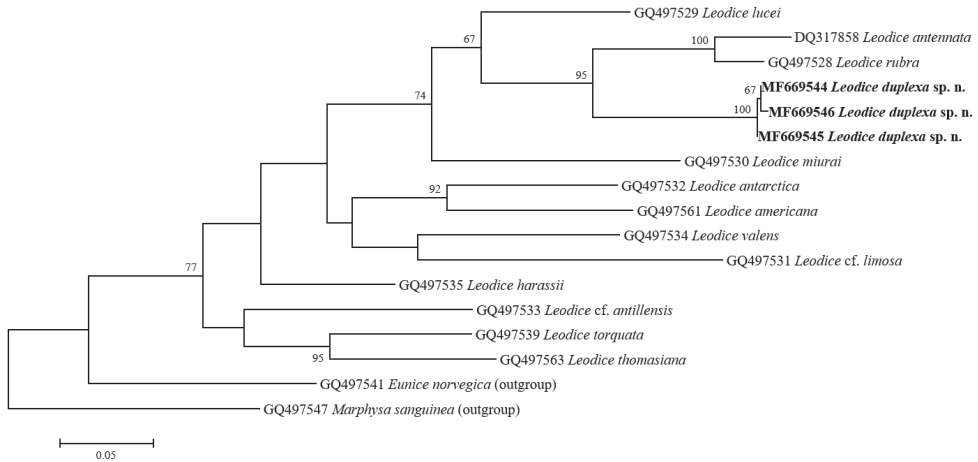


Figure 3. Maximum likelihood tree showing phylogenetic relationship based on COI sequences of 13 *Leodice* species with two outgroup taxa (*Eunice norvegica* and *Marphysa sanguinea*).

Acknowledgments

This work was supported by the National Marine Biodiversity Institute of Korea as a part of the ‘Securement, Analysis and Evaluation of Marine Invertebrate Bioresources (2017M00600)’.

References

- Arias A, Fernández-Álvarez FÁ, Martins R, Anadón N (2015) Rediscovery and redescription of *Leodice laurillardii* (Quatrefages, 1866) comb. nov. (Annelida: Eunicidae)-a rare European polychaete or just an overlooked species? *Zootaxa* 3964(4): 475–481. <https://doi.org/10.11646/zootaxa.3964.4.6>
- Carrera-Parra LF, Salazar-Vallejo SI (1998) A new genus and 12 new species of Eunicidae (Polychaeta) from the Caribbean Sea. *Journal of the Marine Biological Association of the United Kingdom* 78(1): 145–182. <https://doi.org/10.1017/S0025315400040005>
- Day JH (1967) A monograph on the Polychaeta of Southern Africa. Part 1. Errantia. British Museum (Natural History), London, 458 pp. <https://doi.org/10.5962/bhl.title.8596>
- Fauchald K (1970) Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allan Hancock Monographs in Marine Biology* 5: 1–335.
- Fauchald K (1992) A review of the genus *Eunice* (Eunicidae: Polychaeta) based upon type material. *Smithsonian Contributions to Zoology* 523: 1–422. <https://doi.org/10.5479/si.00810282.523>
- Hartman O (1944) Polychaetous Annelids. Part V. Eunicea. *Allan Hancock Pacific Expeditions* 10(1): 1–237.

- Hsueh PW, Li YH (2014) New species and new records of eunicids (Polychaeta, Eunicidae) from Taiwan. *Zootaxa* 3802(2): 151–72. <https://doi.org/10.11646/zootaxa.3802.2.1>
- Imajima M, Hartman O (1964) Polychaetes of Japan. Part II. Allan Hancock Foundation Publications. Occasional Papers 26: 239–452.
- Imajima M (2007) Annelida, Polychaeta III. Seibutsu Kenkyusha Co., Ltd., Tokyo, 499 pp.
- Lamarck JB (1818) Histoire Naturelle des Animaux sans Vertèbres, présentant les caracteres généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s’y rapportent; précédées d’une Introduction offrant la Détermination des caractères essentiels de l’animal, sa distinction du végétal et des autres corps naturels, en fin, l’Exposition des Principes fondamentaux de la Zoologie. Vol. 5. Deterville & Verdiere, Paris, 612 pp.
- León-González JA, Rivera CG, Romero MY (2004) Sublittoral Eunicidae and Onuphidae (Polychaeta) from soft bottom off El Salvador, eastern Pacific. *Journal of the Marine Biological Association of the United Kingdom* 84(1): 93–101. <https://doi.org/10.1017/S0025315404008951h>
- Miura T (1977) Eunicid Polychaetous Annelids from Japan-I. *Bulletin de la Société franco-japonaise d’océanographie* 15: 1–20.
- Miura T (1986) Japanese Polychaetes of the genera *Eunice* and *Euniphysa*: Taxonomy and branchial distribution patterns. *Publication of the Seto Marine Biological Laboratory*, 31: 269–325. <https://doi.org/10.5134/176125>
- Savigny JC (1820) Système des annélides, principalement de celles des côtes de l’Égypte et de la Syrie, offrant les caractères tant distinctifs que naturels des Ordres, Familles et Genres, avec la Description des Espèces. Description de l’Égypte ou Recueil des Observations et des Recherches qui ont été faites en Égypte pendant l’Expédition de l’Armée Française, publié par les Ordres de sa Majesté l’Empereur Napoléon le Grand, *Histoire Naturelle* 1(3): 1–128.
- Schulze A (2006) Phylogeny and Genetic Diversity of Palolo Worms (Palola, Eunicidae) from the Tropical North Pacific and the Caribbean. *Biological Bulletin* 210(1): 25–37. <https://doi.org/10.2307/4134534>
- Steiner TM, Nogueira JM, Amaral AC (2002) *Eunice rubra* Grube (Annelida, Polychaeta, Eunicidae), a redescription based on the holotype and Brazilian specimens. *Revista Brasileira de Zoologia* 19(1): 243–259.
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Wu X, Sun R, Liu R (2013a) A new species of *Eunice* (Polychaeta: Eunicidae) from Hainan Island, South China Sea. *Chinese Journal of Oceanology and Limnology* 31(1): 134–139. <https://doi.org/10.1007/s00343-013-2014-5>
- Wu X, Sun R, Liu R, Xu K (2013b) Two new species of *Eunice* Cuvier, 1817 (Polychaeta, Eunicidae) from the coral reefs of Hainan Island with a key to 16 species of *Eunice* from China seas. *Zootaxa* 3652(2): 249–264. <https://doi.org/10.11646/zootaxa.3652.2.3>

- Zanol J, Fauchald K, Paiva PC (2007) A phylogenetic analysis of the genus *Eunice* (Eunicidae, Polychaete, Annelida). *Zoological Journal of the Linnaean Society* 150(2): 413–434. <https://doi.org/10.1111/j.1096-3642.2007.00302.x>
- Zanol J, Halanych K, Struck T, Fauchald K (2010) Phylogeny of the bristle worm family Eunicidae (Eunicida, Annelida) and the phylogenetic utility of noncongruent 16S, COI and 18S in combined analyses. *Molecular Phylogenetics and Evolution* 55: 660–676. <https://doi.org/10.1016/j.ympev.2009.12.024>
- Zanol J, Halanych K, Fauchald K (2014) Reconciling taxonomy and phylogeny in the bristle-worm family Eunicidae (polychaete, Annelida). *Zoologica Scripta* 43(1): 79–100. <https://doi.org/10.1111/zsc.12034>

Revision of the genus *Ptomaphagus* Hellwig from eastern Asia (Coleoptera, Leiodidae, Cholevinae)

Cheng-Bin Wang¹, Michel Perreau², Jan Růžička¹, Masaaki Nishikawa³

1 Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 21 Praha 6, Czech Republic **2** IUT Paris Diderot, Université Paris Diderot, Sorbonne Paris Cité, case 7139, 5 rue Thomas Mann, F-75205 Paris cedex 13, France **3** Kashiwagaya 1112-16, Ebina, 243-0402 Japan

Corresponding author: Jan Růžička (ruzickajan@fzp.czu.cz)

Academic editor: B. Guéorguiev | Received 22 August 2017 | Accepted 12 October 2017 | Published 14 November 2017

<http://zoobank.org/763EF053-AFAA-4111-9CA9-6060F9E09E70>

Citation: Wang C-B, Perreau M, Růžička J, Nishikawa M (2017) Revision of the genus *Ptomaphagus* Hellwig from eastern Asia (Coleoptera, Leiodidae, Cholevinae). ZooKeys 715: 69–92. <https://doi.org/10.3897/zookeys.715.20497>

Abstract

The species belonging to the genus *Ptomaphagus* Hellwig, 1795 (Coleoptera, Leiodidae, Cholevinae, Ptomaphagini) from eastern Asia are assigned to three species groups. Group *yasutoshii* has a single species: *P.* (s. str.) *yasutoshii* Nishikawa, 1993 from Taiwan, China. Group *nepalensis* with three species: *P.* (s. str.) *nepalensis* Perreau, 1988 from Nepal and *P.* (s. str.) *masumotoi* Nishikawa, 2011 from Thailand are redescribed, and *P.* (s. str.) *piccoloi* Wang, Růžička, Nishikawa, Perreau & Hayashi, 2016 is recorded for the first time from China (Zhejiang). Group *sibiricus* with seven species, including two newly described Chinese ones *P.* (s. str.) *funiu* **sp. n.** from Henan, and *P.* (s. str.) *haba* **sp. n.** from Yunnan, and five known species: *P.* (s. str.) *chenggongii* Wang, Nishikawa, Perreau, Růžička & Hayashi, 2016, *P.* (s. str.) *hayashii* Wang, Růžička, Perreau, Nishikawa & Park, 2016, *P.* (s. str.) *kuntzeni* Sokolowski, 1957 (distribution records from Myanmar excluded), *P.* (s. str.) *sibiricus* Jeannel, 1934 and *P.* (s. str.) *tingtingtae* Wang, Nishikawa, Perreau, Růžička & Hayashi, 2016. Specimens of other undescribed species of the group *sibiricus* are also recorded, revealing a high diversity of this genus in eastern Asia, especially in central and north Sichuan, China, which essentially remains to be investigated. Relevant morphological characters of the examined species are illustrated with colour plates, and their known distributions are mapped. A key to species of *Ptomaphagus* from eastern Asia is provided.

Keywords

Cholevinae, eastern Asia, Leiodidae, new species, *Ptomaphagus*, species group, taxonomy

Introduction

The genus *Ptomaphagus* belongs to the subtribe Ptomaphagina of the tribe Ptomaphagini (Leiodidae, Cholevinae) and was introduced by Hellwig (1795) based on a single species *Tritoma sericea* Fabricius, 1787 (= *Silpha subvillosa* Goeze, 1777) from Europe, which was fixed as the type species of the genus by monotypy. It is the most speciose genus (including 138 known species worldwide) in the tribe Ptomaphagini. However, the nominotypical subgenus, which is limited to the Palaearctic and north Oriental Regions has only 30 species (Perreau 2000, Nishikawa 2011, Wang et al. 2016a, 2016b, 2016c).

Considering the fauna of China, only four representatives of the subgenus *Ptomaphagus* s. str. had been recorded from Taiwan Island, two of which were just recently described in a previous paper in this series (Wang et al. 2016b). For the vast mainland of China, there were no records of this genus before this study.

In this paper, two new species are described: *Ptomaphagus* (s. str.) *funiu* sp. n. from Henan Province, China and *P.* (s. str.) *haba* sp. n. from Yunnan Province, China. *P.* (s. str.) *piccoloi* Wang, Růžička, Nishikawa, Perreau & Hayashi, 2016 is recorded for the first time from China (Zhejiang Province). Several unidentified *Ptomaphagus* species from central and north Sichuan Province are discussed here also, without descriptions due to the limited number of available specimens. This reveals a high diversity in this region. Moreover, *P.* (s. str.) *nepalensis* Perreau, 1988 from Nepal and *P.* (s. str.) *masu-motoi* Nishikawa, 2011 from Thailand are redescribed, and record of *P.* (s. str.) *kuntzeni* Sokolowski, 1957 from Myanmar is discounted. Relevant morphological characters of the examined species are illustrated with colour plates, and their known distributions are mapped. All species from eastern Asia are assigned to one of three species groups, and a key to all the investigated taxa is provided.

Materials and methods

Specimens were relaxed and softened in a hot saturated solution of potassium hydroxide for 4 minutes (for mounted dry specimens) or 8 minutes (for alcohol-preserved specimens), and then transferred to distilled water to rinse the residual potassium hydroxide off and stop any further bleaching. The softened specimens were moved into glycerine and dissected there to observe morphological details. After examination, the body parts were mounted on a glass coverslip with Euparal Mounting Medium for future studies. Habitus photographs were taken using a Canon macro photo lens MP-E 65mm on a Canon 550D. Observations, photographs, and measurements of morphological details were performed using an Olympus BX53 microscope with an Olympus DP73 camera. The final deep focus images were created with Zerene Stacker 1.04 stacking software. Adobe Photoshop CS6 was used for post-processing. Exact label data are cited, while authors' remarks and addenda are placed in square brackets; separate label lines are indicated by a slash (/), and separate labels are indicated by a double slash (/). Measurements are averages taken from 5 specimens.

The material examined for this study is deposited in the following collections and museums (with names of curators in parentheses):

BMNH	Natural History Museum (formerly British Museum), London, United Kingdom (M. Barclay)
CAPE	Collection of Andreas Pütz, Eisenhüttenstadt, Germany
CCBW	Collection of Cheng-Bin Wang, Chengdu, China
CJRZ	Collection of Jan Růžička, Prague, Czech Republic
CMNE	Collection of Masaaki Nishikawa, Ebina, Japan
CMPR	Collection of Michel Perreau, Paris, France
CMSB	Collection of Michael Schülke, Museum für Naturkunde Berlin, Germany (J. Frisch)
CPMG	Collection of Pier Mauro Giachino, Torino, Italy
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland (G. Cuccodoro)
MNHN	Muséum National d'Histoire Naturelle, France, Paris (T. Deuve, A. Taghavian)
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden (J. Bergsten)
NMPC	Národní muzeum, Prague, Czech Republic (M. Fikáček, J. Hájek)
NSMT	National Museum of Nature and Science, Tsukuba, Japan (S. Nomura)

The following measurements in millimetres (mm) were made:

AL	(antennal length): length between the antennal base and the apex
BTW	(basitarsal width): maximum width of male proximal protarsomere
EBL	(extended body length): summation of HL, PL, ELL and length of exposed scutellum, preventing the error introduced by exposed or retracted head
ELL	(elytral length): length between the posterior end of scutellum and the elytral apex
ELW	(elytral width): widest part of both elytra combined
EW	(eye width): maximum width of a single compound eye in dorsal view
HL	(head length): length between the anterior apex of clypeus and the posterior margin of occipital carina along the midline
HW	(head width): maximum width of head (usually including eyes)
PL	(pronotal length): length of the pronotum along the midline
PW	(pronotal width): maximum width of pronotum
TW	(tibial width): maximum width of male protibia (excluding spines along outer margin etc.)

Results

Genus *Ptomaphagus* Hellwig, 1795

Distribution. Holarctic, north Oriental, north Neotropical.

Subgenus *Ptomaphagus* s. str.

Distribution. Palearctic, north Oriental.

Key to species of *Ptomaphagus* Hellwig from eastern Asia

- 1 Body length ≥ 4.3 mm (Wang et al. 2016b: Fig. 2A–D); antennomere III much longer than II (Wang et al. 2016b: Fig. 5A); VI subquadrate, length/width = 0.8 (Wang et al. 2016b: Fig. 5A); metathoracic wings absent; aedeagus with median lobe turning to right at apex (Wang et al. 2016b: Fig. 6F–I); spermatheca discoid in distal part (Wang et al. 2016b: Fig. 7A–C); China (Taiwan) (group *yasutoshii*) ***P. (s. str.) yasutoshii* Nishikawa**
- Body length usually ≤ 4.3 mm; antennomere III shorter than or as long as II; VI transverse, length/width ≤ 0.5 ; metathoracic wings fully developed; aedeagus with median lobe not turning to right at apex; spermatheca not discoid in distal part...2
- 2 Body length ≤ 3.0 mm, except *P. (s. str.) masumotoi* approaches 3.5 mm; spermatheca sinuous or coiled in distal part (Figs 3F; 5F) (group *nepalensis*) **3**
- Body length ≥ 3.5 mm; spermatheca simply curved in distal part (Figs 7F; 9G) (group *sibiricus*) **5**
- 3 Elytral apices with sexual dimorphism, rounded in male but acuminate in female (Wang et al. 2016a: Fig. 5G–H); male abdominal ventrite VIII rounded at posterior edge and with a small median notch (Wang et al. 2016a: Fig. 5I); China (Zhejiang), Japan ***P. (s. str.) piccoloi* Wang, Růžička, Nishikawa, Perreau & Hayashi**
- Elytral apices without sexual dimorphism, similarly rounded in both sexes; male abdominal ventrite VIII emarginate at posterior edge **4**
- 4 Male basal three protarsomeres less expanded (Fig. 2C); spiculum gastrale of genital segment with about 2/5 of length protruding beyond anterior edge of epipleurite IX (Fig. 2J); aedeagus with the apex of median lobe lanceolate (Fig. 3A, C); Nepal ***P. (s. str.) nepalensis* Perreau**
- Male basal three protarsomeres strongly expanded (Fig. 4C); spiculum gastrale of genital segment with about 1/5 of length protruding beyond anterior edge of epipleurite IX (Fig. 4J); aedeagus with the apex of median lobe oblong (Fig. 5A, C); Thailand ***P. (s. str.) masumotoi* Nishikawa**
- 5 Spermatheca not coiled in proximal part (Wang et al. 2016a: Fig. 4G); China (Taiwan), Japan ***P. (s. str.) kuntzeni* Sokolowski**
- Spermatheca coiled in proximal part (Figs 7F; 9G) **6**
- 6 Male abdominal ventrite VIII distinctly emarginate at posterior edge (Fig. 8I); in lateral view, aedeagal median lobe abruptly and strongly bent ventrally in apical part (Fig. 9C); China (Yunnan) ***P. (s. str.) haba* sp. n.**
- Male abdominal ventrite VIII rounded or subtruncate at posterior edge; in lateral view, aedeagal median lobe not abruptly and strongly bent ventrally in apical part **7**

- 7 Male abdominal ventrite VIII without a small median notch (Fig. 6I); aedeagus very short and stout (Fig. 7A–B); China (Henan) ***P. (s. str.) funiu* sp. n.**
- Male abdominal ventrite VIII with a small median notch; aedeagus long and slender **8**
- 8 Spiculum gastrale of genital segment with about 3/8 of length protruding beyond anterior edge of epipleurite IX (Wang et al. 2016b: Figs 8J; 11J) **9**
- Spiculum gastrale of genital segment with about 1/5 of length protruding beyond anterior edge of epipleurite IX (Wang et al. 2016c: Figs 2J; 4J) **10**
- 9 Antennomere XI with length/width = 1.9 (Wang et al. 2016b: Fig. 8A); right apicoventral piece of aedeagal median lobe broad (Wang et al. 2016b: Fig. 9H); spermatheca extended leftwards in proximal part (Wang et al. 2016b: Fig. 10B); China (Taiwan) ***P. (s. str.) chenggongi* Wang, Nishikawa, Perreau, Růžicka & Hayashi**
- Antennomere XI with length/width = 1.3 (Wang et al. 2016b: Fig. 11A); right apicoventral piece of aedeagal median lobe rather small (Wang et al. 2016b: Fig. 9I); spermatheca not extended leftwards in proximal part (Wang et al. 2016b: Fig. 10C); China (Taiwan) ***P. (s. str.) tingtingae* Wang, Nishikawa, Perreau, Růžicka & Hayashi**
- 10 Aedeagus stouter (Wang et al. 2016c: Fig. 5A); right apicoventral piece of median lobe much wider and subpentagonal (Wang et al. 2016c: Fig. 5C); apical half of median lobe thicker in lateral view (Wang et al. 2016c: Fig. 5B); Russia (Far East), South Korea ***P. (s. str.) sibiricus* Jeannel**
- Aedeagus much larger and more slender (Wang et al. 2016c: Fig. 3A); right apicoventral piece of median lobe slenderly lanceolate (Wang et al. 2016c: Fig. 3C); apical half of median lobe much flatter in lateral view (Wang et al. 2016c: Fig. 3B); Russia (Far East) ***P. (s. str.) hayashii* Wang, Růžicka, Perreau, Nishikawa & Park**

Group *yasutoshii*

Diagnosis. This group is characterised by the following combination of characters: (1) body length ≥ 4.3 mm; (2) antennomere III much longer than II; VI subquadrate, length/width = 0.8; (3) metathoracic wings absent; (4) aedeagus with median lobe turning to right at apex; (5) spermatheca discoid in distal part. Species included:

P. (s. str.) yasutoshii Nishikawa, 1993 (China (Taiwan))

= *P. (s. str.) smetanai* Perreau, 1996

Group *nepalensis*

Diagnosis. This group is characterised by the following combination of characters: (1) body length ≤ 3.0 mm, except *P. (s. str.) masumotoi* approaches 3.5 mm; (2) anten-

nomere III shorter than or almost as long as II; VI transverse, length/width ≤ 0.5 ; (3) metathoracic wings fully developed; (4) aedeagus with median lobe not turning to right at apex; (5) spermatheca sinuous or coiled in distal part. Species included:

P. (s. str.) *masumotoi* Nishikawa, 2011 (Thailand)

P. (s. str.) *nepalensis* Perreau, 1988 (Nepal)

P. (s. str.) *piccoloi* Wang, Růžicka, Nishikawa, Perreau & Hayashi, 2016 (China (Zhejiang), Japan)

***Ptomaphagus* (s. str.) *nepalensis* Perreau, 1988**

Figs 1A–B; 2A–J; 3A–F

Ptomaphagus (s. str.) *nepalensis* Perreau, 1988: 1005 (*Ptomaphagus*; type locality: Népal, district de Lalitpur, Phulcoki [ca. 27°34'N 085°25'E], 2600 m; MHNG); Perreau, 2000: 363 (*Ptomaphagus* (s. str.); in catalog); Perreau, 2004: 178 (*Ptomaphagus* (*Ptomaphagus*); in catalog); Perreau, 2015: 249 (*Ptomaphagus* (*Ptomaphagus*); in catalog).

Material examined. Type material. Paratypes: 1♂, NEPAL, Kath- / mandu District // Phulcoki 2600 m / 20.IV.1982 / A. & Z. Smetana // PARATYPE (MHNG); 1♂, NEPAL Lalitpur / Distr. Phulcoki / 2600 m 16.X.[19]83 / Smetana & Löbl // *Ptomaphagus* / *nepalensis* / Perreau 1988 // PARATYPE // MHNG / ENTO / 00003344 (MHNG); 1♀, NEPAL Lalitpur / Distr. Phulcoki / 2600 m 14.X.[19]83 / Smetana & Löbl // PARATYPE // MHNG / ENTO / 00003345 (MHNG); 1♀, NEPAL Lalitpur / Distr. Phulcoki / 2650 m 15.X.[19]83 / Smetana & Löbl // PARATYPE // MHNG / ENTO / 00003346 (MHNG); 1♀, NEPAL Lalitpur / Distr. Phulcoki / 2650 m 14.X.[19]83 / Smetana & Löbl // PTOMAPHAGUS / NEPALENSIS n. sp. / M. PERREAU det. 1987 // PARATYPE // MHNG / ENTO / 00003347 (MHNG); 1♀, NEPAL Lalitpur / Distr. Phulcoki / 2700 m 15.X.[19]83 / Smetana & Löbl // PARATYPE (MHNG); 1♂, NEPAL, Kath- / mandu District // Phulcoki 2600 m / 20.IV.1982 / A. & Z. Smetana // PARATYPE // MHNG / ENTO / 00003343 (MHNG); 1♀, NEPAL, Kath- / mandu District // Phulcoki 2600 m / 22.IV.1982 / A. & Z. Smetana // PARATYPE // MHNG / ENTO / 00003342 (MHNG); 2♂♂, NEPAL: distr. / Kathmandu: Phulcoki / 2500 m, 28–29.IV.[19]84 / Löbl - Smetana (CMPR).

Redescription. *Male.* EBL: 2.9–3.0 mm. Length of different body parts: HL : AL : PL : ELL = 0.5 : 0.9 : 0.7 : 1.6 mm; width: HW : EW : PW : ELW = 0.8 : 0.1 : 1.1 : 1.1 mm. Proportion of antennomeres from base to tip in μm (length \times width): 132 \times 54, 89 \times 50, 69 \times 50, 45 \times 52, 47 \times 60, 38 \times 72, 74 \times 89, 29 \times 90, 67 \times 97, 75 \times 103, 137 \times 94.

Habitus (Fig. 1A) elongated oval, regularly convex and sublustrous. Well pigmented: mostly blackish brown; mouthparts, basal three or four antennomeres and apical half of ultimate antennomere, protarsi, and apex of meso- and metatarsi more or less yellowish. Dorsum continually clothed with fine, recumbent, yellowish pubescence.

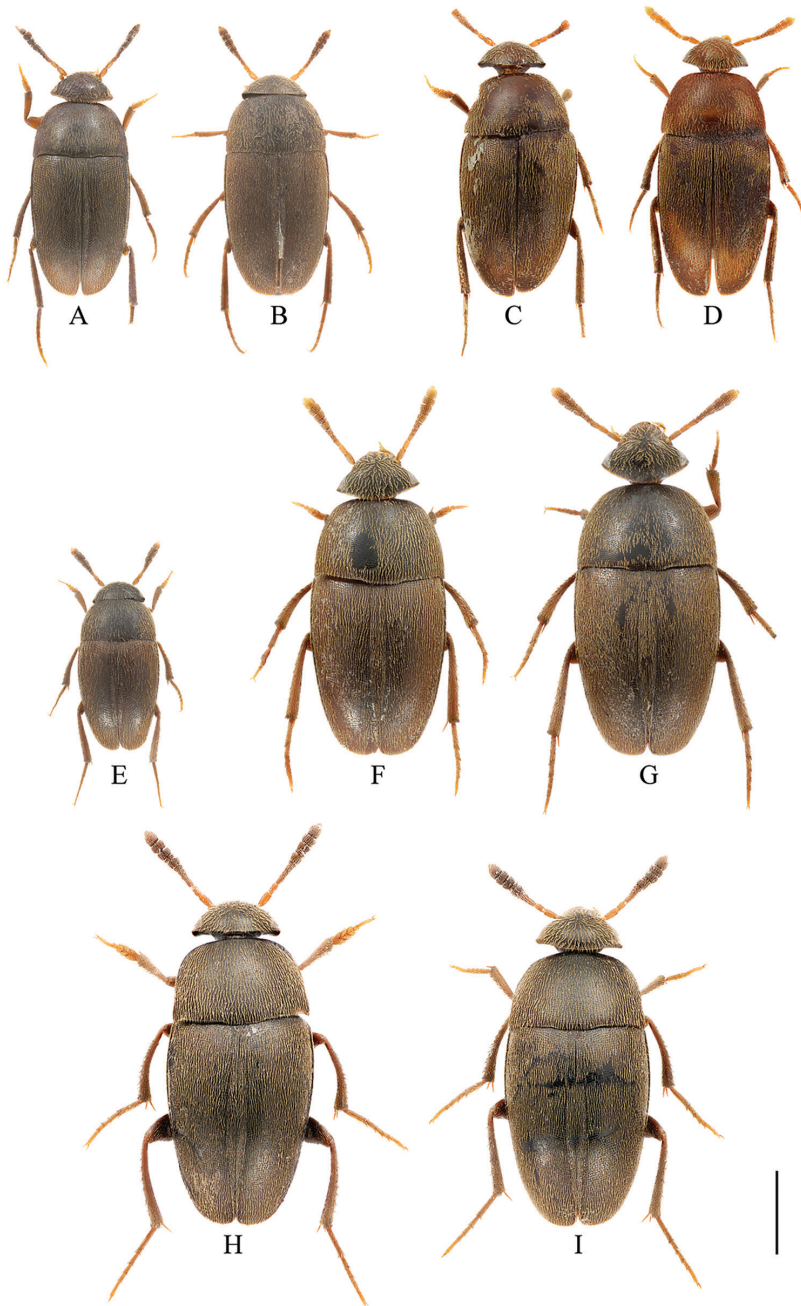


Figure 1. Habitus of *Ptomaphagus* (s. str.) spp. (dorsal view). **A–B** *P.* (s. str.) *nepalensis* Perreau, 1988 **A** ♂ (paratype; Nepal) **B** ♀ (paratype; Nepal) **C–D** *P.* (s. str.) *masumotoi* Nishikawa, 2011 **C** ♂ (paratype; Thailand) **D** ♀ (holotype; Thailand) **E** *P.* (s. str.) *piccoloi* Wang, Růžička, Nishikawa, Perreau & Hayashi, 2016 ♂ (China: Zhejiang) **F–G** *P.* (s. str.) *funiu* sp. n. **F** ♂ (holotype; China: Henan) **G** ♀ (paratype; China: Henan) **H–I** *P.* (s. str.) *haba* sp. n. **H** ♂ (holotype; China: Yunnan) **I** ♀ (paratype; China: Yunnan). Scale bar: 1 mm.

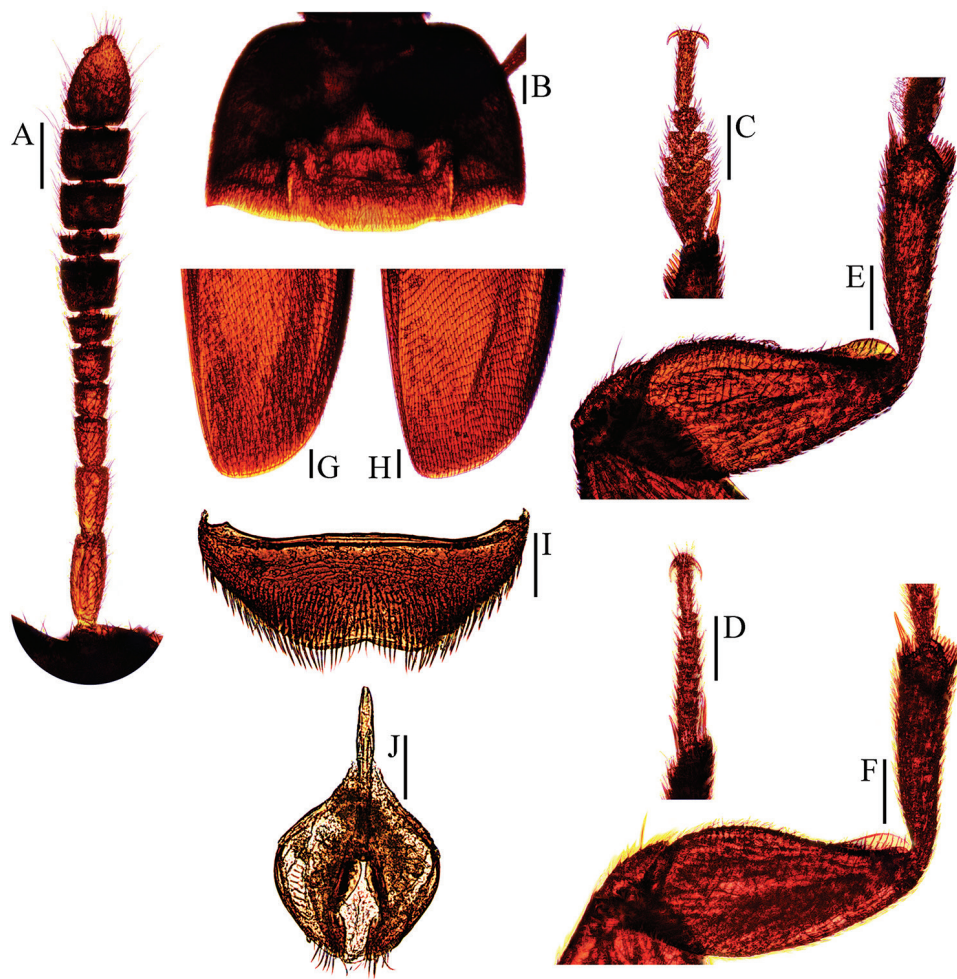


Figure 2. *Promaphagus* (s. str.) *nepalensis* Perreau, 1988 (♂: paratype; ♀: paratype). **A** antenna ♂ (dorsal view) **B** pronotum ♂ (dorsal view) **C** protarsus ♂ (dorsal view) **D** protarsus ♀ (dorsal view) **E** protibia and profemur ♂ (ventral view) **F** protibia and profemur ♀ (ventral view) **G** elytral apex ♂ (dorsoapical view) **H** elytral apex ♀ (dorsoapical view) **I** ventrite VIII ♂ (ventral view) **J** genital segment ♂ (ventral view). Scale bars: 0.1 mm.

Insertions of pubescence on dorsal surfaces of pronotum, elytra and femora aligned along transverse striolations; interspace between two striolations glabrous.

Head transverse, $HW/HL = 1.5$. Clypeofrontal suture absent. Clypeus with anterior margin almost straight. Compound eyes well developed, $EW/HW = 0.1$. Antennae (Fig. 2A) slender, $AL/HW = 1.1$; antennomere III shorter than II; VI with length/width = 0.5; XI pear-shape.

Pronotum (Fig. 2B) transverse, widest just before hind angles, $PW/PL = 1.5$. Sides gently arched, gradually narrowing from posterior to anterior; hind angles slightly pro-

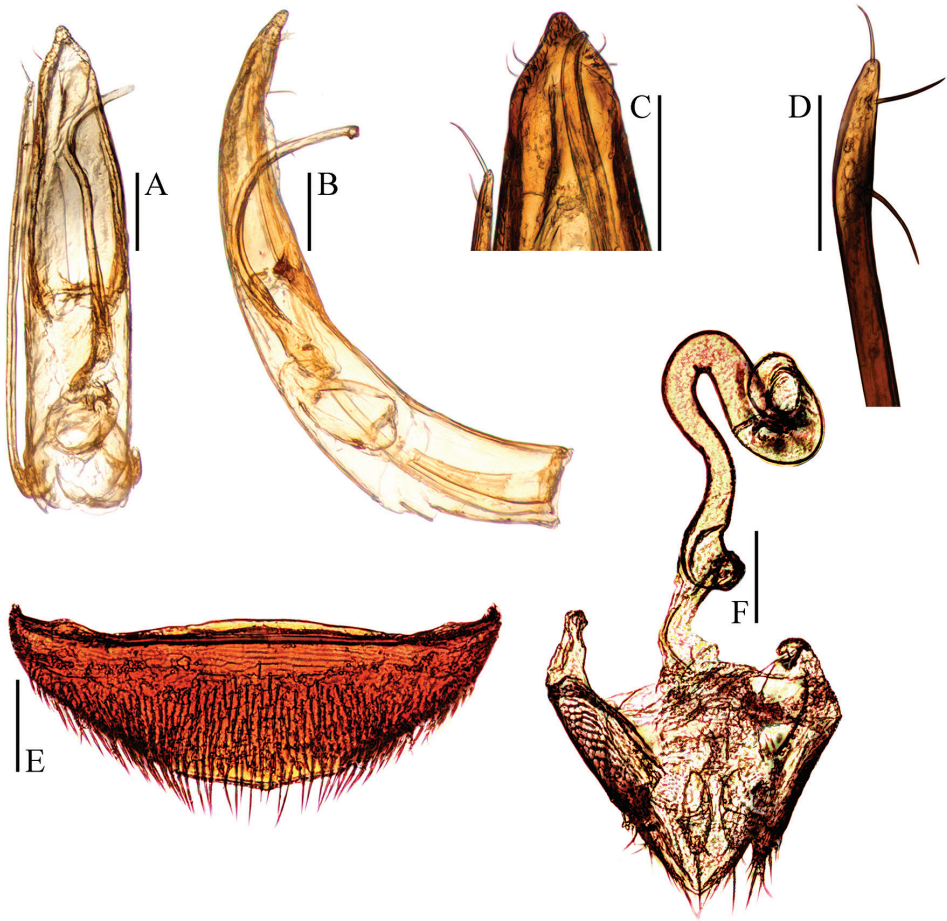


Figure 3. *Ptomaphagus* (s. str.) *nepalensis* Perreau, 1988 (♂: paratype; ♀: paratype). **A** aedeagus (dorsal view) **B** aedeagus (lateral view) **C** aedeagal apex (dorsal view) **D** paramere apex (lateral view) **E** ventrite VIII ♀ (ventral view) **F** spermatheca, genital segment and ovipositor (ventral view). Scale bars: 0.1 mm.

jected backwards and subacute. Posterior margin widely but shortly protruded in middle part, emarginate near hind angles.

Elytra oval, widest at about basal 2/7, $ELL/EW = 1.4$. Sides weakly arched, gradually narrowing from widest part to apices; apices (Fig. 2G) rounded. Sutural striae present. Metathoracic wings fully developed.

Prolegs robust, with basal three protarsomeres (Fig. 2C) expanded: $TW/BTW = 1.3$. Protibiae (Fig. 2E) expanded towards apex. Profemora broad. Mesotibiae arcuate, mesotarsi simply linear. Metatibiae slender, straight, but relatively short.

Abdominal ventrite VIII (Fig. 2I) distinctly emarginate at posterior edge, and much deeper at median. Spiculum gastrale of genital segment (Fig. 2J) with about 2/5 of length protruding beyond anterior edge of epipleurite IX.

Aedeagus (Fig. 3A) rather long and slender, with median lobe gradually narrowing towards a lanceolate apex and terminated to a widely subrounded knob in dorsal view; opening of genital orifice situated on dorsal surface, deeply cut inwards on preapical left margin of median lobe. Ventral surface of the apex of the median lobe (Fig. 3C) inserted with two ventrally oriented setae on the left side and three ventrally oriented setae on the right side; parameres narrow, reaching about apical 1/7 of median lobe, each apex (Fig. 3D) with two long lateral setae and one shorter apical seta. In lateral view (Fig. 3B), median lobe slender, regularly bent ventrally, and gradually tapering to a round apex. Endophallus with stylus quite slender, a transverse nodule in middle region, a cheliform complex just below base of stylus, and a circular complex in the basal region.

Female. Similar to male in general appearance (Fig. 1B), including elytral apices (Fig. 2H), but distinguished by the following characteristics: protarsi (Fig. 2D) simply linear; protibiae (Fig. 2F) narrower; abdominal ventrite VIII (Fig. 3E) almost rounded at posterior edge and slightly protruded at median; genital segment and ovipositor as shown in Fig. 3F; spermatheca (Fig. 3F) sinuous or coiled in distal part, not coiled in proximal part.

Distribution. Nepal.

***Ptomaphagus* (s. str.) *masumotoi* Nishikawa, 2011**

Figs 1C–D; 4A–J; 5A–F

Ptomaphagus (s. str.) *masumotoi* Nishikawa, 2011: 97 (*Ptomaphagus* (*Ptomaphagus*); type locality: NW Thailand, Chiang Mai, Doi Inthanon [ca. 18°42'N, 98°59'E], 1750 m; NSMT).

Material examined. Type material. Holotype: ♀, Doi Inthanon / 1750 m, Chiang / Mai, Thailand / 9-XI-1995 / K. MASUMOTO leg. // Holotype / *Ptomaphagus* (*Ptomaphagus*) / *masumotoi* M. Nishikawa, / 2011 / Design. M. Nishikawa, 2011 / # MNC 146Ch2P ♀ (NSMT). **Paratype:** 1♂, same data as holotype except: # MNC 147Ch2P ♂ (NSMT).

Redescription. Male. EBL: 3.4 mm. Length of different body parts: HL : AL : PL : ELL = 0.6 : - : 0.8 : 2.0 mm; width: HW : EW : PW : ELW = 0.8 : 0.1 : 1.3 : 1.5 mm. Proportion of antennomeres from base to tip in μm (length \times width): 121 \times 57, 105 \times 62, 71 \times 65, 48 \times 70, 53 \times 82, 35 \times 92, 94 \times 111, 28 \times 101, 83 \times 112 (last two antennomeres missing).

Habitus (Fig. 1C) elongated oval, regularly convex and sublustrous. Well pigmented: mostly brown; mouthparts, basal three antennomeres and apical half of ultimate antennomere, protarsi, and apex of meso- and metatarsi more or less paler. Dorsum continually clothed with fine, recumbent, yellowish pubescence. Insertions of pubescence on dorsal surfaces of pronotum, elytra and femora aligned along transverse striations; interspace between two striations glabrous.

Head transverse, HW/HL = 1.5. Clypeofrontal suture absent. Clypeus with anterior margin gently rounded. Compound eyes well developed, EW/HW = 0.1. Antennae

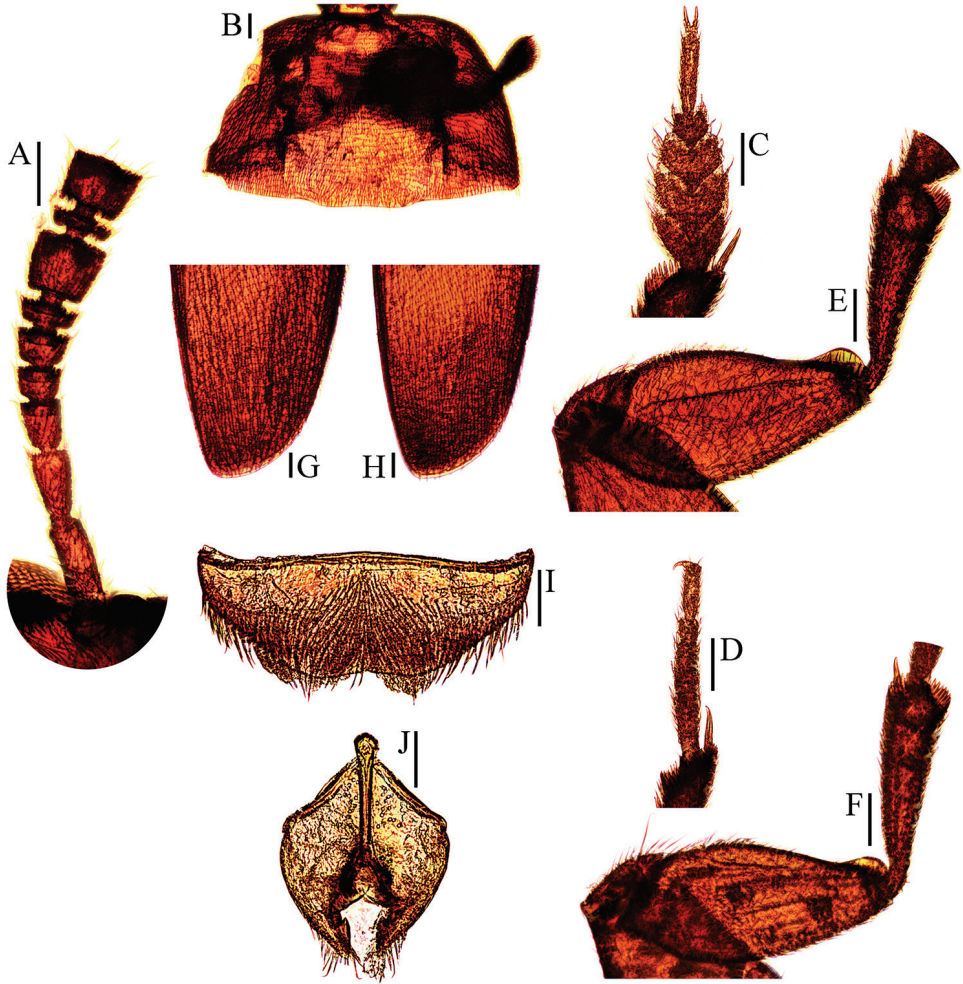


Figure 4. *Ptomaphagus* (s. str.) *masumotoi* Nishikawa, 2011 (♂: paratype; ♀: holotype). **A** antenna ♂ (dorsal view) **B** pronotum ♂ (dorsal view) **C** protarsus ♂ (dorsal view) **D** protarsus ♀ (dorsal view) **E** protibia and profemur ♂ (ventral view) **F** protibia and profemur ♀ (ventral view) **G** elytral apex ♂ (dorsoapical view) **H** elytral apex ♀ (dorsoapical view) **I** ventrite VIII ♂ (ventral view) **J** genital segment ♂ (ventral view). Scale bars: 0.1 mm.

(Fig. 4A) slender; antennomere III shorter than II; VI with length/width = 0.4; X and XI of holotype missing.

Pronotum (Fig. 4B) transverse, widest around hind angles, PW/PL = 1.6. Sides gently arched, simply narrowing from posterior to anterior; hind angles not projected backwards and bluntly rounded. Posterior margin widely protruded in middle part, emarginate near hind angles.

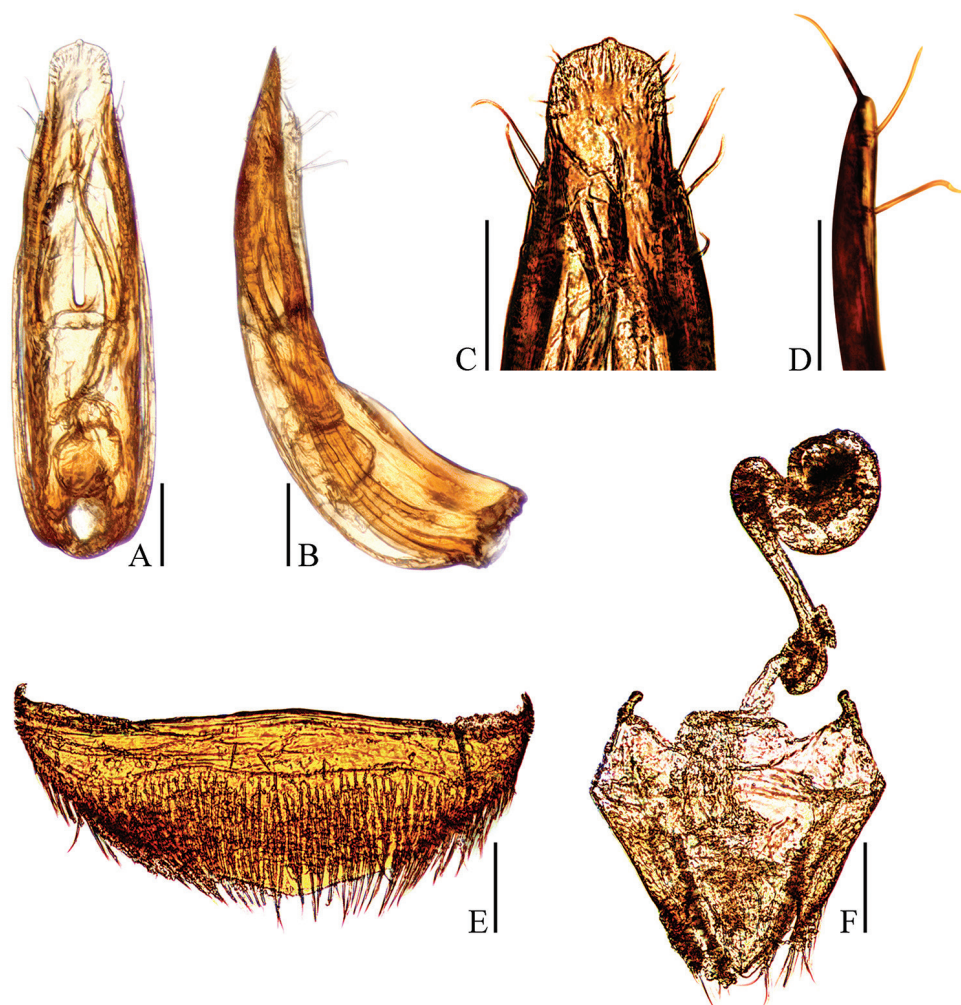


Figure 5. *Ptomaphagus* (s. str.) *masumotoi* Nishikawa, 2011 (♂: paratype; ♀: holotype). **A** aedeagus (dorsal view) **B** aedeagus (lateral view) **C** aedeagal apex (ventral view) **D** paramere apex (lateral view) **E** ventrite VIII ♀ (ventral view) **F** spermatheca, genital segment and ovipositor (ventral view). Scale bars: 0.1 mm.

Elytra oval, widest at about basal $2/7$, $ELL/EW = 1.4$. Sides weakly arched, gradually narrowing from widest part to apices; apices (Fig. 4G) narrowly rounded. Sutural striae present. Metathoracic wings fully developed.

Prolegs robust, with basal three protarsomeres (Fig. 4C) strongly expanded: $TW/BTW = 1.0$. Protibiae (Fig. 4E) strongly expanded towards apex. Profemora broad. Mesotibiae gently arcuate, mesotarsi simply linear. Metatibiae straight, but relatively short and thick.

Abdominal ventrite VIII (Fig. 4I) emarginate at posterior edge. Spiculum gastrale (Fig. 4J) of genital segment with about 1/5 of length protruding beyond anterior edge of epipleurite IX.

Aedeagus (Fig. 5A) slender, with median lobe gradually narrowing towards an oblong apex and terminated to a shortly rounded knob in dorsal view; opening of genital orifice situated on dorsal surface, deeply cut inwards on preapical left margin of median lobe. Ventral surface of the apex of the median lobe (Fig. 5C) inserted with five ventrally oriented setae on the left side and six ventrally oriented setae on the right side; parameres narrow, reaching about apical 1/7 of median lobe, each apex (Fig. 5D) with two long lateral setae and one similar apical seta. In lateral view (Fig. 5B), median lobe regularly bent ventrally but almost straight in apical half, and gradually tapering to a acuminate apex. Endophallus with stylus quite slender, a transverse nodule in middle region, a cheliform complex just below base of stylus, and a circular complex in the basal region.

Female. Similar to male in general appearance (Fig. 1D), including elytral apices (Fig. 4H), but distinguished by the following characteristics: protarsi (Fig. 4D) simply linear; protibiae (Fig. 4F) slightly narrower; abdominal ventrite VIII (Fig. 5E) slightly protruded at median of posterior edge; genital segment and ovipositor as shown in Fig. 5F; spermatheca (Fig. 5F) sinuous or coiled in distal part, not coiled in proximal part.

Distribution. Thailand.

Ptomaphagus (s. str.) *piccoloi* Wang, Růžička, Nishikawa, Perreau & Hayashi, 2016
Figs 1E; 10A, G

Material examined. 1♂, CHINA: Zhejiang (CH07-39), / Hangzhou Pref., Tianmu Shan [天目山], 40 / km WNW Linan, water reservoir, / 30°20'56"N, 119°18'42"E, 300 / m, plant refuse, litter from rock edges, 17.VI.2007, leg. A. Pütz (CAPE).

Remarks. This species is recorded for the first time from China.

Distribution. China (Zhejiang), Japan.

Group *sibiricus*

Diagnosis. This group is characterized by the following combination of characters: (1) $3.5 \text{ mm} \leq \text{body length} \leq 4.3 \text{ mm}$; (2) antennomere III shorter than or as long as II; VI transverse, length/width ≤ 0.5 ; (3) metathoracic wings fully developed; (4) aedeagus with median lobe not turning to right at apex; (5) spermatheca simply curved in distal part. Species included:

P. (s. str.) *chenggongi* Wang, Nishikawa, Perreau, Růžička & Hayashi, 2016 (China (Taiwan))

P. (s. str.) *funiu* sp. n. (China (Henan))

P. (s. str.) *haba* sp. n. (China (Yunnan))

P. (s. str.) *hayashii* Wang, Růžicka, Perreau, Nishikawa & Park, 2016 (Russia (Far East))

P. (s. str.) *kuntzeni* Sokolowski, 1957 (China (Taiwan), Japan)

= *P.* (s. str.) *amamianus* Nakane, 1963

P. (s. str.) *sibiricus* Jeannel, 1934 (Russia (Far East), South Korea)

P. (s. str.) *tingtingae* Wang, Nishikawa, Perreau, Růžicka & Hayashi, 2016 (China (Taiwan))

***Ptomaphagus* (s. str.) *funiu* sp. n.**

<http://zoobank.org/8DA08857-FB58-4688-8E00-38E054A82C3D>

Figs 1F–G; 6A–J; 7A–F

Type material. Holotype. ♂, China, W Henan, 9.–10.VI. / Funiu Shan [伏牛山], 33°31'N, 111°56'E / BAOTIANMAN, 1500–1750 m / Jaroslav Turna leg., 2008 (CPMG). **Paratypes.** 1♀, same data as holotype (CJRZ); 1♂, same data as holotype except: 15.V.–5.VI / 2009 (CMPR).

Diagnosis. Aedeagus (Fig. 7A) very short and stout, with median lobe gradually narrowing towards a widely lanceolate apex and terminated to a rounded knob in dorsal view. In lateral view (Fig. 7B), median lobe very thick, gently bent ventrally, and gradually tapering towards a thin apex.

Description. Male. EBL: 3.9 mm. Length of different body parts: HL : AL : PL : ELL = 0.6 : 1.0 : 1.1 : 2.1 mm; width: HW : EW : PW : ELW = 1.0 : 0.1 : 1.5 : 1.6 mm. Proportion of antennomeres from base to tip in µm (length × width): 154 × 61, 117 × 61, 87 × 65, 55 × 72, 57 × 87, 46 × 100, 80 × 117, 34 × 124, 77 × 138, 89 × 146, 141 × 131.

Habitus (Fig. 1F) elongated oval, regularly convex and sublustrous. Well pigmented: mostly blackish brown; mouthparts, basal three or four antennomeres and apical half of ultimate antennomere, protarsi, and apex of meso- and metatarsi more or less paler. Dorsum continually clothed with fine, recumbent, yellowish pubescence. Insertions of pubescence on dorsal surfaces of pronotum, elytra and femora aligned along transverse striolations; interspace between two striolations glabrous.

Head quite transverse, HW/HL = 1.7. Clypeofrontal suture absent. Clypeus with anterior margin gently rounded. Compound eyes well developed, EW/HW = 0.1. Antennae (Fig. 6A) slender, AL/HW = 1.0; antennomere III shorter than II; VI with length/width = 0.5; XI pear-shape.

Pronotum (Fig. 6B) transverse, widest directly before hind angles, PW/PL = 1.5. Sides gently arched, narrowing from posterior to anterior; hind angles slightly projected backwards and acute. Posterior margin widely protruded in middle part, emarginate near hind angles.

Elytra oval, widest at about basal 1/5, ELL/EW = 1.3. Sides weakly arched, gradually narrowing from widest part to apices; apices (Fig. 6G) widely rounded. Sutural striae present. Metathoracic wings fully developed.

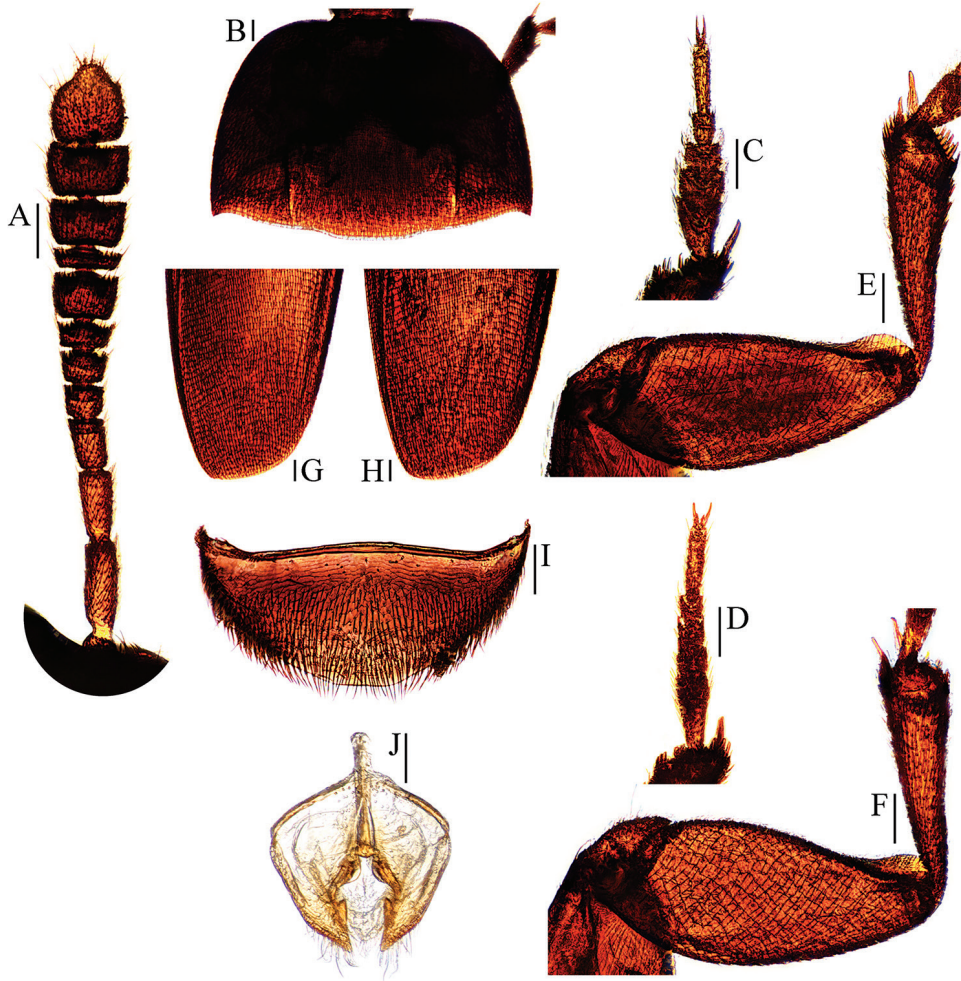


Figure 6. *Ptomaphagus* (s. str.) *funiu* sp. n. (♂: paratype; ♀: paratype). **A** antenna ♂ (dorsal view) **B** pronotum ♂ (dorsal view) **C** protarsus ♂ (dorsal view) **D** protarsus ♀ (dorsal view) **E** protibia and profemur ♂ (ventral view) **F** protibia and profemur ♀ (ventral view) **G** elytral apex ♂ (dorsoapical view) **H** elytral apex ♀ (dorsoapical view) **I** ventrite VIII ♂ (ventral view) **J** genital segment ♂ (ventral view). Scale bars: 0.1 mm.

Prolegs robust, with basal three protarsomeres (Fig. 6C) less expanded: TW/BTW = 1.5. Protibiae (Fig. 6E) expanded towards apex. Profemora broad. Mesotibiae arcuate, mesotarsi simply linear. Metatibiae slender and straight.

Abdominal ventrite VIII (Fig. 6I) simply subrounded at posterior edge. Spiculum gastrale of genital segment (Fig. 6J) with about 1/3 of length protruding beyond anterior edge of epipleurite IX.

Aedeagus (Fig. 7A) very short and stout, with median lobe gradually narrowing towards a widely lanceolate apex and terminated to a rounded knob in dorsal view;

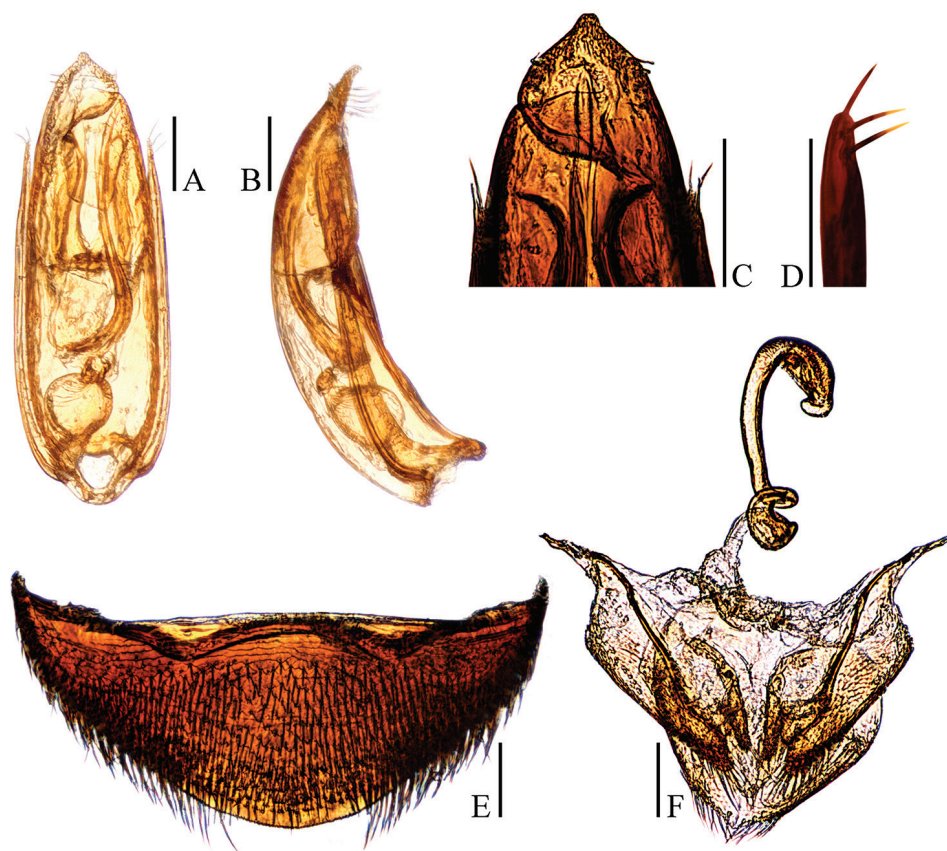


Figure 7. *Ptomaphagus* (s. str.) *funiu* sp. n. (♂: paratype; ♀: paratype). **A** aedeagus (dorsal view) **B** aedeagus (lateral view) **C** aedeagal apex (ventral view) **D** paramere apex (lateral view) **E** ventrite VIII ♀ (ventral view) **F** spermatheca, genital segment and ovipositor (ventral view). Scale bars: 0.1 mm.

opening of genital orifice situated on dorsal surface, deeply cut inwards on preapical left margin of median lobe. Ventral surface of the apex of the median lobe (Fig. 7C) inserted with 5 ventrally oriented setae on the left side and 6 ventrally oriented setae on the right side; parameres narrow, reaching about apical 1/5 of median lobe, each apex (Fig. 7D) with 2 lateral setae and 1 similar apical seta. In lateral view (Fig. 7B), median lobe very thick, gently bent ventrally, and gradually tapering towards a thin apex. Endophallus with stylus quite slender, a subelliptical nodule in middle region, a cheliform complex just below base of stylus, and a circular complex in the basal region.

Female. Similar to male in general appearance (Fig. 1G), including elytral apices (Fig. 6H), but distinguished by the following characteristics: protarsi (Fig. 6D) simply linear; protibiae (Fig. 6F) slightly narrower; abdominal ventrite VIII (Fig. 7E) round at posterior edge; genital segment and ovipositor as shown in Fig. 7F; spermatheca (Fig. 7F) curved in distal part, coiled in proximal part, and stem slightly arcuate.

Distribution. China (Funiu Mts. in Henan).

Etymology. The specific epithet is from the Chinese name (in Pinyin) of the type locality “Funiu Shan”, and means “prostrate cow”.

***Ptomaphagus* (s. str.) *haba* sp. n.**

<http://zoobank.org/5A165BE7-0FA5-4439-BFFE-869871DB61C0>

Figs 1H–I; 8A–J; 9A–G

Type material. *Holotype*. ♂, CHINA - YUNNAN / HABASHAN [哈巴山] - Habashan Mts. / 12.–16.6.2004, 3500– / 4000 m, 27°19'N, 100°08'E / lgt. Fouqué R.+H. (WGS 84) (NMPC). *Paratypes*. 9♂♂, 10♀♀, same data as holotype (1♀ in NMPC, 1♂1♀ in BMNH, 1♂1♀ in CCBW, 5♂♂5♀♀ in CJRZ, 1♂1♀ in CMNE, 1♂1♀ in CMPR).

Diagnosis. Aedeagus (Fig. 9A) long and slender, with median lobe gradually narrowing towards a lanceolate apex and terminated to an obtusely rounded knob in dorsal view (Fig. 9B). In lateral view (Fig. 9C), median lobe slender, regularly bent ventrally but abruptly stronger in apical part, and gradually tapering towards a thin apex.

Description. *Male*. EBL: 3.9–4.1 mm (4.0 mm in holotype). Length of different body parts: HL : AL : PL : ELL = 0.6 : 1.1 : 1.0 : 2.2 mm; width: HW : EW : PW : ELW = 1.0 : 0.1 : 1.5 : 1.6 mm. Proportion of antennomeres from base to tip in μm (length \times width): 176 \times 74, 130 \times 75, 88 \times 77, 58 \times 89, 64 \times 101, 38 \times 118, 80 \times 142, 28 \times 136, 84 \times 162, 98 \times 158, 186 \times 140.

Habitus (Fig. 1H) elongated oval, regularly convex and sublustrous. Well pigmented: mostly dark brown to blackish brown; mouthparts, basal two or three antennomeres and apical half of ultimate antennomere, protarsi, and apex of meso- and metatarsi brownish. Dorsum continually clothed with fine, recumbent, yellowish pubescence. Insertions of pubescence on dorsal surfaces of pronotum, elytra and femora aligned along transverse striolations; interspace between two striolations glabrous.

Head quite transverse, HW/HL = 1.6. Clypeofrontal suture absent. Clypeus with round anterior margin. Compound eyes well developed, EW/HW = 0.1. Antennae (Fig. 8A) slender, AL/HW = 1.1; antennomere III shorter than II; VI with length/width = 0.3; XI pear-shape.

Pronotum (Fig. 8B) transverse, widest at hind angles, PW/PL = 1.5. Sides gently arched, narrowing from posterior to anterior, and sensibly constricted above hind angles; hind angles slightly projected backwards and obtusely subrounded. Posterior margin widely protruded in middle part, emarginate near hind angles.

Elytra oval, widest at about basal 1/5, ELL/EW = 1.4. Sides weakly arched, gradually narrowing from widest part to apices; apices (Fig. 8G) rounded. Sutural striae present. Metathoracic wings fully developed.

Prolegs relatively slender, with basal three protarsomeres (Fig. 8C) expanded: TW/BTW = 1.2. Protibiae expanded towards apex. Profemora broad. Mesotibiae arcuate, mesotarsi simply linear. Metatibiae slender and slightly arcuate.

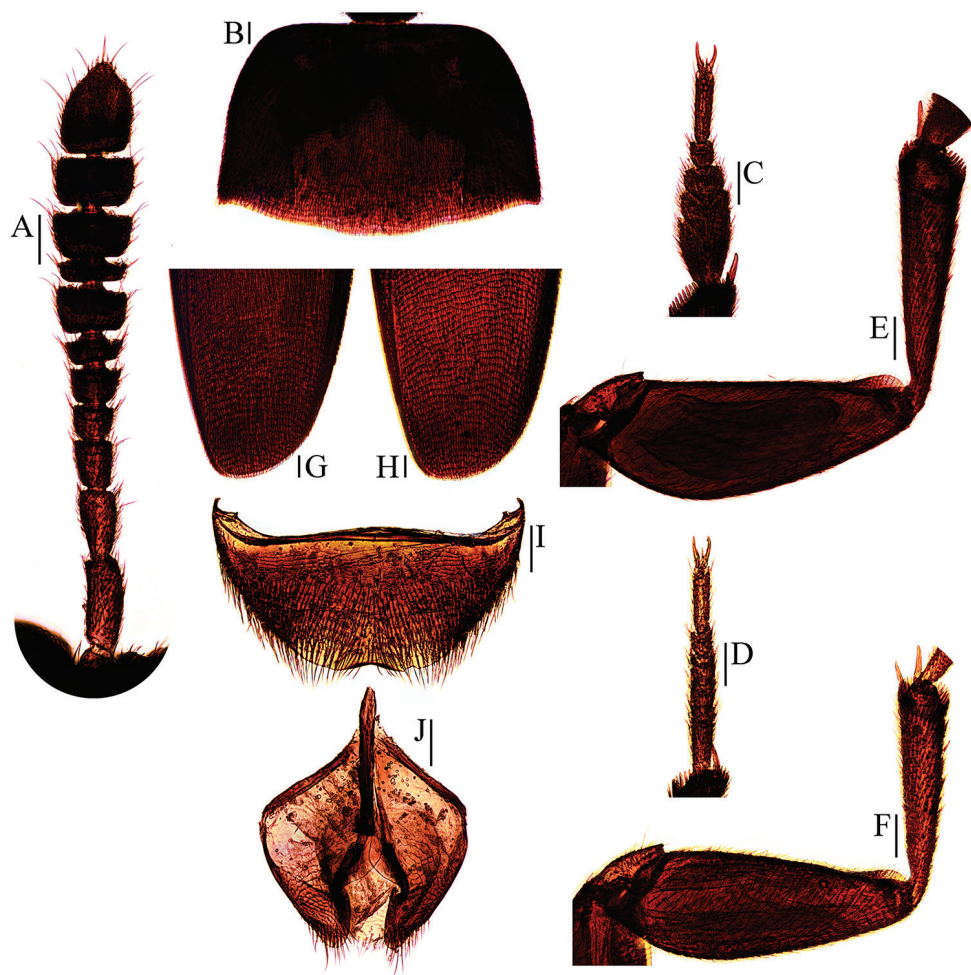


Figure 8. *Ptomaphagus* (s. str.) *haba* sp. n. (♂: paratype; ♀: paratype). **A** antenna ♂ (dorsal view) **B** pronotum ♂ (dorsal view) **C** protarsus ♂ (dorsal view) **D** protarsus ♀ (dorsal view) **E** protibia and profemur ♂ (ventral view) **F** protibia and profemur ♀ (ventral view) **G** elytral apex ♂ (dorsoapical view) **H** elytral apex ♀ (dorsoapical view) **I** ventrite VIII ♂ (ventral view) **J** genital segment ♂ (ventral view). Scale bars: 0.1 mm.

Abdominal ventrite VIII (Fig. 8I) distinctly emarginate at posterior edge. Spiculum gastrale of genital segment (Fig. 8J) with about 1/3 of length protruding beyond anterior edge of epipleurite IX.

Aedeagus (Fig. 9A) long and slender, with median lobe gradually narrowing towards a lanceolate apex and terminated to an obtusely rounded knob in dorsal view (Fig. 9B); opening of genital orifice situated on dorsal surface, deeply cut inwards on preapical left margin of median lobe. Ventral surface of the apex of the median lobe (Fig. 9D) inserted with 6 ventrally oriented setae on both sides; parameres narrow,

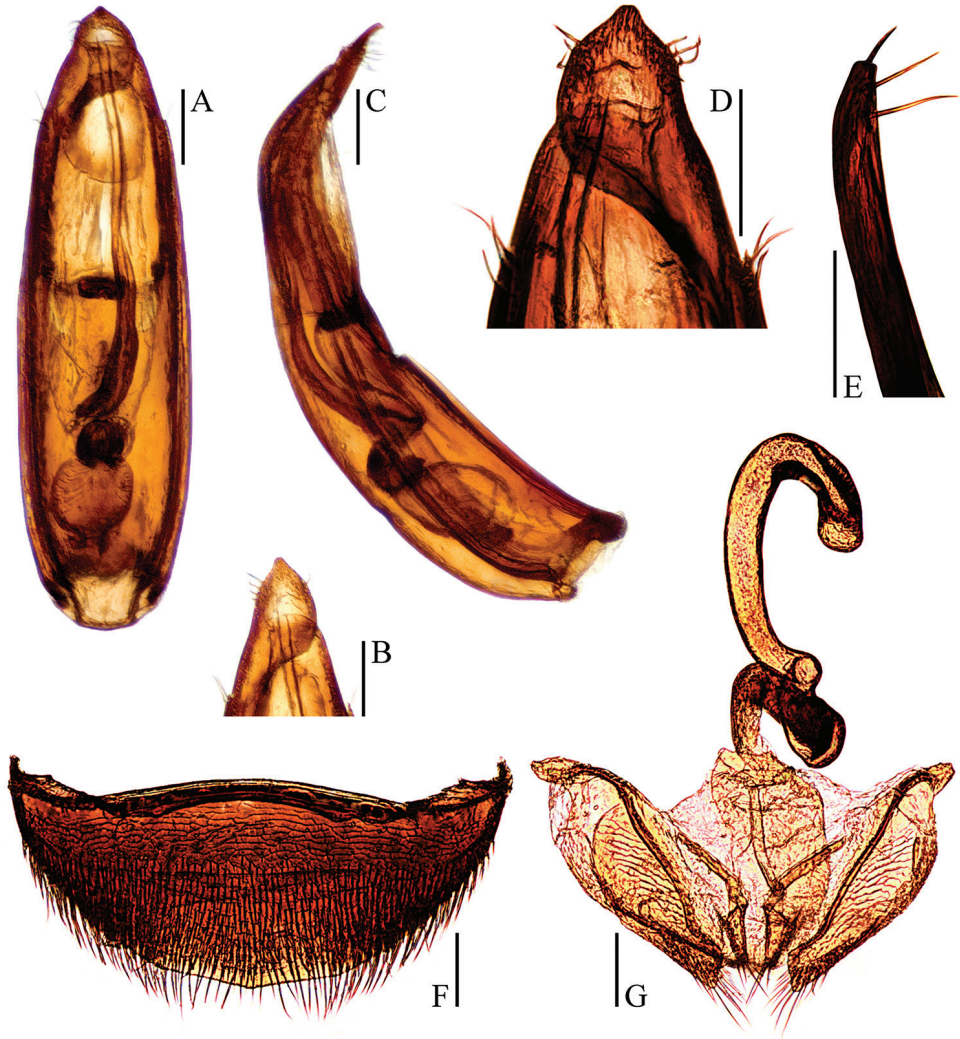


Figure 9. *Ptomaphagus* (s. str.) *haba* sp. n. (♂: paratype; ♀: paratype). **A** aedeagus (dorsal view) **B** aedeagal apex (dorsal view) **C** aedeagus (lateral view) **D** aedeagal apex (ventral view) **E** paramere apex (lateral view) **F** ventrite VIII ♀ (ventral view) **G** spermatheca, genital segment and ovipositor (ventral view). Scale bars: 0.1 mm.

reaching about apical 1/5 of median lobe, each apex (Fig. 9E) with 2 lateral setae and 1 shorter apical seta. In lateral view (Fig. 9C), median lobe slender, regularly bent ventrally but abruptly stronger in apical part, and gradually tapering towards a thin apex. Endophallus with stylus quite slender, a subelliptical nodule in middle region, a cheliform complex just below base of stylus, and a circular complex in the basal region.

Female. Similar to male in general appearance (Fig. 11), including elytral apices (Fig. 8H), but distinguished by the following characteristics: protarsi (Fig. 8D) simply



Figure 10. Aedeagi of *Ptomaphagus* (s. str.) spp. (**A–F** dorsal view **G–L** lateral view) **A, G** *P.* (s. str.) *piccoloi* Wang, Růžička, Nishikawa, Perreau & Hayashi, 2016 (China: Zhejiang) **B, H** *P.* (s. str.) sp.4 (China: Sichuan) **C, I** *P.* (s. str.) sp.5 (China: Shaanxi) **D, J** *P.* (s. str.) sp.6 (China: Sichuan) **E, K** *P.* (s. str.) sp.7 (China: Shaanxi) **F, L** *P.* (s. str.) sp.8 (China: Shaanxi). Scale bar: 0.1 mm.

linear; protibiae (Fig. 8F) narrower; abdominal ventrite VIII (Fig. 9F) almost rounded at posterior edge and slightly protruded at median; genital segment and ovipositor as shown in Fig. 9G; spermatheca (Fig. 9G) curved in distal part, coiled in proximal part, and stem gently arcuate.

Distribution. China (Haba Mts. in Yunnan).

Etymology. The specific epithet is from the Chinese name (in Pinyin) of the type locality “Habashan”, and means “flower of gold” in the Naxi language.

Other undescribed species of group *sibiricus*

Certain female specimens of *Ptomaphagus* from eastern Asia are possibly assigned to the right species group, but they cannot be identified at species level without the corresponding male individuals; this problem concerns especially females from the group *sibiricus*. The male aedeagus is the most crucial character for separating species.

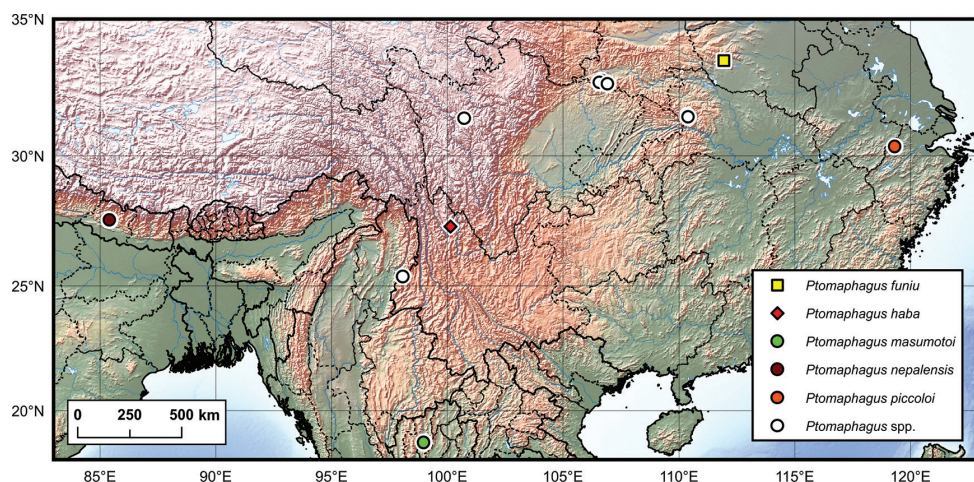


Figure 11. Distribution map of *Ptomaphagus* species from mainland China, Nepal, and Thailand.

The following *Ptomaphagus* species numbered as spp. 1, 2 and 3 have similar spermathecae, all curved in distal part and coiled in proximal part. *Ptomaphagus* spp. 4–8 with only one or two specimens respectively. What is surprising is the syntopic occurrence of four species (spp. 5–8) on a single mountain, Micang Shan (part of the Qinling Mountain Range), even at the same collecting point. For female specimens from the same region, their spermathecae are all curved in the distal part and coiled in the proximal part, similar to each other but with slight differences. Therefore, in consideration of limited specimens and the uncertainty of matching female and male specimens, we refrain from describing these species here and only provide illustrations of their aedeagi in Fig. 10, until such time as more specimens become available from this region.

Ptomaphagus sp. 1 ♀

Material examined. 1♀, N. E. Burma / Kambaiti, 2000 m / 12–17.6.34, Malaise [leg.] // Riksmuseum / Stockholm // *Ptomaphagus* (s. str.) / *kuntzeni* Sok. / det. / Szymczakowski 1964 // 9557 / E91 + // NHRS-JLKB / 000027149 (NHRS).

Remarks. Szymczakowski (1964) reported this female specimen as belonging to *Ptomaphagus* (s. str.) *kuntzeni*. However, Nishikawa (2011) and Wang et al. (2016a) disputed his identification. After dissecting it, we found that the spermatheca is curved in the distal part and coiled in the proximal part, but *P.* (s. str.) *kuntzeni* is so far the only species in the group *sibiricus* in which the spermatheca is not coiled in proximal part. Thus *P.* (s. str.) *kuntzeni* is excluded from the list of known fauna of Myanmar.

***Ptomaphagus* sp. 2 ♀**

Material examined. 2♀♀, China, N Henan, 14.VI.–6.VII. / WANGWUSHAN [王屋山], 1650 m / 35°12'N 112°17'E / Jaroslav Turna leg., 2007 (CPMG).

***Ptomaphagus* sp. 3 ♀**

Material examined. 1♀, CHINA: W-Hubei (Daba Shan) / pass E of Mt. Da Shennongjia, / 12 km NW Muyuping [木鱼坪], 31°30'N, / 110°21'E, 22.VII.2001, / leg. M. Schülke [C01-13E] // dry creek vally, mixed deciduous / forest, dead wood, mushrooms, / moss, 1950–2050 m (sifted) [C01-13E] (CMSB); 1♀, China, W Hubei, 20.VI.–12.VII. / MUYUPING [木鱼坪] S.env. ~1300 m / pit fall traps, 31.45N 110.4E / Jaroslav Turna leg., 2003 (CMPR).

***Ptomaphagus* sp. 4 ♂**

Figs 10B, H

Material examined. 1♂, CHINA - NW Sichuan / between Shangliusuo-Luhua / 5 km E of Luhua [芦花镇], 2400 m, shrubs / 7-28.VI.2004, leg. R. Fabbri (CPMG).

***Ptomaphagus* sp. 5 ♂**

Figs 10C, I

Material examined. 2♂♂, China, SW Shaanxi, 21.V.–10.VI. / Micang Shan [米仓山], 32°43'N, 106°34'E / LIPING, for park [forest park], 1700–1850 m / Jaroslav Turna leg., 2009 (CPMG).

***Ptomaphagus* sp. 6 ♂**

Figs 10D, J

Material examined. 1♂, China, N Sichuan, 5.VI.–9.VII. / Micang Shan [米仓山], 1385 m / DABA, 32°40'N 106°55'E / Jaroslav Turna leg., 2007 (CPMG).

***Ptomaphagus* sp. 7 ♂**

Figs 10E, K

Material examined. 1♂, China, SW Shaanxi, 21.V.–10.VI. / Micang Shan [米仓山], 32°43'N, 106°34'E / LIPING, for park [forest park], 1700–1850 m / Jaroslav Turna leg., 2009 (CPMG).

***Ptomaphagus* sp. 8 ♂**

Figs 10F, L

Material examined. 1♂, China, SW Shaanxi, 24.V.–30.VI. / Micang Shan [米仓山], 32°47'N, 106°40'E / LIPING for park [forest park], 1500–1600 m / Jaroslav Turna leg., 2011 (CPMG).

***Ptomaphagus* spp. ♀♀**

Material examined. 7♀♀, China, SW Shaanxi, 21.V.–10.VI. / Micang Shan [米仓山], 32°43'N, 106°34'E / LIPING, for park[forest park] , 1700–1850 m / Jaroslav Turna leg., 2009 (CPMG); 1♀, China, N Sichuan, 5.VI.–9.VII. / Micang Shan [米仓山], 1385 m / DABA, 32°40'N 106°55'E / Jaroslav Turna leg., 2007 (CPMG).

Acknowledgements

We would like to express our sincere thanks to Maxwell V. L. Barclay (BMNH), Pier Mauro Giachino (Torino, Italy), Yasuhiko Hayashi (Kawanishi, Japan), Hideto Hoshina (Fukui University, Fukui, Japan), Alfred F. Newton (Field Museum of Natural History, Chicago, USA), Stewart B. Peck (Carleton University, Ottawa, Canada), Vadim Zinchenko (Russian Academy of Sciences, Siberian Branch, Novosibirsk, Russia) and Hong-Zhang Zhou (Institute of Zoology, Chinese Academy of Sciences, Beijing, China) for their considerable help in our study. We are obliged to Pavel Jakubec (Czech University of Life Sciences, Prague, Czech Republic) for helping with habitus photographs with the camera system. All the collectors mentioned in the text are acknowledged for their field work. We thank Maxwell V. L. Barclay for linguistic revision of the text. We are grateful to Pier Mauro Giachino, Leonardo Latella (Verona, Italy) and Borislav Guéorguiev (National Museum of Natural History, BAS, Sofia, Bulgaria), reviewers who provided constructive comments on previous versions of the manuscript. This study was supported by the Ministry of the Interior of the Czech Republic (no. VI20152018027).

References

- Hellwig JCL (1795) *Favna etrusca sistens Insecta quae in provinciis Florentina et Pisana praesertim collegit Petrus Rossius*, in *Regio Pisano Aethenaeo Publ. prof. et Soc. Ital. Tomus primus*. C. G. Fleckeisen, Helmstadii, 457 pp.
- Nishikawa M (1993) Occurrence of a new apterous species of *Ptomaphagus* (Coleoptera, Cholevidae) in Taiwan. *Elytra* (Tokyo) 21(1): 123–128.
- Nishikawa M (2011) A new *Ptomaphagus* (Coleoptera: Leiodidae: Cholevinae) from Northwest Thailand. *Special Publication of the Japanese Society of Scarabaeoidology* 1: 97–102.

- Perreau M (1988) Les Cholevidae himalayiens du Muséum d'Histoire naturelle de Genève. *Revue suisse de Zoologie* 95: 1005–1018. <https://doi.org/10.5962/bhl.part.81947>
- Perreau M (2000) Catalogue des Coléoptères Leiodidae, Cholevinae et Platypsyllinae. *Mémoires de la Société entomologique de France* 4: 1–460.
- Perreau M (2004) Family Leiodidae Fleming, 1821. In: Löbl I, Smetana A (Eds) *Catalogue of Palaearctic Coleoptera. Volume 2: Hydrophiloidea – Histeroidea – Staphylinioidea*. Apollo Books, Stenstrup, 133–203.
- Perreau M (2015) Family Leiodidae Fleming, 1821. In: Löbl I, Löbl D (Eds) *Catalogue of Palaearctic Coleoptera. Volume 2/1. Hydrophiloidea – Staphylinioidea*. Revised and updated edition. Brill, Leiden & Boston, 180–290.
- Szymczakowski W (1964) Analyse systématique et zoogéographique des Catopidae (Coleoptera) de la région orientale. *Acta Zoologica Cracoviensia* 9: 55–289.
- Wang C-B, Nishikawa M, Perreau M, Růžička J, Hayashi Y (2016b) Revision of the genus *Ptomaphagus* Hellwig (Coleoptera, Leiodidae, Cholevinae) from Taiwan Island. *ZooKeys* 609: 43–62. <https://doi.org/10.3897/zookeys.609.9327>
- Wang C-B, Růžička J, Nishikawa M, Perreau M, Hayashi Y (2016a) Revision of the genus *Ptomaphagus* Hellwig (Coleoptera, Leiodidae, Cholevinae) from Japan. *ZooKeys* 607: 119–144. <https://doi.org/10.3897/zookeys.607.9074>
- Wang C-B, Růžička J, Perreau M, Nishikawa M, Park S-J (2016c) Revision of the genus *Ptomaphagus* Hellwig (Coleoptera, Leiodidae, Cholevinae) from the Russian Far East and the Korean Peninsula. *ZooKeys* 637: 33–45. <https://doi.org/10.3897/zookeys.637.9384>

Relocation of *Dodecaseta* McCammon & Stull, 1978 (Annelida, Capitellidae) in *Notodasus* Fauchald, 1972

María E. García-Garza¹, Jesus A. de León-González¹, Leslie H. Harris²

1 Universidad Autónoma de Nuevo León, Facultad de Ciencias Biológicas, Laboratorio de Biosistemática, AP 5 “F”, San Nicolás de los Garza, Nuevo León, México **2** Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007, U.S.A.

Corresponding author: María E. García-Garza (maria.garciagza@uanl.edu.mx)

Academic editor: Greg Rouse | Received 2 June 2017 | Accepted 26 September 2017 | Published 21 November 2017

<http://zoobank.org/7AA61B68-2056-4C0C-AFFF-070071A5FE57>

Citation: García-Garza ME, de León-González JA, Harris LH (2017) Relocation of *Dodecaseta* McCammon & Stull, 1978 (Annelida, Capitellidae) in *Notodasus* Fauchald, 1972. ZooKeys 715: 93–101. <https://doi.org/10.3897/zookeys.715.13936>

Abstract

The capitellid polychaete genus *Dodecaseta* McCammon & Stull, 1978 is relocated in *Notodasus* Fauchald, 1972. Two species are redescribed based on examination of type material and three new combinations are proposed: *Notodasus oraria* (McCammon & Stull, 1978), *N. eibyeyacobseni* (Green, 2002). *N. fauchaldi* (Green, 2002). *N. kristiani* (García-Garza et al., 2009), is synonymized under *N. oraria*. Some comments on *Dasybranchus lumbricoides* Grube, 1878 are included.

Keywords

Polychaeta, Capitellidae, *Dodecaseta*, *Notodasus*, new combinations

Introduction

The study of capitellid polychaetes has been complex. Determination at the generic level is based mainly on the number of thoracic segments, the number of chaetigers with capillary chaetae, a mixture of capillaries and hooded hooks, complete (with notopodium and neuropodium), or incomplete (with notopodium only) first chaetiger, as well as the position of the transition between thorax and abdomen (Fauchald 1977). However, these characters have caused erroneous determinations when the organisms

are in initial stages of growth since the capitellids display great morphological variability in these characters at different stages of development (Blake 2000).

Capitellids in early developmental stages have the first three segments with capillary chaetae while the following segments bear hooded hooks which will later be replaced by capillary chaetae in subsequent stages (Ewing 1984, George 1984). In addition to its simple morphological structure, and sometimes due to improper relaxation, fixation and preservation of specimens, confusion can occur in the establishment of new genera or species and misidentifying species by identifying immature stages. With this variability in the chaetal formula we may infer that some monotypic genera could be described from juvenile organism however this needs an in depth study of each case. In this work a review of a species belonging to *Dodecaseta* McCammon and Stull, 1978, confirmed that these species have morphological characters placing them in *Notodasus* Fauchald, 1972.

Material and methods

Material from the Natural History Museum of Los Angeles County, Allan Hancock Foundation Polychaete Collection (LACM-AHF) and the Colección Poliquetológica de la Universidad Autónoma de Nuevo León (UANL). Methyl green staining was used to determine specific patterns of glandular areas. Specimens were submerged for a maximum of two minutes in a solution of methyl green in 70% ethanol and washed in several alcohol changes (Warren et al. 1994). Photographs were taken with a stereomicroscope Olympus SZ61 equipped with a digital camera Olympus C-7070. Editing of photos was performed using Adobe Photoshop CS6.

Taxonomy

Order Capitellidae Fauchald, 1977

Family Capitellidae Grube, 1862

Genus *Notodasus* Fauchald, 1972

***Notodasus* Fauchald, 1972**

Notodasus Fauchald, 1972: 246–247, Pl.51 fig. a-c; García-Garza 2009: 101; García-Garza, et. al. 2009: 810; García-Garza and de León-González 2011: 35; Magalhães and Bailey-Brock 2012: 28.

Dodecaseta McCammon & Stull, 1978: 40–43, figs 1–3; Green 2002: 311.

Type species. *Notodasus magnus* Fauchald, 1972

Diagnosis. Thorax with 11 chaetigers with bilimbate capillary chaetae first chaetiger biramous. First two abdominal chaetigers with bilimbate capillaries in both rami, subsequent chaetigers with hooded hooks. Lateral organs and branchiae present.

Remarks. The genus *Dodecaseta* was established by Mc Cammon and Stull (1978) to include *Dodecaseta oraria*, a species from Southern California. These authors considered that *D. oraria* differed from the genus *Notodasus* by presenting the first thoracic chaetiger biramous and capillary chaetae in the first abdominal segments. In the original description of *Notodasus*, Fauchald (1972) described the genus with the first chaetiger being uniramous. García-Garza et al. (2009) reviewed the *Notodasus* genus based on the examination of type material, and they observed that the holotype *N. magnus* (type species of the genus) has the first chaetiger biramous, not uniramous as originally described.

The holotype of *D. oraria* is a small specimen of 12 mm long and 0.8 mm wide (LACM-AHF POLY 1248). McCammon and Stull (1978) included 12 specimens in the original description, but they did not include variation in body size of these specimens. Based on this discrepancy in the description (and other factors) we believe that the genus *Dodecaseta* should be synonymized with the genus *Notodasus*.

Blake (2000) had previously felt that *Dodecaseta* should be synonymized with *Notomastus* since the only known species form the Southern California Bight varied from *Notomastus* only in that it has notochaetae in the first abdominal chaetiger, and the presence of abdominal capillaries is not a considered generic character of capitellids.

Green (2002) expands the genus *Dodecaseta*, in order to describe two new species from the Andaman Sea (*D. fauchaldi* and *D. eibyejacobseni*) including the following characters, 12 and 13 chaetigers with capillary chaetae, with the last one or two transitional in appearance with expanded neuropodial lobes, and protruded lateral organs. However, the ammended diagnosis proposed by Green for *Dodecaseta* agrees with the diagnosis of the genus *Notodasus* Fauchald, 1972. Consequently, we believe that *D. fauchaldi* and *D. eibyejacobseni* should also be reassigned to the genus *Notodasus*.

***Notodasus oraria* (McCammon & Stull, 1978), comb. n.**

Figure 1

Dodecaseta oraria Mc Cammon & Stull, 1978: 41–43, figs 1–3.

Notodasus kristiani García-Garza et al., 2009: 809–823, figs 5A–D, 8E; García-Garza and de León-González 2011: 17–52; Magalhães and Bailey-Brock 2012: 33, figs 24a–d, 25c–d.

Material examined. Type material *Dodecaseta oraria* Holotype (LACM-AHF POLY 1248); Paratype (LACM-AHF POLY 1250), Palos Verdes Península, California, USA, 30–180 m; *Notodasus kristiani* Holotype (UANL 6515), Varadero beach, Guaymas, Sonora, Mexico [27°54'04.3"N, 110°52'07.7"W], 1 m, July 01 2005, 20 Paratypes (UANL 6517), 2 Paratypes (LACM-AHF POLY 2213), 1 Paratype (MNNH

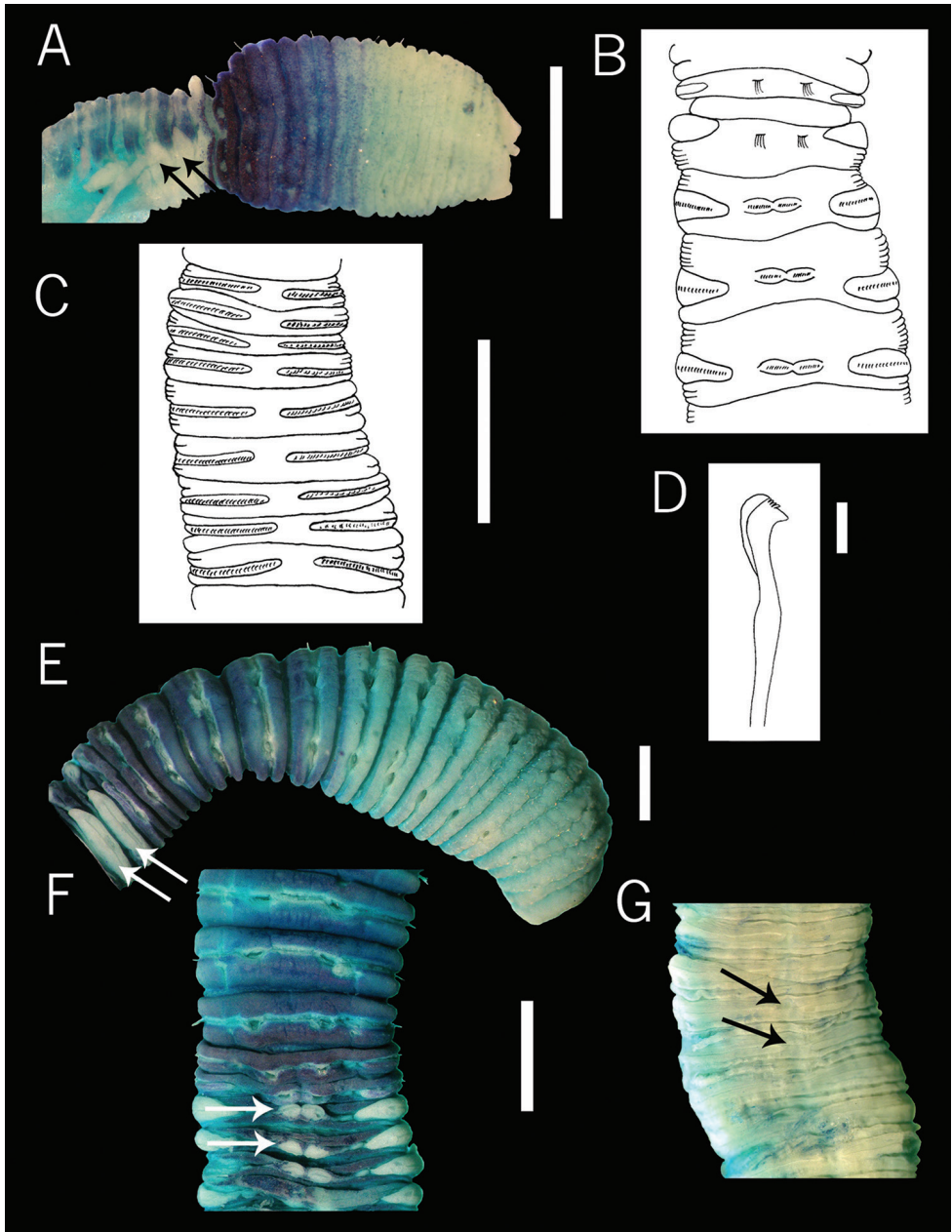


Figure 1. Holotypes of *Dodecaseta oraria* McCammon & Stull (**A–D**), and *Notodasus kristiani* (García-Garza et al., 2009) (**E–G**). **A** anterior end, lateral view **B** chaetiger 12-16, dorsolateral view **C** chaetigers 36-46, ventral view **D** neurohook from chaetiger 88, lateral view **E** anterior end, lateral view **F** chaetigers 9-17, dorsal view **G** chaetigers 19-27. Methyl green stain **A–C, E–G**. Scale bars: **A, B, C, E, F, G** = 1 mm, **D** = 15µm.

1508), 1 Paratype (ZMH POL), Varadero beach, Guaymas, Sonora, [27°54'04.3"N, 110°52'07.7"W], 1 m, July 01 2005, coll. J.A. de León-González (JALG) and M.E. García-Garza (MEG-G).

Additional material examined. *Notodasus kristiani*, two specimens (ECO-SUR), Municipal beach, Los Angeles Bay, Baja California, Mexico [28°56'32.3"N, 113°33'57.2"W] 1 m, May 24 1986, coll. P. Sánchez and E. Espinosa. One specimen (UANL 6515), Estero Rancho Nuevo, Santa Marina Bay, Baja California Sur, [24°19'15"N, 111°25'05"W] 3 m, June 21 1998, coll. JALG.

Redescription. Holotype of *D. oraria* incomplete with 89 segments, 12 mm long, 0.8 mm wide in abdomen. Color in alcohol white-translucent. Prostomium conical with palpo. Eyespots not seen. Peristomium to the eighth thoracic chaetiger tessellated, remaining segments smooth. Thorax with 11 chaetigers, with bilimbate capillaries in both rami, first chaetiger biramous, transition between thorax and abdominal segments marked by abrupt shorting of abdominal segments. (Fig. 1A). Thoracic and abdominal segments biannulate. Notopodia lateral in first thoracic segments, in subsequent segments located dorsally. Lateral organs, between notopodia and neuropodia throughout body, those of thoracic region closer to notopodium; thoracic lateral organs larger than abdominals. Genital pores not seen. Notopodial lobes of abdominal chaetigers 3–7 fused dorsally (Fig. 1B, F), each line of hooded hooks completely separated, with around 18–20 hooks per fascicle. Neuropodial lobes project to dorsal region and separate ventrally, with chaetal fascicles with about 77–80 hooded hooks (Fig. 1A, C). Notopodial and neuropodial abdominal hooded hooks similar along body, with long anterior shaft, bulbous node, indistinct constriction, developed shoulder, short hood, posterior shaft longer than anterior one. Four rows of teeth above triangular main fang, basal row with five teeth, middle basal row with seven, middle apical row with nine and distal row with two teeth (Fig. 1D). Branchiae emerge from a ventral pore. Pygidium not seen.

Methyl green staining pattern. Peristomium and first 6 segments without staining apparently, post-chaetal part of segment 7, segments 8 to 10 and pre-chaetal part of segment 11 moderately stained, and segments 12 and 13 dark green (Fig. 1A, E).

Habitat. Mud with high content of organic matter (Varadero beach), in soft sediments retained into Nastier boxes (Santa Marina bay), and mud pockets between *Mytilus edulis* beds (Los Angeles Bay, Municipal beach).

Distribution. USA: Southern California Bight, Waianae outfall and Mamala Bay, Sand Island outfall, Hawaii; Mexico: Gulf of California and western coast of Baja California.

Remarks. Type material of *Dodecaseta oraria* was examined and compared with type material of *Notodasus kristiani*, and we found similar morphological characters in both species: lateral notopodia in the first thoracic segments, in subsequent segments located dorsally; abdominal notopodial lobes fused dorsally (Fig. 1B, F); neuropodial lobes expanded to the dorsal side (Fig. 1A–B, E–F) and separated ventrally (Fig. 1C, G).

Based on examining type material of both species, we conclude that the specimens identified as *D. oraria* were juveniles exhibiting variation in chaetal counts, leading to a mis-identification. We conclude therefore, that *Dodecaseta oraria* is a junior synonym of *Notodasus kristiani*.

***Notodasus fauchaldi* (Green, 2002), comb. n.**

Figure 2

Dodecaseta fauchaldi Green, 2002: 312–313, fig. 23A–I.

Material examined. Type material. *Dodecaseta fauchaldi* Paratype (LACM AHF POLY 2100) St. E-20 m/BC, North Pacific Ocean, Andaman Sea, Thailand, [8°30'N, 98°12'E] 21 m, 22 April 1996, muddy sand, coll. S. Bussarawit, Charatsee Aungtonya.

Redescription. Paratype incomplete (lacking posterior end) with 44 segments, 19 mm long, 0.71 mm wide in abdomen. Color in alcohol light brown. Prostomium conical with palpode, eyespots present. Peristomium to seventh thoracic chaetiger with epithelium longitudinally striated, remaining segments smooth. Thorax with 11 chaetigers, with bilimbate capillaries in both rami first chaetiger biramous. Transition between thorax and abdomen marked by a slight reduction in the size of the first two abdominal segments (Fig. 2B). Thoracic and abdominal segments biannulated, notopodia lateral in first thoracic segments, in subsequent segments located dorsally (Fig. 2A). Lateral organs between notopodia and neuropodia throughout body, those of thoracic region closer to notopodium. In segments 12 and 13 the lateral organs protrude, just as abdominal ones. Genital pores not seen. Abdominal chaetigers 1–9 with notopodial lobes fused dorsally (Fig. 2B), each line of hooded hooks completely separated, with around 13 hooks per fascicle. Neuropodial lobes projected to dorsal region and separate ventrally (Fig. 2C), chaetal fascicles with 81 hooded hooks. Notopodial and neuropodial abdominal hooded hooks similar throughout, with long anterior shaft, bulbous node, indistinct constriction, developed shoulder, short hood, posterior shaft longer than anterior one, four rows of teeth above triangular main fang (Fig. 2D). Pygidium not examined.

Methyl green staining pattern. Peristomium and first seven chaetigers with light green, chaetiger 9–11 with moderate green, chaetiger 12th and pre-chaetal part of the 13th dark green (Fig. 2A). Abdominal chaetiger with two longitudinal bands stained with an intense green, disrupted by neuropodial lobes and lateral organs (Fig. 2B); with a longitudinal ventral line stained with a moderate green along the body (Fig. 2C).

Habitat. Sediment characterized as sandy mud, muddy sand and sand with shell fragments, 21 to 55 m.

Distribution. Only known for the type locality, Andaman Sea, Thailand.

Remarks. In the description of *D. fauchaldi*, Green (2002) mentioned that the species had a tessellated epithelium up to chaetiger 4 or 5, hooded hooks with three lines of small teeth over the principal fang, and the ventral abdominal segments did not stain with methyl green. However the paratype reviewed has tessellated epithelium from the peristomium to segment 7, hooded hooks with four lines of small teeth over the principal fang, and methyl green staining revealed a longitudinal abdominal line with moderate green along ventral body. It is worth mention that in Green's description, the legend of figure 23 B, F and G has a mistake, in figure B chaetiger 9–14, must actually be 11–16; in figure F chaetiger 10–15, must actually be 12–17, and in figure G chaetiger 10–14, must be 12–16.

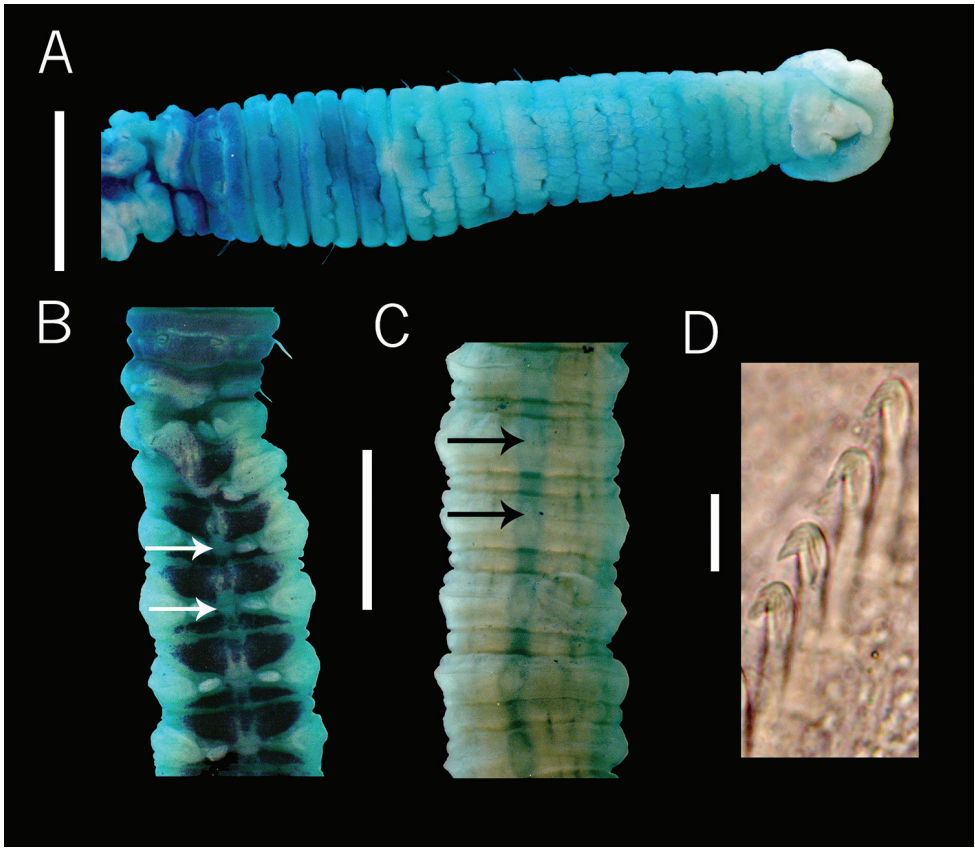


Figure 2. Paratype of *Dodecaseta fauchaldi* (Green, 2002). **A** anterior end, dorsal view **B** chaetigers 12-19, dorsal view **C** chaetigers 21-26, ventral view **D** neurohook of chaetiger 40, lateral view. Methyl green stain **A**. Scale bars: **A–C** = 1mm, **D** = 15 µm.

***Notodasus eibyejacobseni* (Green, 2002), comb. n.**

Dodecaseta eibyejacobseni Green, 2002: 249-343, fig. 24A–G

Remarks. The type material of *Dodecaseta eibyejacobseni* could not be review because it could not be located in the Phuket Marine Biological Center (Aungtonya, per. comm.). However, the original description of Green (2002) and the figure 24 A–G, provides evidence of morphological characters that are present in the genus *Notodasus*. Thus, we considered that this species needs be reassigned to the genus *Notodasus*.

Green (2002) states that she compared specimens of *N. eibyejacobseni* with specimens identified by Hartman (1947) as *Dasybranchus lumbricoides* Grube, 1878 (LACM-AHF n 2222,1451-42, n2170, 14913-F2676), from intertidal areas of southern California, lower California and other parts of western Mexico. Green found similarities between Hartman's specimens and her own specimens from the BIOSHELF material. However,

as *D. lumbricoides* was originally described from Pandanon Island (Philippines) there is a possibility that specimens from Thailand by Green and those from California and Mexico by Hartman do not belong to the same species as demonstrated below.

We reviewed some lots collected in California and identified by Olga Hartman and Kristian Fauchald as *D. lumbricoides*: LACM AHF POLY-N-1450-42, N1451-42; LACM AHF POLY-N 2221; LACM AHF POLY-N 1284/14884-F2637 and LACM AHF POLY-N 14905/F2663 (by O. Hartman), and LACM AHF POLY-N-1746 (by K. Fauchald). Specimens of the first four lots, all correspond to *Notodasus harrisae* García-Garza et al., 2009; specimen LACM AHF POLY-N 1284/14884-F2637 correspond to *Notodasus oraria* new combination; and specimen LACM AHF POLY-N 14905/F2663 correspond to *Dasybranchus platyceps* Hartman, 1947.

Ewing (1984) reported *D. lumbricoides* from the northern Gulf of Mexico, Florida however, based on his description, these specimens belong in the genus *Notodasus* but we do not have access to specimens in order to corroborate our observations.

Acknowledgements

We thank for Charatsee Aungtonya, curator of the Phuket Marine Biological Center (PMBC), for the information on the type material; and to Sergio I. Salazar-Vallejo, El Colegio de la Frontera Sur (ECOSUR), who allowed us to revise the material in their collections. We thank María Ana Tovar Hernández who reviewed an earlier draft of this manuscript. Pat Hutchings an anonymous reviewer for critical comments on the manuscript. The study was funded by Programa de Apoyo a la Investigación Científica y Tecnológica de la Universidad Autónoma de Nuevo León (PAICyT) CN541-15.

References

- Blake JA (2000) Family Capitellidae Grube, 1862 In: Blake JA, Hilbig B, Scott PV (Eds) Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Volumen 7. The Annelida Part 4, Polychaeta: Flabelligeridae to Sternaspidae: Santa Barbara Museum of Natural History, California, 47–96.
- Ewing RM (1984) Family Capitellidae Grube, 1862. In: Uebelacker JM, Johnson PG (Eds) Taxonomic guide to the polychaetes of the northern Gulf of Mexico Vol. II. Barry A. Vittor & Associates, Inc., Mobile, Alabama, 14.1–14.47.
- Fauchald K (1972) Benthic polychaetous annelids from deep water off Western Mexico and adjacent areas in the Eastern Pacific Ocean. Allan Hancock Monographs in Marine Biology 7: 1–575.
- Fauchald K (1977) The polychaete worms. Definitions and keys to the Orders, Families and Genera. Natural History Museum of Los Angeles County, Science Series 28: 1–190.
- García-Garza ME (2009) Capitellidae Grube, 1862. In: de León-González JA, Bastida-Zavala JR, Carrera-Parra LF, García-Garza ME, Peña-Rivera A, Salzar-Vallejo SI, Solis-Weiss V

- (Eds) Poliquetos (Anelida: Polychaeta) de México y América Tropical. Universidad Autónoma de Nuevo León, Monterrey, México, 101–114.
- García-Garza ME, VD Hernández-Valdez, JA de León-González (2009) Generic revision of *Notodasus* Fauchald, 1972 (Polychaeta: Capitellidae) with descriptions of four new species from the coasts of Mexico. *Scientia Marina* 73(4): 809–823. <https://doi.org/10.3989/scimar.2009.73n4809>
- García-Garza ME, JA de León-González (2011) Review of the Capitellidae (Annelida, Polychaeta) from the Eastern Tropical Pacific region, with notes on selected species. *Zookeys* 151: 17–52. <https://doi.org/10.3897/zookeys.151.1964>
- George JD (1984) The behavior and life history of a mangrove-dwelling capitellid (Polychaeta). In: Hutchings PA (Ed.) *Proceedings of First International Polychaete Conference*, Sydney, Linnean Society of New South Wales, 323–337.
- Green KD (2002) Capitellidae (Polychaeta) from the Andaman Sea. *Phuket Marine Biological Center Special Publication* 24: 249–343.
- Hartman O (1947) Polychaetous annelids. Part VII. Capitellidae. *Allan Hancock Pacific Expeditions* 10(4-5): 391–481.
- Magalhães-Wagner F, Bailey-Brock JH (2012) Capitellidae Grube, 1862 (Annelida: Polychaeta) from the Hawaiian Islands with description of two new species. *Zootaxa* 3581(1): 1–5.
- Mc Cammon JA, Stull JK (1978) A new genus and species of Capitellidae (Polychaeta) from California. *Bulletin. Southern California Academy of Sciences* 77(1): 40–43.
- Warren LM, Hutchings PA, Doyle S (1994) A revision of the genus *Mediomastus* Hartman, 1944 (Polychaeta: Capitellidae). *Records of the Australian Museum* 46: 227–256. <https://doi.org/10.3853/j.0067-1975.46.1994.6>

Integrative overview of the herpetofauna from Serra da Mocidade, a granitic mountain range in northern Brazil

Leandro J.C.L. Moraes¹, Alexandre P. de Almeida², Rafael de Fraga¹,
Rommel R. Rojas², Renata M. Pirani¹, Ariane A.A. Silva¹,
Vinícius T. de Carvalho², Marcelo Gordo², Fernanda P. Werneck¹

1 Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, 69067-375, Manaus, Amazonas, Brazil **2** Departamento de Biologia, Universidade Federal do Amazonas, Av. General Rodrigo Octávio Jordão Ramos 3000, 69077-000, Manaus, Amazonas, Brazil

Corresponding author: *Leandro J.C.L. Moraes* (leandro.jclm@gmail.com)

Academic editor: *A. Herrel* | Received 14 August 2017 | Accepted 4 October 2017 | Published 22 November 2017

<http://zoobank.org/FF11D309-E66F-43F5-95E3-148E1F0D5728>

Citation: Moraes LJCL, Almeida AP, Fraga R, Rojas RR, Pirani RM, Silva AAA, de Carvalho VT, Gordo M, Werneck FP (2017) Integrative overview of the herpetofauna from Serra da Mocidade, a granitic mountain range in northern Brazil. ZooKeys 715: 103–159. <https://doi.org/10.3897/zookeys.715.20288>

Abstract

The Brazilian mountain ranges from the Guiana Shield highlands are largely unexplored, with an understudied herpetofauna. Here the amphibian and reptile species diversity of the remote Serra da Mocidade mountain range, located in extreme northern Brazil, is reported upon, and biogeographical affinities and taxonomic highlights are discussed. A 22-days expedition to this mountain range was undertaken during which specimens were sampled at four distinct altitudinal levels (600, 960, 1,060 and 1,365 m above sea level) using six complementary methods. Specimens were identified through an integrated approach that considered morphological, bioacoustical, and molecular analyses. Fifty-one species (23 amphibians and 28 reptiles) were found, a comparable richness to other mountain ranges in the region. The recorded assemblage showed a mixed compositional influence from assemblages typical of other mountain ranges and lowland forest habitats in the region. Most of the taxa occupying the Serra da Mocidade mountain range are typical of the Guiana Shield or widely distributed in the Amazon. Extensions of known distribution ranges and candidate undescribed taxa are also recorded. This is the first herpetofaunal expedition that accessed the higher altitudinal levels of this mountain range, contributing to the basic knowledge of these groups in remote areas.

Keywords

Amazonia, bioacoustics, biogeography, lowland forest, morphology, mountain, mtDNA, Pantepui, phylogenetic relationships

Introduction

Scientific interest in mountain ranges arises primarily because they are characterized by a geographical isolation associated with differential availability of topographical, climatic, and edaphic conditions along the altitudinal gradients (Haslett 1997, Martinelli 2007, Körner et al. 2017). These characteristics provide ideal conditions for the development of unique evolutionary lineages and occurrence of a variety of endemic taxa (Lomolino 2001, Rull 2005, Hoorn et al. 2013, Nogué et al. 2013). This speciation hotspot pattern occurs in the mountain ranges of northern South America (Guiana Shield highlands), which lies on the ancient terrain of the Cratonic Guiana Shield (Hershkovitz 1969, Désamóré et al. 2014, Salerno et al. 2012, Bonaccorso and Guayasamin 2013). Despite a history of different concepts and geographic boundaries (Mayr and Phelps 1967, Huber 1988a, Kok 2013a), these high altitude areas are considered as a distinct biogeographic region (Morrone 2014), presenting biotic affinities with the megadiverse Amazon and Andean regions (Duellman 1979, Salerno et al. 2012, Mannion et al. 2014).

Initial discoveries concerning the amphibian and reptile diversity from Guiana Shield highlands were reported by localized expeditions at the transition between the nineteenth and twentieth centuries (Boulenger 1900, Roze 1958a, b). Knowledge increased exponentially when helicopters facilitated access to remote mountains (Aubrecht et al. 2012), leading to several expeditions focused on describing the assemblages of particular localities. Such studies brought to prominence several endemic taxa from the highlands (e.g., Gorzula 1992, Myers 1997, Myers and Donnelly 1992, 1996, 2001, 2008, MacCulloch et al. 2007, Barrio-Amorós and Brewer-Carias 2008, Kok 2008, 2009a, 2009b, 2010, 2013b, 2015, Kok and Rivas 2011, Kok et al. 2010, 2011, 2015), and some resulted in broad outlines of the main biogeographical patterns of these taxa (e.g., Hoogmoed 1979, Duellman 1999, Gorzula and Señaris 1999, McDiarmid and Donnelly 2005).

More recently, studies have shown that diversification and evolutionary patterns of distinct species were associated with the landscape history of the region (Kok et al. 2012, 2017, Salerno et al. 2012, 2015, Vacher et al. 2017). While several intriguing patterns have been found for some highland lineages, such as recent diversification and low genetic divergence among mountains (Salerno et al. 2012, Kok et al. 2012, 2017), overall knowledge on the geographical and altitudinal distribution patterns of amphibians and reptiles from Guiana Shield highlands and their drivers are far from being fully understood. One of the main reasons is the occurrence of huge sampling gaps, mostly due to the short-term nature of inventories and to the difficult and costly access to highland areas, some of which remain unexplored (Aubrecht et al. 2012). The sampling deficiency in the Brazilian region of the Guiana Shield highlands highlights the impor-

tance of exploring these areas for biodiversity and biogeography assessments. Sampling in novel mountain ranges will most likely result in the discovery of new taxa and unique lineages, and geographical range extensions, all of which can contribute to the conservation of these threatened regions (Rull et al. 2016).

Furthermore, most specimens currently collected during biological inventories are identified using morphological characteristics. However, given the pervasive occurrence of cryptic diversity (Vences et al. 2005, Vences and Wake 2007), particularly in Neotropical amphibians and reptiles (Fouquet et al. 2007a, c, Geurgas and Rodrigues 2010, Oliveira et al. 2016, Kok et al. 2016), other methods are being used to reveal the hidden diversity in remote areas with difficult access. For example, molecular techniques may contribute to indicate the presence of undescribed species and detect cryptic speciation through divergence in DNA sequences, and this short-term result might take longer to be achieved using a single taxonomic data source (Vences et al. 2005, Vences and Wake 2007, Fouquet et al. 2007a, Paz and Crawford 2012).

Recently, a multidisciplinary initiative conducted an expedition (“Biodiversity of the Serra da Mocidade”) to inventory the biological diversity of distinct taxonomic groups in the poorly known region of the Serra da Mocidade, a remote granitic mountain range located in northern Brazil (INPA, 2016), highly isolated from other mountains and with difficult access. Here we present and discuss the diversity of amphibians and reptiles of the area and their biotic affinities, using an integrative approach combining morphological, bioacoustical and molecular analyses to identify specimens. We found remarkable records, and make observations concerning species taxonomy, ecology and distribution patterns in the Guiana Shield highlands region.

Materials and methods

Study area

The Guiana Shield highlands region is located in northern South America, within the limits of Venezuela, Guyana, Suriname, and Brazil (Fig. 1), and is composed of mountain ranges covered by dense forests, shrubby vegetation or moss forests, surrounded by a lowland matrix of either tropical forests or savanna ecosystems (Mayr and Phelps 1967, Huber 1988b, McDiarmid and Donnelly 2005). These ancient mountains date to the Precambrian period (1.8–2.5 billion years) (Santos et al. 2003, Nogué et al. 2009, Kok 2013a), and have two main geological origins: sedimentary rocks, which are currently exposed as abrupt vertical elevations with tabular tops (called “tepui”) and igneous-metamorphic rocks, which lie beneath the sedimentary rocks and may also be exposed as granitic uplifts with a mountain-like appearance (Steyermark 1986, Schubert and Briceño 1987, Huber 1995, Hoorn and Wesselingh 2010).

This study was conducted at Serra da Mocidade (Figs 1, 2), a complex of granitic mountains located in extreme northern Brazil, within the limits of Caracaraí municipality, Roraima state, with a mean altitudinal level of 1,000 m above sea level

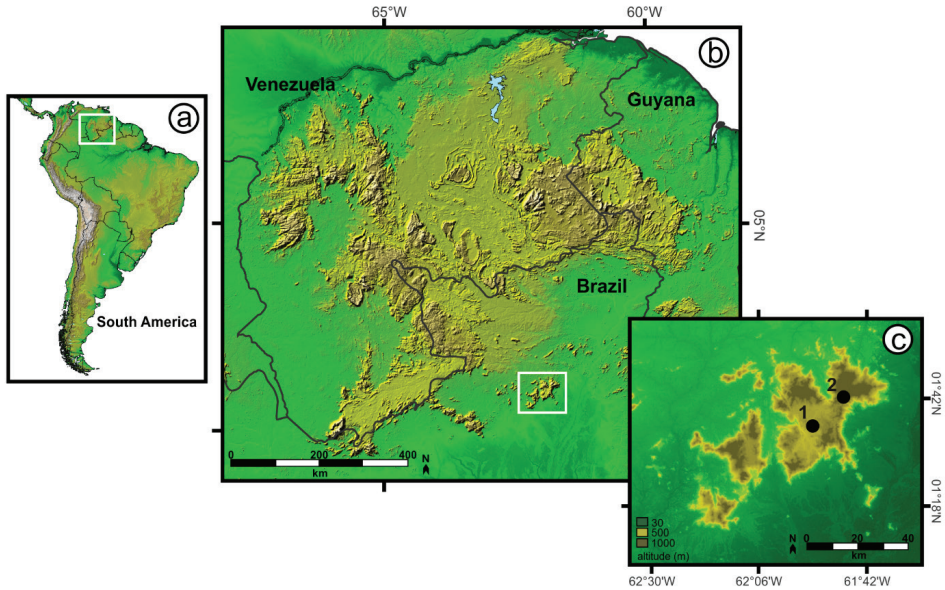


Figure 1. Study area. Location of **a** the main Guiana Shield highlands region in northern South America, and **b** the Serra da Mocidade mountain range. A larger scale map of mountain range **c** shows the location of the two field base camps.

(hereafter, asl) and peaks over 1,900 m asl. The Serra da Mocidade area is protected by a federal conservation unit (Parque Nacional da Serra da Mocidade), an indigenous Yanomami territory and a military area, property of the Brazilian Army (Ferreira et al. 2014, Ministério do Meio Ambiente 2016). This mountain range is isolated in relation to other Guiana Shield highlands mountains, with the closest mountain range (Serra do Aracá) ca. 100 km distant to the west.

The lowland regional climate has low annual temperature variation, ranging from 24° C to 27° C (average 26° C), a rainy season from April to September and a dry season from October to March (Alvares et al. 2013). Annual rainfall exceeds 2,500 mm (Sombroek 2001, Alvares et al. 2013). Daily thermal oscillation increases at higher altitudes, where temperatures are lower and the influence of wind is stronger, preventing establishment of taller forests (Haslett 1997). The base and lower slopes of the mountain range are covered by dense tropical submontane and montane rainforests, while increased humidity at higher altitudes fosters the development of extensive epiphyte and moss coverage on tree trunks (Ministério do Meio Ambiente 2016).

Sampling areas and species survey

Logistic support from the Brazilian Army allowed aerial access at altitudes only accessible by helicopters, and the installation of two base camps from which it was possible



Figure 2. Serra da Mocidade. Panoramic views of the Serra da Mocidade mountain range (**a**) and a typical granitic inselberg formation (**b**), covered by montane forest. Photographs by Thiago Laranjeiras.

to reach different altitudinal levels (Fig. 1). At base camp #1 at 600 m asl ($01^{\circ}36'N$, $61^{\circ}54'W$), we sampled areas in the foothills of the mountains, while base camp #2 at 1,060 m ($01^{\circ}42'N$, $61^{\circ}47'W$) allowed access to altitudinal levels of 960 m asl ($01^{\circ}42'N$, $61^{\circ}48'W$) and 1,365 m asl ($01^{\circ}43'N$, $61^{\circ}45'W$). Altitudinal levels closer to the camp (900–1,100 m asl) were sampled more intensively due to difficult access in the areas located at 1,365 m asl, which we sampled during a single operation. Although herpetofaunal rapid inventories already have been conducted in the lowlands of this region (Ministério do Meio Ambiente 2016), this is the first expedition that reached the higher altitudes of this mountain range.

Surveys were conducted in two teams, each with three trained herpetologists, one from each base camp (first team at base camp #1 for 15 to 23 January 2016, and second team at base camp #2 for 25 January to 06 February 2016), totaling 22 days of field work and 66 man-days of sampling effort. To maximize characterization of the regional herpetofaunal diversity we used six complementary survey methods to detect individuals: (1) active surveys (Heyer et al. 1994) conducted during day and night, where individuals were visually detected or heard in as many microhabitat as possible and manually captured; (2) pitfall traps (Campbell and Christman 1982, Heyer et al. 1994), installed in two sampling lines, each of ten 60-liters buckets spaced every 10 meters (total sampling line length 100 m), and buried in the ground with the opening at the surface level, interleaved with a pole-supported plastic fence, the lower part of which was buried in the ground; (3) trammel nets, which were installed in streams near the base camps, in order to catch turtles, aquatic amphibians and squamates (Campbell and Christman 1982); (4) hook with meat bait, specifically for turtles; (5) glue traps, installed in fallen logs and tree trunks aiming capture of arboreal squamates and (6) shotgun. All traps were visited every 24 hours or less throughout the sampling period at each base camp. Specimens obtained using methods other than the ones cited above were considered as occasional encounters (Martins and Oliveira 1998, Heyer et al. 1994).

Collection and species identification

Specimens were killed with an injection of Thiopental® or Lidocaine, fixed with 10% formalin, and preserved in 70% ethanol. We removed muscle or liver tissue from specimens before the fixation process and stored it in absolute ethanol. Voucher specimens and tissue samples were deposited in the Collections of Amphibians and Reptiles (INPA-H) and of Genetics Resources (INPA-HT) of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil, respectively.

Taxonomic identifications were performed using morphological, bioacoustical, and molecular analyses, following the taxonomic arrangements of Frost (2017) for amphibians and Uetz and Hošek (2017) for reptiles, with modifications by Pyron et al. (2013), Pinto-Sánchez et al. (2015), and Karin et al. (2016).

Morphology

The specimens' morphologies were analysed according to original descriptions, taxonomic and phylogenetic revisions, dichotomous keys, field guides and results from similar expeditions from Guiana Shield highlands (Boulenger 1900, Boulenger 1911, Roze 1958a, 1958b, 1961, 1987, Rivero 1961, 1970, Vial and Jimenez-Porras 1967, Heyer 1970, 1994, Lutz 1973, Duellman 1979, 1999, Hoogmoed 1979, 1990, Peters and Donoso-Barros 1986, Rebouças-Spieker and Vanzolini 1990, Donnelly and Myers 1991, Gorzula 1992, Dixon et al. 1993, O'Shea and Stimson 1993, Ávila-Pires 1995, Myers 1997, Myers

and Donnelly 1996, 1997, 2001, 2008, Gorzula and Señaris 1999, Lescure and Marty 2000, MacCulloch and Lathrop 2002, 2009, Hollowell and Reynolds 2005, McDiarmid and Donnelly 2005, Miralles et al. 2005, Señaris and Ayarzagüena 2005, Barrio-Amorós and Molina 2006, Bergmann and Russell 2007, Fouquet et al. 2007a, 2007b, 2014, 2015a, 2015b, Hawkins et al. 2007, MacCulloch et al. 2007, Barrio-Amorós and Brewer-Carias 2008, Guayasamin et al. 2008, 2009, Harvey 2008, Kok and Castroviejo-Fisher 2008, Vogt 2008, Lima and Prudente 2009, Ávila-Pires et al. 2010, Kok 2010, 2013a, Miralles and Carranza 2010, Castroviejo-Fisher et al. 2011, Maciel and Hoogmoed 2011, Hedges and Conn 2012, Mendes-Pinto et al. 2012, Motta et al. 2012, Rivas et al. 2012, Cisneros-Heredia 2013, Cole et al. 2013, Jungfer et al. 2013, Lavilla et al. 2013, 2017, Murphy and Jowers 2013, Passos et al. 2013, Gehara et al. 2014, Sá et al. 2014, van Dijk et al. 2014, Wallach et al. 2014, Feitosa et al. 2015, dos Santos et al. 2015, Ribeiro-Júnior 2015a, 2015b, Dewynter et al. 2016a, 2016b, 2016c, 2016d, Oliveira et al. 2016, Ribeiro-Júnior and Amaral 2016, 2017, Orrico et al. 2017, Kok et al. 2017, Vacher et al. 2017), as well as through comparisons with other voucher specimens deposited at INPA-H collection. We investigated external meristic, morphometric and colouration characters. For colour in life we used photographs taken during the expedition, and for morphometric comparisons we measured: the snout-vent length (SVL) of amphibians, lizards, snakes and crocodilians, the caudal length of snakes (CL), and carapace length (CAL) and width (CW) of chelonians. Specimens examined are listed in Suppl. material 1.

Bioacoustics

The calls from some amphibian species were recorded in uncompressed wav format, with a Zoom H1 Handy Recorder (Zoom Corporations, Tokyo, Japan) equipped with an internal microphone, distant about 1–2 m to the emitter. The calls were digitised and analysed using Raven Pro. 1.5 (Cornell Laboratory of Ornithology) at a sampling frequency of 44 KHz and 16-bit resolution. Call structures were visually analysed in the spectrograms, and we measured the following quantitative parameters, considered in amphibian taxonomy (Köhler et al. 2017): call duration (s), inter-call interval (s), pulse duration (s), pulse rate (pulses/s) and dominant frequency (kHz), summarized in mean values \pm standard deviation. The data were compared to calls described in the literature for each analysed species (Cardoso and Haddad 1984, Hoogmoed 1990, Donnelly and Myers 1991, Fouquet et al. 2007b, Morais et al. 2012, Fouquet et al. 2015).

Molecular analyses for uncertain species

When specimens were part of groups already considered as a complex of multiple species or when we considered the possibility of an undescribed taxon, we explored their taxonomic status using DNA sequences of mitochondrial gene 16S, a standard marker for amphibians and reptiles (Vences et al. 2012). Genomic DNA was isolated from

collected tissues using a commercial kit (Wizard, Promega Corp., Madison, WI), and target region amplified via the Polymerase Chain Reaction (PCR) using primers 16Sar and 16Sbr (Palumbi et al. 1991). Purified PCR products were sequenced using the Big Dye Terminator sequencing kit (Applied Biosystems, Waltham, USA) in automated sequencer ABI 3130 XL (Applied Biosystems, Waltham, USA) at Thematic Laboratory of Molecular Biology at INPA.

DNA sequences obtained were compared with those available for closely related taxa in GenBank (Benson et al. 2014). Sequences were manually edited and aligned with CLUSTAL X algorithm run on MEGA 6.06 software (Tamura et al. 2013). Using the same software, we generated maximum likelihood (ML) phylogenetic trees for each taxonomic group inferred by 5,000 bootstrap replicates, and estimated genetic distances between main lineages of each taxon using uncorrected pairwise distances. Although the threshold of the genetic distance percentage that represents an interspecific variation is arbitrary and varies according to the group diversification, we followed Fouquet et al. (2007a, c) and considered the possibility of new taxa when genetic distances were above 3%. In these cases, the final definition of the taxonomic status of a given specimen was thus the result of an integrated interpretation of morphological, bioacoustical, and molecular results.

Diversity and biogeographical comparisons

In order to investigate the relationship between the recorded diversity and sampling effort, as well as to identify differences in species richness between altitudinal levels, we performed extrapolated rarefaction curves (Chao et al. 2014) with presence-absence data, considering the total sampling and at distinct altitudinal levels separately (600 and >900 m asl). We also compile results of herpetofaunal inventories conducted in main nearby habitats to compare the species richness and composition and detect the faunistic affinities of the Serra da Mocidade diversity. These habitats include several mountain ranges part of Guiana Shield highlands, with over five known species (data compiled from Boulenger 1895a, 1895b, 1900, Burt and Burt 1931, Roze 1958a, 1958b, 1987, Rivero 1961, 1966, Lancini 1968, Ayarzagüena 1983, Duellman and Hoogmoed 1984, Zweifel 1986, McDiarmid and Paolillo 1988, Robinson 1989 Mägdefrau et al. 1991, Donnelly and Myers 1991, Ayarzagüena et al. 1992, Donnelly et al. 1992, Gorzula 1992, Ayarzagüena and Señaris 1993, Señaris and Ayarzagüena 1993, Myers et al. 1993, Señaris et al. 1994, Williams et al. 1996, Myers 1997, Myers and Donnelly 1997, 2001, 2008, Fuentes and Barrio-Amorós 2004, McDiarmid and Donnelly 2005, Ouboter et al. 2007, Watling and Ngadino 2007, Barrio-Amorós and Brewer-Carias 2008, Barrio-Amorós and Duellman 2009, Carvalho et al. 2010, Castroviejo-Fisher et al. 2011, Ouboter and Jairam 2012, Fouquet et al. 2015a, Fraga et al. 2017, Rojas-Runjaic et al. 2017, INPA-H voucher specimens), as well as lowland forests and open habitats (*savana*, *campina* and anthropized areas) in northern South America, with focus on the Brazilian territory (data compiled from O'Shea 1989, 1998, Martins 1998, Mac-

Culloch and Reynolds 2013, IBAMA 2014, ICMBio 2014, Gordo et al. 2014, Señaris et al. 2014, Silva 2016, INPA-H voucher specimens). The similarity in species composition between Serra da Mocidade and these habitats was graphically investigated through multivariate ordination using a non-metric multidimensional scaling (NMDS) (Clarke 1993), with qualitative data and the Jaccard index as a similarity measure. Rarefaction curves and NMDS ordination were generated using the R statistical software packages iNEXT (Chao et al. 2014) and vegan (Oksanen et al. 2017), respectively.

To identify biogeographical patterns and evaluate the contribution of adjacent regions to the composition of the local herpetofauna at Serra da Mocidade, we classified species according to their known geographical distribution, delimiting boundaries of biogeographic regions based on the main geological compartments for Northern South America (Gibbs and Barron 1993, Aleixo and Rossetti 2007, Hoorn and Wesselingh 2010), already known to influence the biotic distribution (Ávila-Pires et al. 1995, Aleixo and Rossetti 2007). Therefore, the species were classified in the following categories, which decrease in geographical scale: Widely distributed in Amazonia (WD), for species with wide geographical ranges throughout this region; Western Amazonia (WA) and Eastern Amazonia (EA) for species typical of these macro-regions, influenced by sedimentary basin of the Amazonas River and crystalline shields, respectively; Andes (AN) for species typical of this mountain range of western South America; Guiana Shield (GS), for species occurring in the lowlands of crystalline basement north of the Amazonas River; Guiana Shield highlands (GH), for species occurring mainly in the uplands of this mountainous complex; Potentially endemic to the Serra da Mocidade region (PE), for species potentially restricted to the studied mountain range. Finally, we also considered species that occur at punctual restricted localities outside of their main geographical range (PR) and at transition zones between Amazonia and other biomes (TZ). To evaluate the contribution of these regions in shaping the local herpetofauna, we calculated a relative percentage, dividing the number of species from each biogeographical region in relation to the total number of recorded species, for both amphibians and reptiles.

To verify the contribution of altitudinal generalists and specialists to the species composition of the Serra da Mocidade herpetofauna, we also classified species according to their known altitudinal range as reported in the literature, as lowland (occurring mainly below 500 m asl) and upland (occurring mainly above 500 m asl) species (Hoogmoed 1979, McDiarmid and Donnelly 2005). The relative contribution of these assemblages was also evaluated by dividing the number of species from each group in relation to the total number of recorded species, for both amphibians and reptiles, considering the total sampling and samples from distinct altitudinal levels.

Results

A total of 305 specimens (232 amphibians, 58 squamates, 13 chelonians, and two crocodilians) was recorded, belonging to 51 species (23 amphibians, 24 squamates, three chelonians, and one crocodilian) from 25 families (Table 1). The most diverse

Table 1. Recorded species. List of amphibians and reptiles recorded at the Serra da Mocidade mountain range, with respective sample sizes at each distinct altitudinal level (m above sea level), sampling methods, morphological data, and species' geographical and altitudinal distributions. Sampling methods: (AS) Active survey; (PT) Pitfall traps; (TN) Trammel nets; (HM) Hook with meat bait; (GT) Glue traps; (SG) Shotgun; (OE) Occasional encounters. Morphological measurements: (SVL) Snout-vent length; (CL) Caudal length; (CAL) Carapace length; (CW) Carapace width. Geographical distribution: (WD) Widely distributed in Amazonia; (WA) Western Amazonia; (EA) Eastern Amazonia; (AN) Andes; (GS) Guiana Shield; (GH) Guiana Shield highlands; (PE) Potentially endemic to the Serra da Mocidade region; (PR) Punctual restricted localities; (TZ) Transition zones between Amazonia and other biomes. Altitudinal range: (L) Lowland (below 500 m asl); (U) Upland (above 500 m asl).

Taxon	Altitude (m asl)					Sampling method	Morphological measurements (mm)	Geographic distribution	Altitudinal range
	600	960	1,060	1,365	14				
Amphibia	89	28	101	14					
Gymnophiona			3						
Rhinatrematidae			1						
Epicrionops sp.			1			OE	SVL 83.5	PE ^s	U ^l
Siphonopidae			2						
Brasiloryphlus sp.			2			OE		PE ^{s,l}	U ^l
Anura	91	28	98	14					
Allophrynidae	1								
Allophryne ruthveni Gaige, 1926	1					AS	SVL 28.1	WD [†]	L ^{##}
Aromobatidae	25	4	23	8					
Anomaloglossus apiau Fouquet, Souza, Nunes, Kok, Curcio, Carvalho, Grant & Rodrigues, 2015	25	4	23	8		AS, OE	SVL 15–23	GH ^{†,s}	U ^{s,s}
Bufonidae	3		3						
Rhacobo guttatus (Schneider, 1799)	3		3			AS	SVL 147–167	WD [†]	L, U ^{##}
Rhinella marina (Linnaeus, 1758)	5						SVL 21–44	WD [†]	L ^{##}
Rhinella marjyi Fouquet, Gaucher, Blanc & Vélez-Rodriguez, 2007	1		13	1		AS, PT, OE	SVL 50–70	GS ^{†,s}	L, U [#]
Craugastoridae	10	8	11	2					
Pristimantis aff. vilarsi	10	8	11	2		AS	SVL 17–56.9	GH ^{†,s}	L, U ^{##}
Centrolenidae	5	4	8						
Hyalinobatrachium aff. taylora	4	2	1			AS	SVL 18–21	PE ^{†,s}	U ^{##}

Taxon	Altitude (m asl)				Sampling method	Morphological measurements (mm)	Geographic distribution	Altitudinal range
	600	960	1,060	1,365				
<i>Vitreorana ritae</i> (Lutz, 1952)	1	2	7		AS	SVL 17–22	GS, PR†	L, U ^{##}
Hemiphractidae								
<i>Stefania</i> sp.		2						
Hylidae					AS, OE	SVL 52, 54	PE†§	U†
<i>Boana boans</i> (Linnaeus, 1758)	11	10	40	3				
<i>Boana multifasciata</i> (Günther, 1859)	8	2	9		AS, OE	SVL 82–111	WD†	L, U ^{##}
<i>Boana xerophylla</i> (Duméril & Bibron, 1841)	1		2		AS	SVL 55–72	EA, TZ†	L, U ^{##}
<i>Dendropsophus minutus</i> (Peters, 1872)			1		AS	SVL 57	GS†	L, U ^{##}
<i>Dendropsophus parviceps</i> (Boulenger, 1882)		3	14		AS	SVL 20.5–27	WD†	L, U ^{##}
<i>Osteocephalus taurinus</i> Steindachner, 1862		1	5		AS	SVL 20–27	WD†	L, U ^{##}
Leptodactylidae	2	4	9	3	AS	SVL 64.5–90	WD, TZ†	L, U ^{##}
<i>Adenomera andreae</i> (Müller, 1923)	19							
<i>Leptodactylus guianensis</i> Heyer & de Sá, 2011	1				AS	SVL 24	WD†,††	L ^{##}
<i>Leptodactylus mystaceus</i> (Spix, 1824)	2				AS	SVL 103.7	GS†,††	L†,###
<i>Leptodactylus petersii</i> (Steindachner, 1864)	6				AS, OE	SVL 50–59	WD†,††	L†,###
<i>Physalaemus ephippifer</i> (Steindachner, 1864)	1				AS	SVL 32.5	WD†,††	L†,###
Ranidae	7				AS, PT	SVL 20–28	GS†,††	L†,###
<i>Lithobates palmipes</i> (Spix, 1824)	11							
Reptilia	11				AS	SVL 72–96	WD†	L ^{##}
Squamata	58	2	13					
'Sauria'	43	2	13					
Gymnophthalmidae	34	1	5					
<i>Cercosaura ocellata</i> Wagler, 1830	3							
<i>Tretioscincus oriximinensis</i> Ávila-Pires, 1995	1				PT	SVL 56.5	EA†,†††	L ^{##}
Dactyloidae	2				AS, GT	SVL 53, 55	GS, PR†,††, †††	L, U ^{##}
<i>Anolis punctatus</i> Daudin, 1802	12		2					
<i>Anolis fuscoauratus</i> d'Orbigny, 1837			1		AS	SVL 83	WD†,§§	L, U ^{##}
<i>Anolis planiceps</i> Troschel, 1848	11		1		AS	SVL 40–49	WD†,§§	L, U ^{##}
	1				AS	SVL 40	GS†,§§	L, U ^{##}

Taxon	Altitude (m asl)				Sampling method	Morphological measurements (mm)	Geographic distribution	Altitudinal range
	600	960	1,060	1,365				
Phyllodactylidae								
<i>Thecadactylus rapicauda</i> (Houttuyn, 1782)	4				AS, GT, OE	SVL 92–115	WD [‡]	L [#]
Sphaerodactylidae								
<i>Pseudogonatodes guianensis</i> Parker, 1935	5				AS, GT	SVL 15–17	WD [‡]	L [#]
Polychrotidae								
<i>Polychrus marmoratus</i> (Linnaeus, 1758)	1				SG	SVL 133	WD ^{‡\$\$}	L [#]
Tropiduridae								
<i>Plica plica</i> (Linnaeus, 1758)	2	1	3		AS, PT, SG, OE	SVL 52–141	WD ^{‡\$\$}	L, U [#]
Teiidae								
<i>Ameiva ameiva ameiva</i> (Linnaeus, 1758)	3				SG	SVL 52–85	WD ^{‡##}	L [#]
Scincidae								
<i>Mabuia nigropunctata</i> (Spix, 1825)	4				PT, SG	SVL 72–105	WD ^{‡##}	L [#]
Serpentes								
<i>Colubridae</i>								
<i>Atractus riveroi</i> Roze, 1961	9	1	8		PT	SVL 229–290, CL 29.1–54.5	GH ^{‡,¶}	U [¶]
<i>Chironius fuscus</i> (Linnaeus, 1758)	6				AS	SVL 565, 603, CL 320, 357	WD ^{‡,##}	L, U ^{\$\$\$}
<i>Chironius septentrionalis</i> Dixon, Wiest & Cei, 1993	1		1		AS	SVL 1,480, CL 350	GH ^{‡,##}	L, U ^{‡‡‡,\$\$\$}
<i>Drymobius rhombifer</i> (Günther, 1860)	1				AS	SVL 365, CL 131	WD ^{‡,##}	L, U ^{‡‡‡}
<i>Dipsas catesbyi</i> (Santzen, 1796)	1				OE	SVL 229, CL 89	WD ^{‡,‡‡‡}	L, U ^{‡‡‡}
<i>Dipsas indica indica</i> Laurenti, 1768	1				AS	SVL 520, CL 209	WD ^{‡,##}	L, U [‡]
<i>Dipsas pavonina</i> Schlegel, 1837	1				OE	SVL 275, CL 95	EA, AN ^{‡,‡‡‡}	L, U ^{‡‡‡}
<i>Imantodes cenchoa</i> (Linnaeus, 1758)	1				AS	SVL 713, CL 315	WD ^{‡,##}	L [‡]
<i>Xenodon rabdocephalus rabdocephalus</i> (Wied, 1824)	1				AS	SVL 440, CL 399	WD ^{‡,##}	L [#]
Elapidae								
<i>Micrurus remotus</i> Roze, 1987			1		OE	SVL 42.7, CL 7	WA ^{‡,##}	L, U [#]
Viperidae								
	2	1	2					

Taxon	Altitude (m asl)				Sampling method	Morphological measurements (mm)	Geographic distribution	Altitudinal range
	600	960	1,060	1,365				
<i>Bothrops atrox</i> (Linnaeus, 1758)	1		1		AS, PT	SVL 93.5, 952, CL 17.5, 170	WD ^{‡##}	L, U [#]
<i>Bothrops bilineatus bilineatus</i> (Wied, 1821)		1			AS	SVL 450, 626, CL 80, 104	WD ^{‡##}	L, U [#]
<i>Lachesis muta muta</i> (Linnaeus, 1766)	1				AS	SVL 1,575, CL 175	WD ^{‡##}	L
Testudines	13							
Chelidae	11							
<i>Mesoclemmys gibba</i> (Schweigger, 1812)	10				TN, HM	CAL 109–189, CW 84–138	WD ^{‡,§§§}	L ^{§§§}
<i>Platemys platycephala melanonota</i> Ernst, 1984	1				OE	-	WD ^{‡,§§§}	L ^{§§§}
Testudinidae	2							
<i>Chelonoidis denticulatus</i> (Linnaeus, 1766)	2				OE	-	WD ^{‡,§§§}	L ^{§§§}
Crocodylia	2							
Alligatoridae	2							
<i>Paleosuchus trigonatus</i> (Schneider, 1801)	2				AS	SVL 160, 675	WD ^{‡,###}	L, U ^{###}

[†]Frost 2017, [‡]Uetz and Hošek 2017, [§]Authors personal observations, [|]Maciel and Hoogmoed 2011, ^{*}Fouquet et al. 2015, [#]Fouquet et al. 2007b, ^{††}de Sá et al. 2014, ^{##}Ávila-Pires 1995, ^{§§}Ribeiro-Júnior 2015a, ^{||}Ribeiro-Júnior 2015b, ^{¶¶}Passos et al. 2013, ^{###}Wallach et al. 2014, ^{†††}Lima and Prudente, 2009, ^{###}IUCN 2016, ^{§§§}Dixon et al. 1993, ^{|||}Vial and Jimenez-Porras 1967, ^{¶¶¶}van Dijk et al. 2014, ^{###}Magnusson and Campos 2010, ^{††††}Ribeiro-Júnior and Amaral 2017.

families were Hylidae for amphibians (six species), Dactyloidae for lizards (three species), Colubridae for snakes (six species), and Chelidae for chelonians (two species). Some examples of this diversity and the sampled habitats appear in Figs 3–8. As expected, the species rarefaction curves show that the Serra da Mocidade mountain range still has potential to harbour a greater amphibian and reptile diversity than we record in this short-term sampling (Fig. 9a). Furthermore, the species richness differs between sampled altitudinal levels, tending to decrease in the higher altitudes (above 900 m asl) (Fig. 9b).

The number of specimens recorded during sampling was similar in both camps (149 at base camp #1 vs. 158 at base camp #2), with some species exclusively recorded at distinct altitudinal levels, as with frogs of the genus *Leptodactylus* Fitzinger, 1826 only recorded at 600 m asl or the snakes *Micrurus remotus* Roze, 1987 and *Chironius septentrionalis* Dixon, Wiest & Cei, 1993 only recorded at 1,060 m asl (Fig. 10). Regarding sampling methods, the colubrid *Atractus riveroi* Roze, 1961 and the gymnophthalmid *Cercosaura ocellata* Wagler, 1830 were exclusively recorded using pitfall traps, a method that recorded a total of 15 specimens. Active surveys recorded 252 specimens, eight specimens were collected using shotguns, three using glue traps, ten using trammel nets and hook with bait, and 17 by occasional encounters, including all three caecilians.

Advertisement calls were obtained for a few anuran species, and they were useful to assign or confirm species identification, such as *Dendropsophus minutus* (Peters, 1872), *Rhinella martyi* Fouquet, Gaucher, Blanc & Vélez-Rodriguez, 2007, *Boana boans* (Linnaeus, 1758) and *Anomaloglossus apiau* Fouquet, Souza, Nunes, Kok, Curcio, Carvalho, Grant & Rodrigues, 2015. We obtained DNA sequences from 74 specimens of taxonomically confusing taxa (10 species) to conduct our phylogenetic analyses. These analyses revealed that some species initially thought by us to be new taxa represent taxa already described, for instance *A. apiau*, *R. martyi*, *Dendropsophus parviceps* (Boulenger, 1882), *Vitreorana ritae* (Lutz, 1952) and *Tretioscincus oriximinensis* Ávila-Pires, 1995. Additionally, molecular data indicated the existence of some new candidate species (Padial et al. 2010), such as *Stefania* sp., *Epicrionops* sp. and *Brasilotyphlus* sp. and other taxa that require further studies to clarify their taxonomic status, such as *Pristimantis* aff. *vilarsi* and *Hyalinobatrachium* aff. *taylori*.

Diversity and biogeographical affinities

The species richness of Serra da Mocidade is comparable to that recorded for other mountain ranges in the Guiana Shield highlands region, which harbour a low number of species compared to Guiana Shield lowland forest habitats (Table 2). Regarding the species composition, the amphibians and reptile assemblages of the Serra da Mocidade were evidenced in an intermediate position between the Guiana Shield highlands and lowland forest assemblages, which are distinct from the cluster generated by the lowland open habitat assemblages ($R^2 = 0.74$, stress = 0.14). We note a high divergence in species com-



Figure 3. Amphibian diversity. Examples of amphibians recorded in the Serra da Mocidade mountain range. **a** *Anomaloglossus apiau*, male **b** *Anomaloglossus apiau*, female **c** *Rhaebo guttatus* **d** *Rhinella martyi* **e** *Hyalinobatrachium* aff. *taylori* **f** *Vitreorana ritae* **g** *Dendropsophus minutus* **h** *Dendropsophus parviceps* **i** *Boana boans* **j** *Boana xerophylla*. Photographs by Haroldo Palo Jr. (**c-j**).

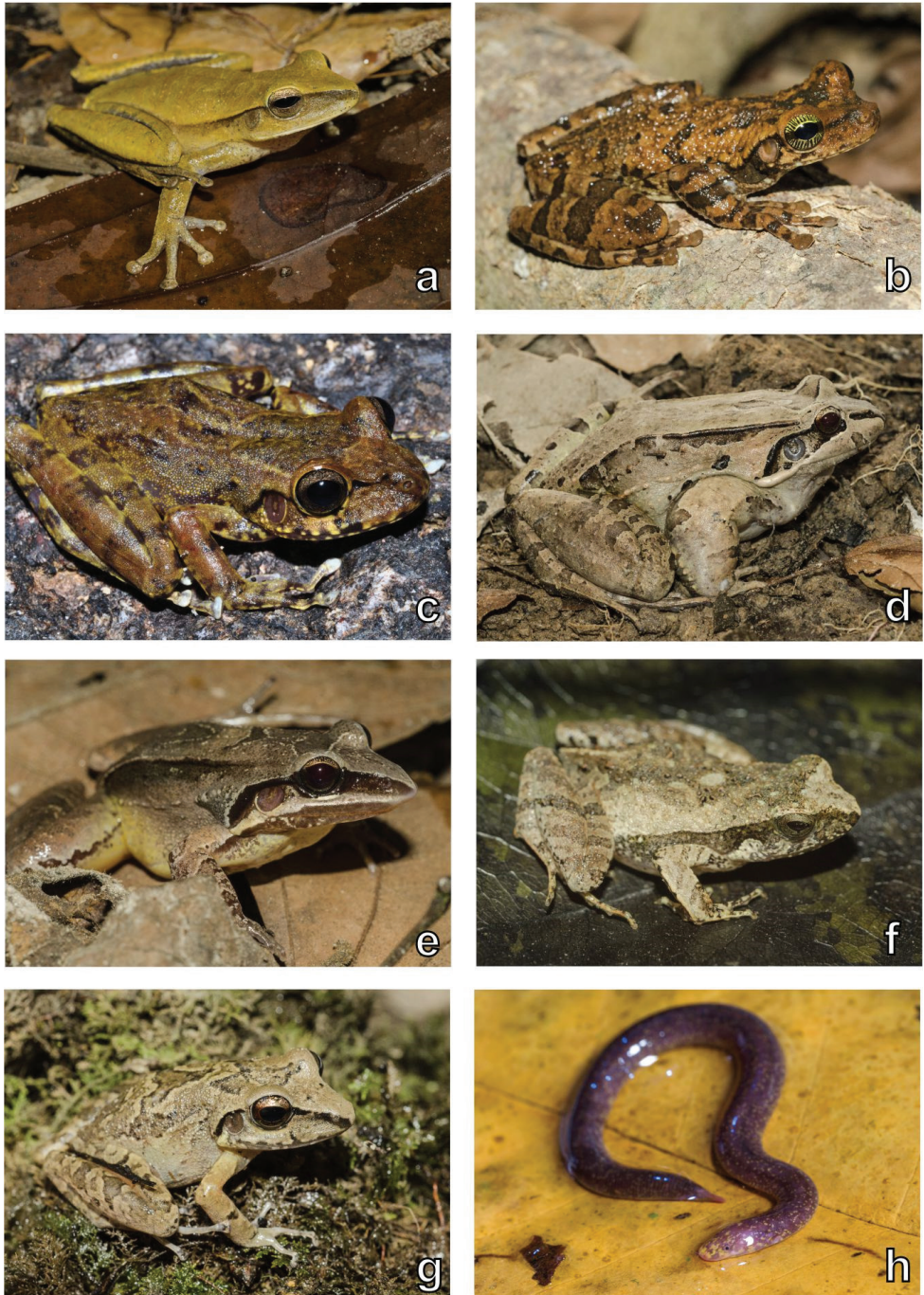


Figure 4. Amphibian diversity. Examples of amphibians recorded in the Serra da Mocidade mountain range. **a** *Boana multifasciata* **b** *Osteocephalus taurinus* **c** *Stefania* sp. **d** *Leptodactylus guianensis* **e** *Leptodactylus mystaceus* **f** *Physalaemus ephippifer* **g** *Pristimantis* aff. *vilarsi* **h** *Epicrionops* sp. Photographs by Haroldo Palo Jr. (**a, b, d–g**), and Marcos Amend (**h**).



Figure 5. Lizard diversity. Examples of lizards recorded in the Serra da Mocidade mountain range. **a** *Anolis fuscoauratus* **b** *Anolis planiceps* **c** *Cercosaura ocellata* **d** *Tretioscincus oriximinensis* **e** *Polychrus marmoratus* **f** *Thecadactylus rapicauda* **g** *Mabuya nigropunctata* **h** *Plica plica*. Photographs by Haroldo Palo Jr. (a–c, e–h) and Marcos Amend (d).



Figure 6. Snake diversity. Examples of snakes recorded in the Serra da Mocidade mountain range. **a** *Chironius septentrionalis* **b** *Chironius fuscus* **c** *Drymobius rhombifer* **d** *Atractus riveroi*, morph 1 **e** *Atractus riveroi*, morph 2 **f** *Dipsas indica indica* **g** *Dipsas pavonina* **h** *Imantodes cenchoa*. Photographs by Haroldo Palo Jr. (**a, b, f–h**) and Marcos Amend (**d, e**).



Figure 7. Snake, chelonian and crocodilian diversity. Examples of snakes, chelonians and the crocodilian recorded in the Serra da Mocidade mountain range. **a** *Xenodon rabdocephalus rabdocephalus* **b** *Micrurus remotus* **c** *Bothrops atrox* **d** *Bothrops bilineatus bilineatus* **e** *Lachesis muta muta* **f** *Mesoclemmys gibba* **g** *Platemys platycephala melanonota* **h** *Paleosuchus trigonatus*. Photographs by Haroldo Palo Jr. (**a**, **c**, **e-h**).



Figure 8. Habitat diversity. Examples of habitats sampled in the Serra da Mocidade mountain range. **a** Submontane rainforest at 600 m asl **b** Pacú River, main water body near camp #1 **c** Montane rainforest at 1,060 m asl **d, e** Rocky streams at 1,060 m asl **f** Montane rainforest at 1,365 m asl. Photographs by Ramiro Melinski (**a–c, e–f**).

position of the mountain ranges included in the analyses, because many of these mountains harbour several endemic species. Among these mountain ranges, the herpetofauna of Serra da Mocidade is more similar to that occurring at the geographically close Apiaú and Neblina, as well as to that occurs at the uplands of Nassau and Lely plateaus, which reach lower altitudes than the others mountain ranges included in this analyses (Fig. 9c).

This same mixed influence is corroborated regarding biogeographical regions, as the composition of the amphibian assemblage was most strongly influenced by widely distributed Amazonian forest lineages (47%), but also included species restricted to, or

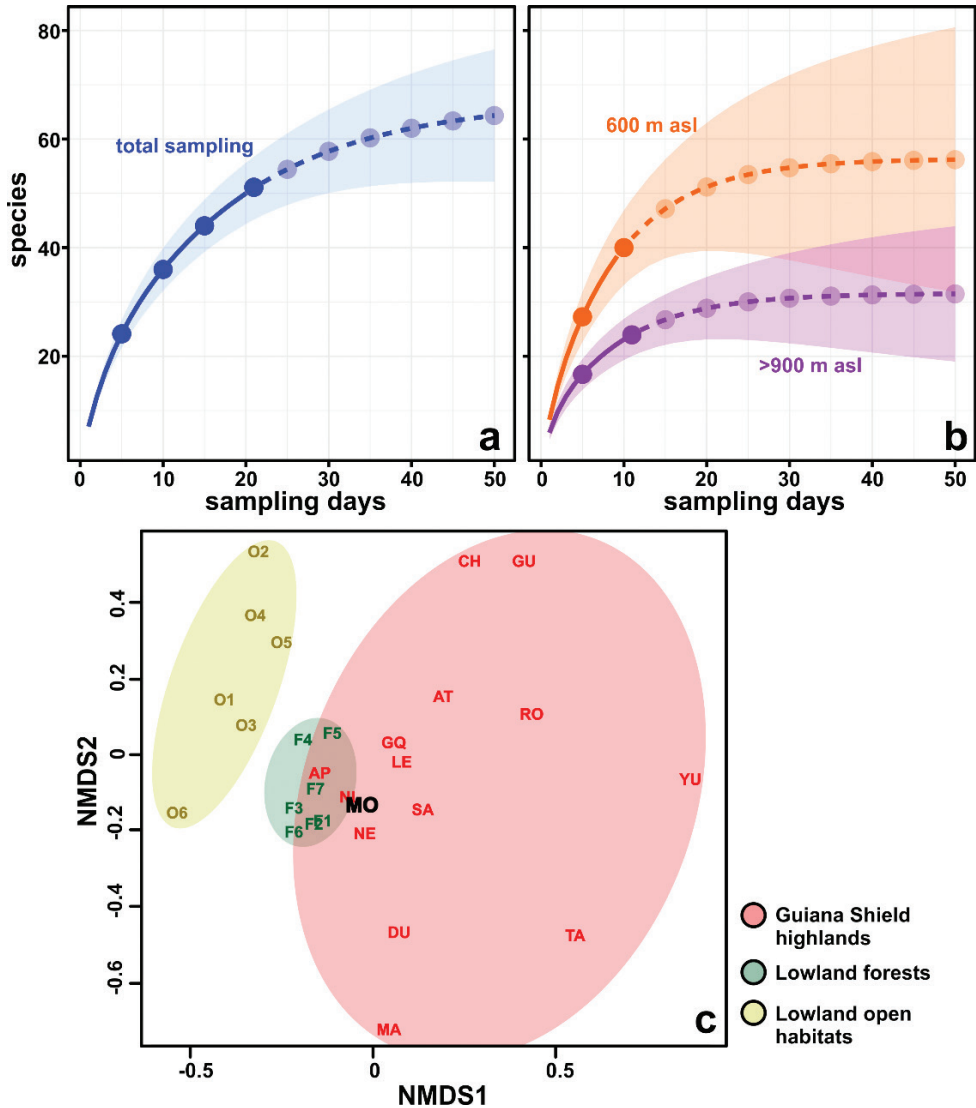


Figure 9. Variation in species richness and composition. **a, b** Extrapolated rarefaction curves showing variation in species richness related to sampling effort at our total sampling **a** and at distinct altitudinal levels **b** of the Serra da Mocidade mountain range. Observed data are in full lines and extrapolated in dashed lines **c** Non-metric multidimensional scaling (NMDS) ordination for amphibian and reptile assemblages from mountain ranges of Guiana Shield highlands and nearby lowland habitats, showing the mixed influence in the Serra da Mocidade composition. Mountain ranges: (MO) Mocidade; (AP) Apiaú; (Du) Duida; (Ma) Marahuaka; (AT) Auyantepui; (Ch) Chimantá; (Gq) Guaiquinima; (NE) Neblina; (TA) Tamacuari; (YU) Yutajé-Corocoro; (RO) Roraima; (SA) Sarisariñama; (NL) Nassau Lely. Lowland habitats: (F1, O1) ESEC Maracá; (F2, O2) PARNA Viruá; (F3, O3) Roraima Lowlands; (F4, O4) Samá and Miang rivers region; (F5, O5) Parque Nacional Canaima; (F6, O6) Parque Nacional da Serra da Mocidade and Estação Ecológica Niquiá; (F7) Kurupukari. References are detailed in the text.

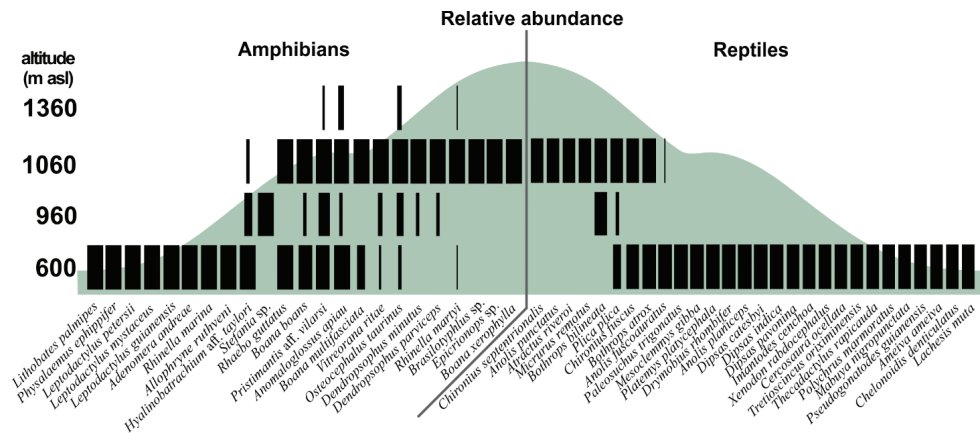


Figure 10. Altitudinal species variation. Altitudinal variation in species composition and relative abundance (width of the black bars) of amphibians and reptiles from our sampling at the Serra da Mocidade mountain range. Note that some species were exclusively recorded in a given altitudinal level while other are altitudinal generalists.

Table 2. Species richness. Herpetofaunal richness variation at some mountain ranges in the Guiana Shield highlands (including data for all altitudinal levels) and at lowland habitats in the region (compiled results of inventories). Data are presented as raw species number/percentage of total herpetofauna and references are detailed in the text.

Mountain range	Amphibians	Reptiles	Total
Mocidade	23/0.45	28/0.55	51
Apiaú	23/0.48	25/0.52	48
Duida	10/0.38	16/0.62	26
Marahuaka	14/0.74	5/0.26	19
Auyantepui	14/0.35	26/0.65	40
Chimantá	8/0.42	11/0.58	19
Guaiquinima	11/0.33	22/0.67	33
Neblina	51/0.45	62/0.55	113
Los Testigos	4/0.67	2/0.33	6
Lema	31/0.53	28/0.47	59
Guanay	4/0.57	3/0.43	7
Yaví	3/0.50	3/0.50	6
Tamacuari	7/0.64	4/0.36	11
Yutajé-Corocoro	6/0.60	4/0.40	10
Roraima	15/0.65	8/0.35	23
Sarisariñama	16/0.44	20/0.56	36
Nassau, Lely	32/0.59	22/0.41	54
Lowland habitats			
Forests	72/0.42	100/0.58	172
Open habitats	40/0.54	33/0.46	73

typical for, the Guiana Shield (22%), Guiana Shield highlands (8%) and Eastern Amazonia (4%). The reptile assemblage composition showed a similar pattern, with most species widely distributed in Amazonia (75%) and smaller proportions of exclusive lineages from the Guiana Shield (7%), Guiana Shield highlands (7%), Eastern Amazonia (7%) and Western Amazonia (3.5%). Some of the taxa we collected are potentially endemic to the Serra da Mocidade mountain range, such as *Stefania* sp., *Epicrionops* sp., *Brasilotyphlus* sp. and *Hyalinobatrachium* aff. *taylori* (Table 1).

Most of the amphibian species we recorded on Serra da Mocidade occur across wide altitudinal ranges along their geographical distribution (43%). Several species are typical from the Amazonian lowlands (35%), and some are typical of the uplands (22%). The reptilian assemblage showed a similar altitudinal pattern: most of the Serra da Mocidade species are generalists in terms of altitudinal range (53.5%) or lowland forms (43%), and few are typical of the uplands (3.5%). When we analysed the distinct assemblages recorded at 600 m asl and above 900 m asl, we found different distribution patterns at a finer scale: at 600 m asl, assemblages were mainly composed of lowland species (47% of amphibians and 52% of reptiles) and altitudinal generalists (42% of amphibians and 48% of reptiles). Above 900 m asl, no elements from lowland forests were recorded for either taxonomic group and assemblages were composed of upland species (33% of amphibians and 11% of reptiles) and altitudinal generalists (67% of amphibians and 89% of reptiles) (Fig. 10).

Remarkable records

Accounts of the remarkable species are provided below, with comments on ecology, taxonomy, morphology, evolutionary distinctiveness, and biogeography.

Epicrionops sp. – The genus *Epicrionops* Boulenger, 1883 is distributed in mountainous habitats of the Andes (seven species) and the Guiana Shield highlands [*Epicrionops niger* (Dunn, 1942)] (Frost 2017). However, the generic position of *E. niger* is uncertain, as recent studies have shown this species to be genetically closer to species in the genus *Rhinatrema* (distributed mainly throughout the Guiana Shield) than to Andean species of *Epicrionops* (Pyron and Wiens 2011, San Mauro et al. 2014). The juvenile specimen recorded at Serra da Mocidade (Fig. 4h) is the first of the genus recorded from Brazil and has a high genetic distance to *E. niger* from Guyana (>15% on the 16S fragment used, Fig. 11). Considering such high molecular divergence and degree of geographical isolation, this taxon represents a new candidate species, needing further studies and samples for its formal description.

Brasilotyphlus sp. – The genera *Microcaecilia* Taylor, 1968 and *Brasilotyphlus* Taylor, 1968 (possibly synonymous by lack of diagnosability—see Maciel and Hoogmoed 2011) are distributed throughout eastern Amazonia, with highest diversity in the Guiana Shield. We found two caeciliid specimens at Serra da Mocidade, both at

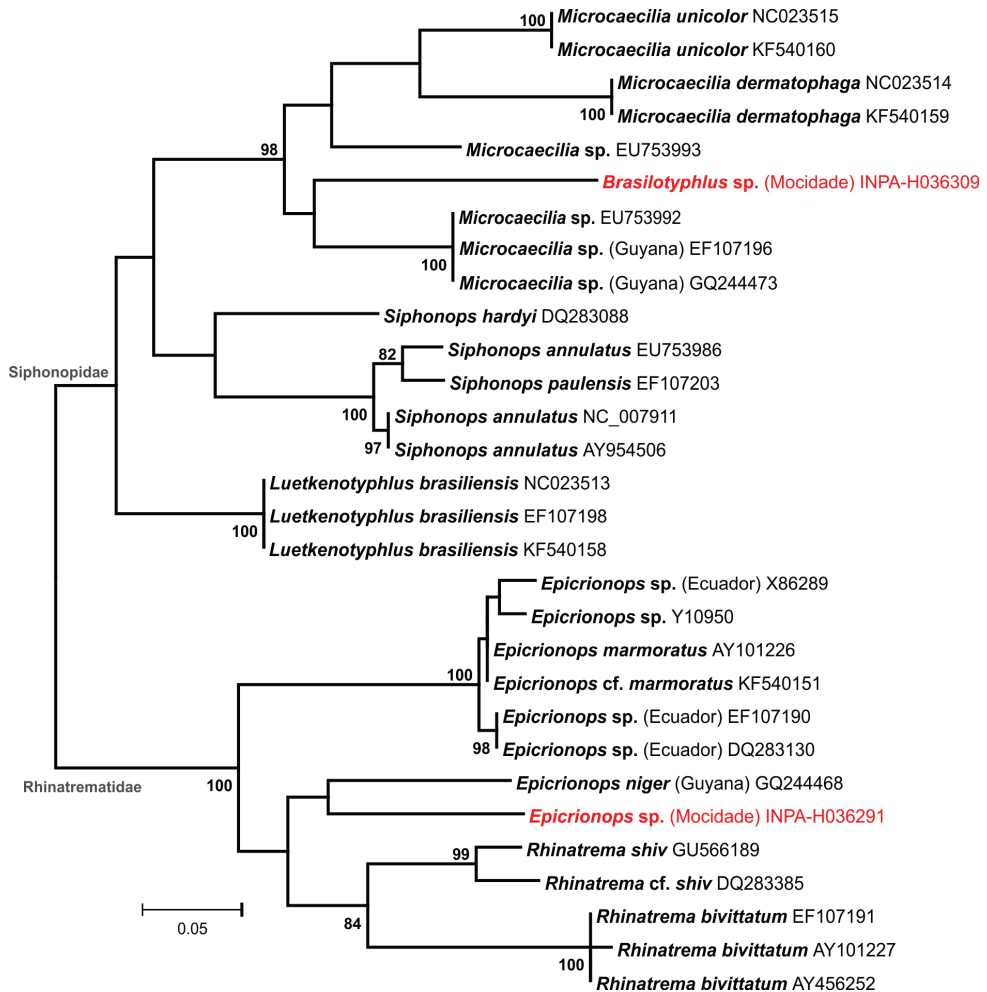


Figure 11. Phylogenetic relationships of caecilians. Maximum likelihood phylogenetic tree of caecilians families Siphonopidae and Rhinatrematidae, based on a 468bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, and specimens from the Serra da Mocidade are highlighted.

1,060 m asl, possessing a diastema between palatine and vomerine teeths, the only known morphological characteristic diagnostic for the genus *Brasilotyphlus* (Maciel et al. 2009, Wilkinson et al. 2013). However, some morphological characteristic distinguish those specimens for other *Brasilotyphlus*, e.g. the lower number of primary annulus (less than 140 vs. more than 141 in the two known species). Although no *Brasilotyphlus* or *Microcaecilia* is known from the Brazilian side of the Guiana Shield highlands region, there is evidence that at least two undescribed species occur there, and one of them is in description process (Maciel and Hoogmoed 2011, Pedro Nunes pers. comm.). Our molecular analyses showed this taxon to be

highly divergent from other *Microcaecilia* with available sequences in GenBank, with a minimum genetic distance of 17% on the 16S fragment used (Fig. 11). Based on these morphological and molecular results, we consider the *Brasilotyphlus* collected at Serra da Mocidade as a new candidate species.

Anomaloglossus apiau – The high endemism levels of the small cryptically coloured terrestrial frogs of the genus *Anomaloglossus* recorded from Guiana Shield highlands mountains (Kok et al. 2012, Vacher et al. 2017), together with the geographical isolation of Serra da Mocidade, led us to immediately suspect that the population found in this mountain range was a new taxon. However, detailed analyses showed that their morphological (Fig. 3a,b), acoustic (Fig. 12, Table 3) and molecular variation (Fig. 13) are consistent with the description of *A. apiau* (Fouquet et al. 2015a), a species previously known only from its type locality, at Serra do Apiaú, a mountain range distant ca. 80 km northeast of Serra da Mocidade. Here we extend the known geographical range of this species. We found the species in all altitudinal levels sampled at Serra da Mocidade, near rocky streams with rapids and waterfalls (Fig. 8d, e).

The population of Serra da Mocidade had adult males with 15–20 mm SVL, and females slightly larger than originally described for *A. apiau* (19–23 mm SVL) (see Fouquet et al. 2015a). As in the population from Serra do Apiaú, specimens from Serra da Mocidade had a high intraspecific polymorphism in colour pattern, and strong sexual dichromatism (Fig. 3a, b). The advertisement call has the same temporal and spectral structure as reported in the species description (long series of paired notes, followed by intervals of silence) (Fig. 12, Table 3). Additionally, the population from Serra da Mocidade occurs within the altitudinal range cited in the original description for the type locality (500–1,400 m asl). Molecular analyses confirmed the similarity between the two populations, with the sample of *A. apiau* from the type locality nested within the Serra da Mocidade clade (Fig. 13). Two subclades from Serra da Mocidade are separated by a low genetic distance (maximum 2% on the 16S fragment used) and occur at different altitudes and drainages. However, this difference is most likely due to natural intraspecific variation, since the genetic distance between populations of *A. apiau* from the type locality and Serra da Mocidade is also below 2%.

This record of *A. apiau* from the Serra da Mocidade (first outside the type locality) is remarkable, since the species was not recorded from the mountain range of the Serra da Maroquinha, located at less than 5 km southeast from the Serra do Apiaú. New studies on the cryptic diversity, evolution and biogeography of the genus *Anomaloglossus* (such as Vacher et al. 2017) should reveal the species limits, geographical patterns and drivers of the diversification in low- and uplands of the Guiana Shield.

Rhinella martyi – *Rhinella martyi* has a confusing taxonomic history, as do many of the small-medium terrestrial forest bufonids in the *Rhinella margaritifera* group (dos Santos et al. 2015). Until recently, this taxon was allocated in the problematic

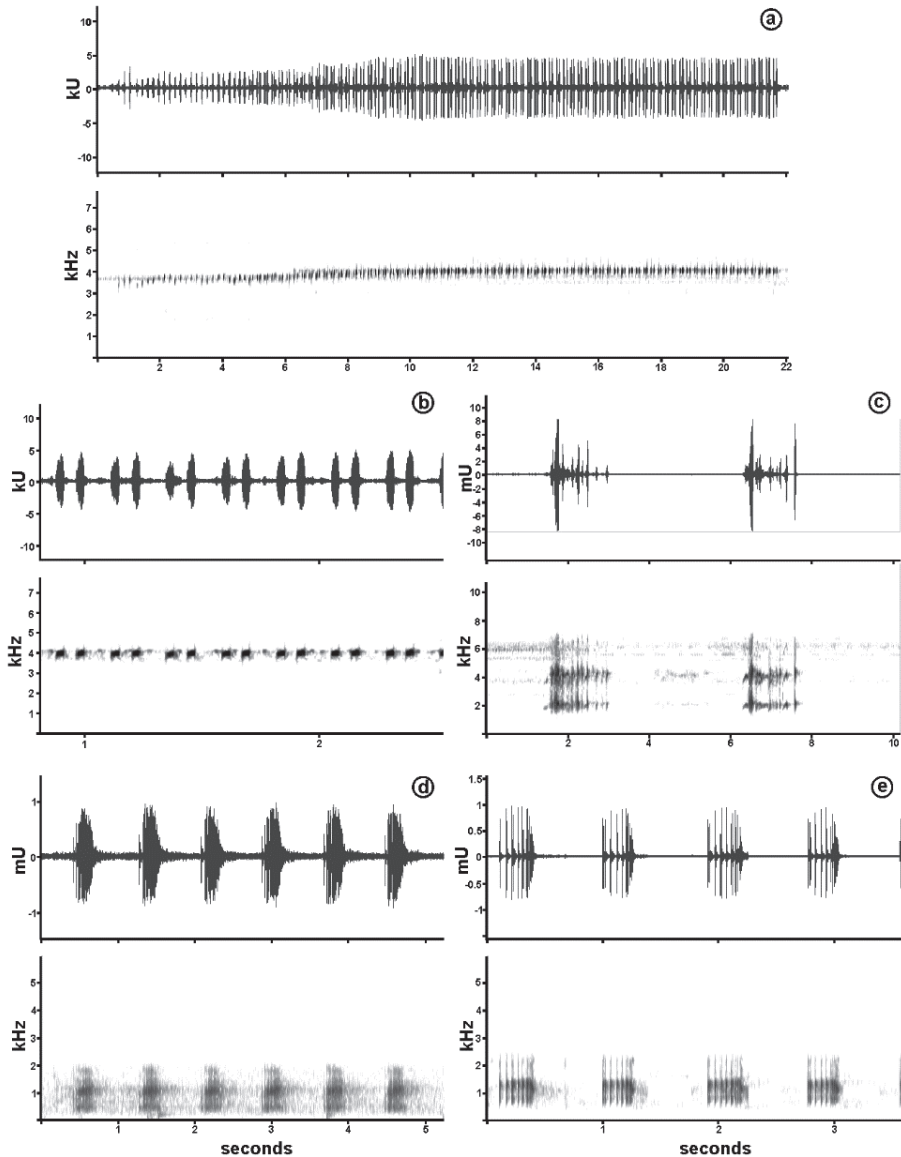


Figure 12. Bioacoustical data. Oscillograms (upper graphs) and sonograms (lower graphs) of advertisement calls of species recorded in the Serra da Mocidade mountain range. **a** *Anomaloglossus apiau*, zoomed at **b** showing the paired pulses **c** *Dendropsophus minutus* **d** *Boana boans* **e** *Rhinella martyi*.

taxon *Rhinella margaritifera* (Laurenti, 1768), but Fouquet et al. (2007a) recognized the presence of distinct lineages occurring in the Guiana Shield. Two of these lineages were later described as the new species *R. lescurei* and *R. martyi* (Fouquet et al. 2007b), but the specific status of the latter was rejected by Ávila-Pires et al. (2010). However, awaiting further integrative revisions of the group, the name

Table 3. Quantitative bioacoustical results. Summary of bioacoustical analyses of advertisement calls of some species recorded from the Serra da Mocidade mountain range, with literature data for comparison. Data are presented as mean, with associated amplitude (–) or standard deviation (\pm).

Species	Locality (References)	Call structure	Call duration (s)	Inter-call interval (s)	Pulse duration (s)	Pulse rate (pulses/s)	Dominant frequency (kHz)
<i>Anomaloglossus apiau</i>	Serra da Mocidade, RR, Brazil	Long trill	19.07 (± 4.89)	15.76 (± 4.12)	0.039 (± 0.002)	8.4 (± 0.67)	4.109 (± 0.148)
<i>Anomaloglossus apiau</i>	Serra do Apiaú, RR, Brazil [†]	Long trill	19.56 (± 11.05)	11.17 (± 7.24)	0.033 (± 0.005)	11.27 (± 0.55)	4.334 (± 0.129)
<i>Dendropsophus minutus</i>	Serra da Mocidade, RR, Brazil	Single note	0.09 (0.04–0.18)	13 (11.2–17.4)	-	-	3.72 (2.1–4.5)
<i>Dendropsophus minutus</i>	Different localities [‡]	Single note	0.11 (0.03–0.2)	14.7 (11.1–18.3)	-	-	3.75 (2.2–5.3)
<i>Boana boans</i>	Serra da Mocidade, RR, Brazil	Long train	0.34 (0.18–0.51)	1.51 (1.27–2.10)	-	-	1.036 (0.9–1.1)
<i>Boana boans</i>	Different localities [‡]	Long train	0.42 (0.18–1.19)	2.05 (0.57–4.7)	-	-	0.648 (0.2–1.1)
<i>Rhinella marmorata</i>	Serra da Mocidade, RR, Brazil	Series of pulses	0.302 (± 0.026)	0.61 (± 0.18)	0.015 (± 0.004)	-	1.237 (± 0.03)
<i>Rhinella marmorata</i>	Guiana Shield lowlands [§]	Series of pulses	0.295 (± 0.013)	-	0.009 (± 0.001)	-	1.169 (± 0.04)

[†] Fouquet et al. 2015, [‡] Cardoso and Haddad 1984, Donnelly and Myers 1991, Morais et al. 2012, [‡] Hoogmoed 1990, [§] Fouquet et al. 2007b.

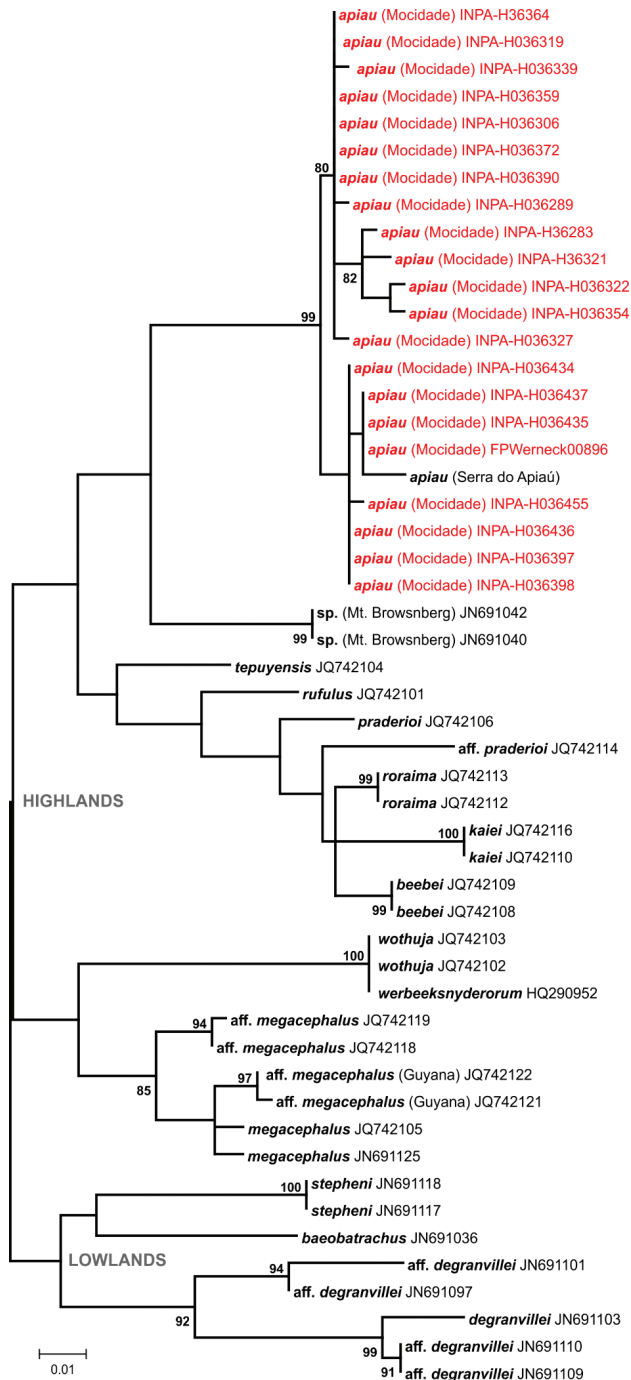


Figure 13. Phylogenetic relationships of *Anomaloglossus*. Maximum likelihood phylogenetic tree of *Anomaloglossus* species, based on a 361bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, and specimens from the Serra da Mocidade are highlighted.

R. martyi was retained (Frost 2017). Both the neotype designated to *Rhinella margaritifera* (Lavilla et al. 2013) and the holotype recently rediscovered (Lavilla et al. 2017), have a different morphology from populations named as *R. martyi* (e.g., by having larger cranial crests and body size). Apparently, *R. martyi* is widely distributed along the northern Guiana Shield, occurring along a broad altitudinal range (Fouquet et al. 2007b).

Individuals of *R. martyi* were found on leaf-litter inside primary forests, and calling males on the banks of streams, mostly at 1,060 m asl (Fig. 3d). Morphological variation among specimens from the Serra da Mocidade mostly fits with the variation proposed in the original species' description, except in a lower variation in adult body size (at Serra da Mocidade, males 50–60 mm SVL, females 62–70 mm SVL), smaller height of supratympanic crests and the bony knob at angle of jaws less developed. The advertisement call recorded at Serra da Mocidade also differs slightly from the species description, with longer pulses and higher dominant frequency (Fig. 12, Table 3). However, the overall morphological and acoustic variation in *R. martyi* is still being clarified (A. Fouquet pers. comm.). Elucidation of the taxonomic status of populations of *Rhinella margaritifera* group from the Guiana Shield still depends on broader integrative revisions.

Pristimantis aff. *vilarsi* – *Pristimantis* is one of the most speciose genus of vertebrates (Padial et al. 2014, Frost 2017). Such high diversity is accompanied by a problematic taxonomy and difficulties in species delimitation (Padial et al. 2014). In the Guiana Shield highlands region, several lineages of *Pristimantis* diversified into lowlands and highland forms (Kok et al. 2011). We found a species from the *Pristimantis conspicillatus* group at the Serra da Mocidade (Fig. 4g). It may represent a new taxon, but its taxonomic status is being evaluated in a broader sense in relation to other *Pristimantis*. Our molecular analyses showed that samples from the Serra da Mocidade are more similar to *Pristimantis vilarsi* (Melin, 1941, redescribed in Barrio-Amorós and Molina 2006) and *Pristimantis zeuctotylus* (Lynch & Hoogmoed, 1977), both species of the *P. conspicillatus* group from the lowlands and uplands of Guiana Shield. The population from Serra da Mocidade has morphological details that distinguish it from these two genetically-related species, as for example the adult body size (SVL): 22–33 mm in males and 31–49 mm in females of *P. vilarsi*, 20–29 mm in males and 30–43 mm in females of *P. zeuctotylus* (Barrio-Amorós and Molina 2006) and 36–46 mm in males and 48–57 mm in females from Serra da Mocidade. *Pristimantis* aff. *vilarsi* occurs across the altitudinal range sampled at Serra da Mocidade and was one of the most abundant anurans in our sampling (along with *A. apiau*). It was recorded on leaf-litter of primary dense forests, but also inhabits rocky outcrops within streams with fast flowing water (Fig. 8d, e).

Hyalinobatrachium aff. *taylori* – The species of *Hyalinobatrachium* from Serra da Mocidade (Fig. 3e) was mainly found at 600 m asl. Most of specimens collected were

juveniles, with few adults varying in body size from 18 to 21 mm SVL. The species is morphologically similar to *Hyalinobatrachium taylori* (Goin, 1968), a taxon widely distributed within the northern Guiana Shield (Castroviejo-Fisher et al. 2011). Both have similar body sizes, snout shape (round in dorsal view and sloping in lateral view), life colouration of dorsum (dark green with small white spots), eyes (grey, black reticulated), hands and feet (yellowish-orange) (Castroviejo-Fisher et al. 2011). However, specimens from Serra da Mocidade differ from *H. taylori* by having white bones instead of green (Señaris and Ayarzagüena 2005, Guayasamin et al. 2009, Castroviejo-Fisher et al. 2011). It is possible that this difference represents an intraspecific variation, since the genetic distance on the 16S fragment used was less than 4% between both taxa (Fig. 14), but bone colouration is a strong character in the genus taxonomy, and green bones is a rare character in *Hyalinobatrachium* (two species), but common in other centrolenid genera, such as *Vitreorana* and *Centrolene* (Guayasamin et al. 2009). In addition, Serra da Mocidade is located far from the known geographical range of *H. taylori*, and the occurrence of this species at this locality would be the first record of the species in Brazil.

The diversity of *Hyalinobatrachium* in the Guiana Shield highlands region appears underestimated, since some lineages were recently described as new species after an integrative revision (Castroviejo-Fisher et al. 2011), and the evolution of lineages in the *H. taylori* complex seem strongly influenced and structured by the altitudinal levels in which they occur, with clades from lowlands and highlands separated by low genetic distances (Castroviejo-Fisher et al. 2011). Considering the uncertainties, and waiting for the results of future detailed studies, we opted to keep this taxon as *H. aff. taylori*.

Vitreorana ritae – The small glassfrog *Vitreorana ritae* is apparently widely distributed in the Guiana Shield (Guayasamin et al. 2009), occupying a wide altitudinal range (see Cisneros-Heredia 2013 for taxonomical accounts and synonymization of *V. oyampiensis* with *V. ritae*). However, single-site records in western Amazonia and south of the Amazon River cloud the delineation of the total species' range and possible connections between populations. The species was found at Serra da Mocidade (Fig. 3f) in riparian vegetation at three altitudinal levels, but with greatest abundance at 1,060 m asl. Specimens from Serra da Mocidade are differentiated from *Vitreorana helenae* (Ayarzagüena, 1992), a morphologically similar taxon from the Guiana Shield highlands region that has yellow eyes and a lime-green dorsum (eyes predominantly gray and a darker green dorsum in *V. ritae*) (Guayasamin et al. 2008). Molecular data also grouped sequences from the Serra da Mocidade with sequences of *V. ritae* from other Guiana Shield localities with less than 2% of genetic distance on the 16S fragment used, while the distinction between *V. ritae* and *V. helenae* lies between 4 and 5% (Fig. 15).

Stefania sp. – The marsupial frog genus *Stefania* have an evolutionary history intrinsically linked to the evolution of the Guiana Shield highlands landscape, as the

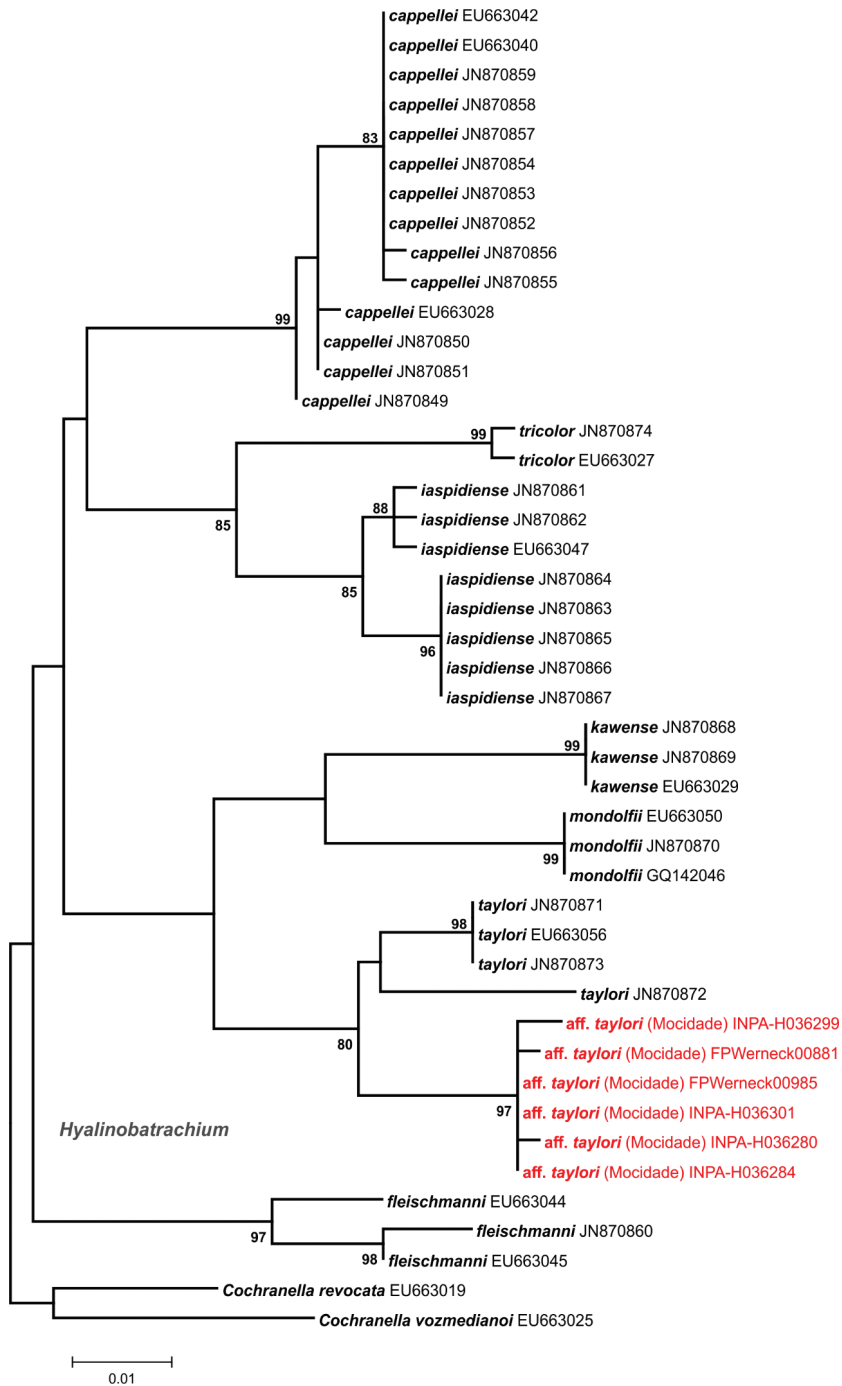


Figure 14. Phylogenetic relationships of *Hyalinobatrachium*. Maximum likelihood phylogenetic tree of *Hyalinobatrachium* species from Guiana Shield, based on a 465bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, and specimens from the Serra da Mocidade are highlighted.

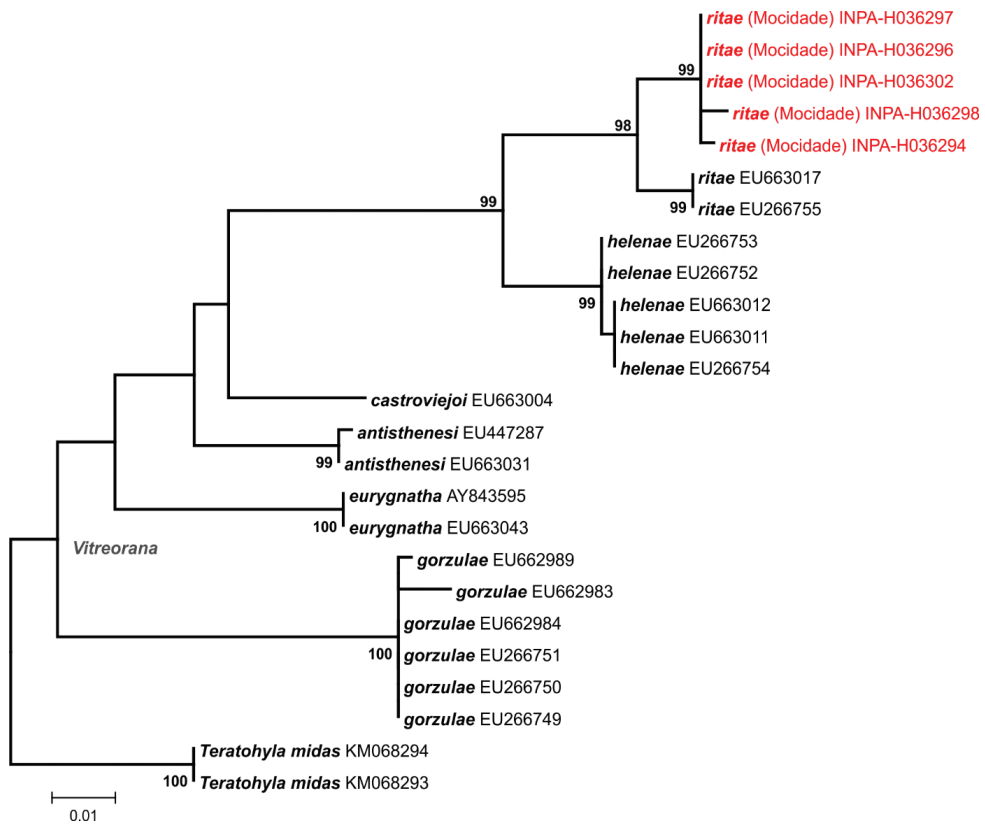


Figure 15. Phylogenetic relationships of *Vitreorana*. Maximum likelihood phylogenetic tree of *Vitreorana* species, based on a 496bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, and specimens from the Serra da Mocidade are highlighted.

genus has a geographical range restricted to this region and high endemism levels in distinct mountain ranges (Duellman and Hoogmoed 1984, Salerno et al. 2012, Duellman 2015, Kok et al. 2016, 2017). We found two adult *Stefania* at 960 m asl on rocky outcrops in rapidly flowing streams (Fig. 8d, e). The specimens from Serra da Mocidade (Fig. 4c) have a large body size (52–54 mm SVL), head wider than long (head length / width = 0.93–0.94), snout rounded in dorsal and lateral views, shagreened dorsum, basal toe webbing, colour pattern in life dorsally yellowish-brown with large rectangular blotches, ventrally gray (lighter in the abdomen) with large whitish patches, and large t-shaped finger and toe discs. The combination of these morphological characters distinguishes these specimens from other congeners (see variation in Rivero 1970, Myers and Donnelly 1997, MacCulloch and Lathrop 2002, Carvalho et al. 2010). The most similar species considering the external morphology is also the one with the closest known geographical distribution (*Stefania tamacuarina* Myers & Donnelly, 1997, which occurs ca. 300 km distant

to the west of the Serra da Mocidade) (Caramaschi and Niemeyer 2005), however these taxa slightly differ in length and shape of snout, dorsal and ventral colouration pattern, as well as size of eye and hands (Myers and Donnelly 1997). The morphological divergence compared to the known congeners is sustained by a high genetic distance (>10% on the 16S gene fragment used), even considering other undescribed taxa detected in a recent phylogenetic analyses of the genus (Kok et al. 2017) (Fig. 16). The population of *Stefania* sp. from Serra da Mocidade is apparently isolated from known ranges of both described and undescribed species, and when confirmed as a new species, will be the third known *Stefania* endemic to a granitic mountain, while other taxa in this genus mainly occur at summits of sandstone mountains (Myers and Donnelly 1997). While new specimen samples (especially adults of *S. tamacuarina*) and DNA sequences are not available, we opted to keep this taxon as a candidate species.

Dendropsophus minutus – The species complex of small arboreal *Dendropsophus minutus* hylids is widely distributed in South America east of Andes, occupying a broad altitudinal range (Frost 2017). The evolutionary history of this complex has been recently revised, showing multiple distinct lineages throughout its wide distribution (Gehara et al. 2014). Several distinct cryptic lineages occur in the Guiana Shield (already noted by Hawkins et al. 2007), which suggests the elevation of the synonymized taxon *Dendropsophus goughi* [species described by Boulenger (1911) and synonymized to *D. minutus* by Lutz (1973)] to specific level for at least one of these lineages. While new studies do not clarify this taxonomic issue, the available name for the population recorded in the Serra da Mocidade is *D. minutus* (Fig. 3g). The specimens recorded share the presence of distinct light stripes in the cloacal region and in some specimens in the heels, and emitted mainly territorial calls (type B *sensu* Cardoso and Haddad 1984), with acoustic parameters within the known variation for the species (Fig. 12, Table 3).

Dendropsophus parviceps – Recent molecular studies on the evolution of the genus *Dendropsophus* found a polyphyletic *Dendropsophus parviceps* species group *sensu* Faivovich et al. 2005 (Fouquet et al. 2011, 2015b, Motta et al. 2012), which harbours small cryptically coloured treefrogs. Recently, a new species of this group (*Dendropsophus counani* Fouquet, Orrico, Ernst, Blanc, Martinez, Vacher, Rodrigues, Ouboter, Jairam & Ron 2015) historically misidentified as *D. parviceps*, was described from the Guiana Shield (Fouquet et al. 2015b). We compared the specimens collected in Serra da Mocidade (Fig. 3h) with known taxa of the *D. parviceps* group, and both morphologic variation and molecular similarity (Fig. 17) reveals their identity as *D. parviceps*. We found a genetic distance of 3% on the 16S fragment used between samples from Serra da Mocidade and the *D. parviceps* sequence available in GenBank, from southwestern Amazonia (Acre state, Brazil), and this phylogenetic divergence can most likely be attributed to intraspecific variation due to wide geographical distance. This species has an ex-

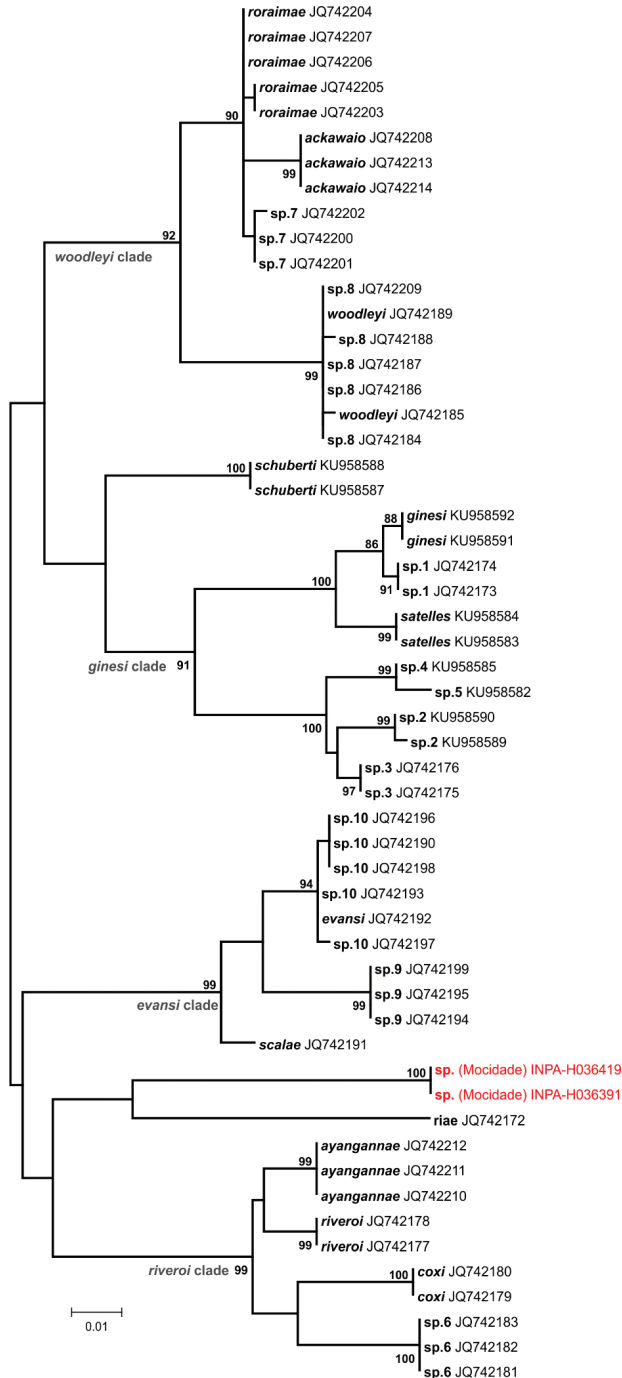


Figure 16. Phylogenetic relationships of *Stefania*. Maximum likelihood phylogenetic tree of *Stefania* species, based in a 536bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, species numbers of undescribed taxa follow Kok et al. (2017) and specimens from the Serra da Mocidade are highlighted.

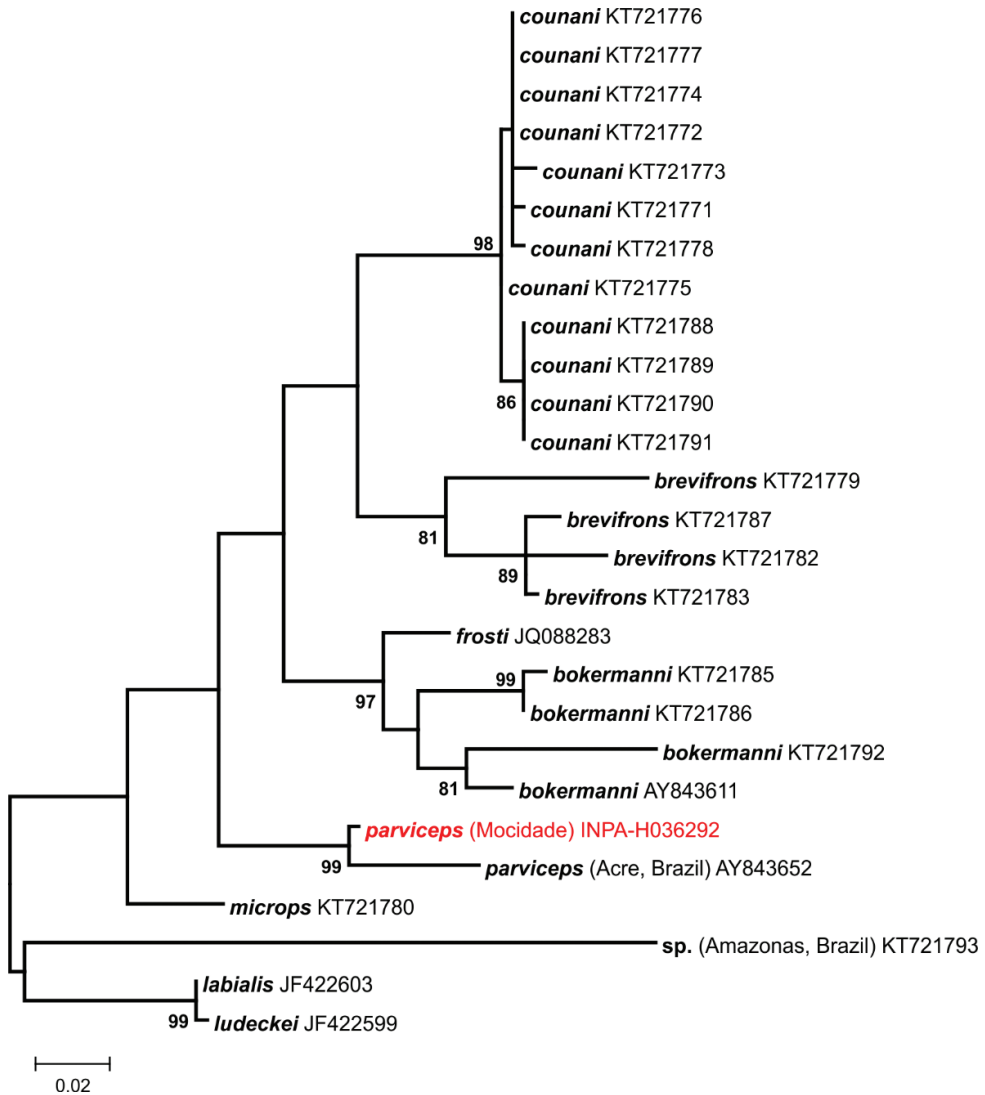


Figure 17. Phylogenetic relationships of *Dendropsophus*. Maximum likelihood phylogenetic tree of some species from *Dendropsophus parviceps* clade, based on a 350bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, and specimens from the Serra da Mocidade are highlighted.

tensive distribution throughout Amazonia, including historical records in other mountain ranges of Guayan Highlands (McDiarmid and Paolillo 1988, Schlüter and Mägdefrau 1991), and present high levels of genetic divergence reported between some populations (Fouquet et al. 2015b). It is likely that future studies will reveal other independent lineages hidden under this name, as was the case of *D. counani*.

Boana boans, *B. multifasciata*, *B. xerophylla* and *Osteocephalus taurinus* – These medium to large sized arboreal hylids have wide geographical ranges in Amazonia: *B. boans* (Fig. 3i) and *O. taurinus* (Fig. 4b) occur throughout almost the entire basin, *B. xerophylla* (Fig. 3j) occurs on the northern Guiana Shield and *B. multifasciata* (Fig. 4a) in eastern Amazonia and in the transition zone between Amazonia and Cerrado, an open savanna biome with its core distribution in central Brazil (Frost 2017). All these taxa are considered as lowland species, but they may occur in lower densities at higher altitudinal levels, having been recorded on other Guiana Shield highlands mountain ranges (Aubrecht et al. 2012). While *B. boans* and *O. taurinus* are typical of primary and secondary Amazonian forests, *B. xerophylla* and *B. multifasciata* occur in drier habitats, having their evolution intrinsically linked to the development and spread of dry habitats in Brazil. The combination of wide geographical range, presence of allopatric populations with distinct body sizes, colours and calls (Duelman 1979, Barrio-Amorós and Brewer-Carias 2008), are evidence for a complex of multiple independent lineages (see details on *B. boans* advertisement call from the Serra da Mocidade in Fig. 12, Table 3). Previous studies investigating the intraspecific variation of these taxa have been conducted (e.g., Jungfer et al. 2013, Guarnizo et al. 2016, Orrico et al. 2017), but a clear definition of specific limits still needs further definition.

Adenomera andreae and *Leptodactylus petersii* – These species are both terrestrial frogs, typical of Amazonian lowlands (Sá et al. 2014, Frost 2017). The intraspecific molecular variation for *A. andreae*, known to be widely distributed in forest habitats of Amazonia, shows divergent lineages endemic to the Guiana Shield (Fouquet et al. 2014). As for *L. petersii*, several studies have investigated the morphological and bioacoustics variation of the species and their close relatives (*Leptodactylus melanonotus* species group) (Heyer 1970, 1994, de Sá et al. 2014), but the high polymorphism and intraspecific variation of species from this group still hinder definitive taxonomic assignment. Further studies with broader datasets may reveal restricted lineages within *L. petersii*.

Lithobates palmipes – This large ranid inhabit forest habitats near to slow-flowing water bodies (lakes, ponds and rivers), is widely distributed in Amazonia, Atlantic Forest and transitional habitats and may represent a species complex. The presence of several gaps in the known species distribution hampers a precise geographical determination (La Marca et al. 2010, Rodrigues et al. 2013). Although the expected occurrence of the species reaches Roraima state and it has already been recorded in nearby areas, no state record has appeared in the literature until this study (nearest documented record at 400 km west of the Serra da Mocidade in Rodrigues et al. 2013). *Lithobates palmipes* abundance also varies considerably across its distributional range (Acosta-Galvis 1999), but the environmental determinants of such variation are still unknown (Ramalho et al. 2011). In the foothills of Serra da Mocidade, the species was abundant in the Pacú River floodplain (Fig. 8b), a tributary of the

Branco River, with more than 11 specimens (adults and larvae) recorded in three sampling nights.

Pseudogonatodes guianensis – *Pseudogonatodes guianensis* is a small leaf-litter lizard widely distributed within Amazonian lowlands (Ávila-Pires 1995, Ribeiro-Júnior 2015b). However, it is a species apparently rare in the Guiana Shield highlands region, where *Coleodactylus septentrionalis* Vanzolini, 1980 is the more abundant sphaerodactylid (Ribeiro-Júnior 2015b). No record of this species from the Roraima state appears in the previous literature, and our finding filling this distribution gap.

Plica plica – This widely distributed arboreal lizard (Ávila-Pires 1995, Rivas et al. 2012) has several distinct lineages with restricted geographical ranges (Murphy and Jowers 2013, Oliveira et al. 2016). However, the genetic divergence between lineages is not clearly reflected in the morphologic variation. A recent study on the morphological variation of the *Plica plica* complex led to the description of several new taxa with restricted distributions and kept *P. plica* as the species with broadest distribution within the Guiana Shield (Murphy and Jowers 2013). Also, a study on the intraspecific genetic variation of this species showed at least two distinct lineages from the region of Serra da Mocidade (Oliveira et al. 2016). We recorded *P. plica* (Fig. 5h) at three altitudinal ranges, and considering such current state of knowledge for the species complex, we retain the specimens from the Serra da Mocidade under this epithet, based in their external morphology.

Mabuya nigropunctata – Specimens of *Mabuya* from Serra da Mocidade (Fig. 5g) were assigned to this name based in morphological characters within the known variation of the species, as for example, the paired prefrontal scales, two pairs of nuchal scales, five supraciliar scales, dorsals scales tricarinate, dark ventral surfaces of hand and feet, which are covered by small tubercles, and a dark lateral band, not limited by dorsal and ventral light stripe. This morphological variation promptly differ this specimens from other *Mabuya* with a geographical distribution known for this region: *Mabuya carvalhoi* Rebouças-Spieker and Vanzolini, 1990 (with fused prefrontals, large granules in ventral surface of hands and feets, three to five pairs of nuchals, five longitudinal light stripes along the body and a blue tail) and *Mabuya bistriata* (Spix, 1825) (with four supraciliars, dorsals smooth, one pair of nuchals, distinct light stripes limiting the dark lateral band and at dorsum, and light ventral surfaces of hands, which are covered by moderately large granules). However, the recorded specimens have an interesting characteristic that differs from the species known morphology (Ávila-Pires 1995, Hedges and Conn 2012): the fusion of frontoparietal scales in a single butterfly-shaped scale. Morphological comparisons with other *M. nigropunctata* specimens collected in the Brazilian Guiana Shield highlands region (on Pico da Neblina, deposited at INPA-H collection) reveal the same pattern on the frontoparietal scales for some specimens, while other specimens from the same locality have the typical pattern of two frontoparietals.

Intraspecific analyses of molecular variation indicated a strong genetic structure and multiple lineages within this widely distributed Amazonian taxon (Miralles et al. 2005, Miralles and Carranza 2010). One of those lineages (which have *Mabuya surinamensis* Hallowell, 1857 as available name) occurs on the Guiana and Brazilian Shields, including the Guiana Shield highlands region (Miralles and Carranza 2010). The dissimilarity in the number of frontoparietals found in the specimens from Northern Brazil may represent typical variation within this lineage, but confirmation awaits further taxonomic studies.

Tretioscincus oriximinensis – The small cryptic specimens of *Tretioscincus* from Serra da Mocidade (Fig. 5d) were collected on leaf-litter of primary dense forest and have morphological characters within the known diagnosis of *T. oriximinensis*: high number of dorsal scales (>30 rows), polygonal scales on tail, in 12 rows and keeled, prefrontal in contact, six gular scales anteriorly, dorsolateral light stripe become paler at middle of the dorsum (Ávila-Pires 1995). In addition, molecular analyses showed low genetic distance on the 16S fragment used (<0.1%) between Serra da Mocidade specimens and a sample of *T. oriximinensis* from Venezuela. Although the species is apparently more abundant in open habitats, the original description also cites some individuals found in forested areas (Ávila-Pires 1995).

There is a subtle morphological divergence between *T. oriximinensis* populations from northern (including Serra da Mocidade) and eastern Amazonia (Ávila-Pires 1995), with differences in number of ventral scales and extension of keels in scales from tail to posterior dorsals. This morphological divergence is reflected at the molecular level (Fig. 18), as we found ca. 4% of genetic distance between samples from this populations. Dissimilarities between the *T. oriximinensis* populations indicate that their taxonomic status deserves to be further investigated.

Atractus riveroi – This groundsnake typical from Guiana Shield highlands was previously known by only two specimens (Roze 1961, Passos et al. 2013). We found three specimens in pitfall traps at the 1,060 m asl altitudinal level: two with a brown dorsal background with dark markings (Fig. 6d) and one with a black dorsal background with small white spots (Fig. 6e) (Passos et al. 2013). For detailed information on morphologic variation and geographical distribution of this species based in these records and new specimens from nearby mountain ranges, see Fraga et al. (2017).

Chironius fuscus and *C. septentrionalis* – Two species of diurnal *Chironius* snakes were recorded at Serra da Mocidade: one is a typical lowland species widely distributed in Amazonia and other ecosystems in South America (*Chironius fuscus* – Fig. 6b), while the other is a upland inhabitant (*Chironius septentrionalis* – Fig. 6a, adult male recorded only at 1,060 m asl, with 1,480 mm SVL, 350 mm caudal length – tail damaged, dorsals 12/12/8, ventrals 179, subcaudals 60, anal plate divided, apical pits on neck scales) (Dixon et al. 1993). The latter species was described as

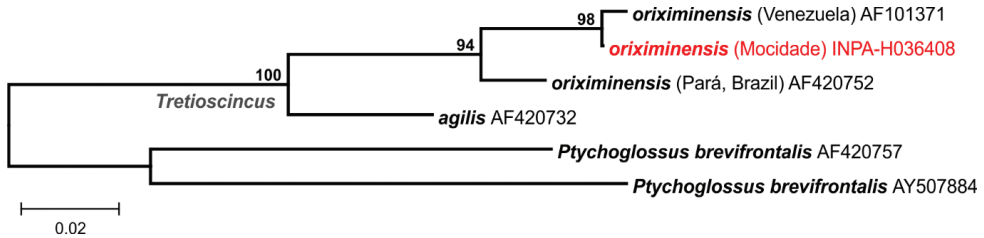


Figure 18. Phylogenetic relationships of *Tretioscincus*. Maximum likelihood phylogenetic tree of *Tretioscincus* species and populations, based on a 427bp fragment of the 16S mtDNA. Only bootstrap values >80% are shown (5,000 replicates). The GenBank accession numbers appear after the names of downloaded sequences, and specimens from the Serra da Mocidade are highlighted.

a subspecies of the widely distributed Amazonian species *Chironius multiventris* Schmidt and Walker, 1943 (Dixon et al. 1993), but a morphologic taxonomic revision elevated it to specific level (Dixon et al. 1993). This species occurs at high altitudinal levels in adjacent Venezuela, but may occur in lowlands on the island of Trinidad (Dixon et al. 1993). This is the first record from Brazil, extending the known distribution by more than 500 km south.

Drymobius rhombifer – Despite being widely distributed in Amazonia (Rivas et al. 2012), this diurnal snake (Fig. 6c) is rarely recorded, apparently due to low densities throughout its range (Stafford and Castro 2010). Our record from Serra da Mocidade is the second known occurrence for the Roraima state, ca. 200 km from the first record (O’Shea and Stimson 1993). Another specimen was collected by one of us (VTC) on the Brazilian Guiana Shield highlands region in a previous expedition to the Neblina mountain range (00°40’N, 65°56’W), in Amazonas state.

Micrurus remotus – The holotype of this small monadal coral snake is from the Guiana Shield highlands region [Cerro de la Neblina (Roze 1987)]. Additional specimens have been recorded in this region and in southern Amazonia (Roze 1987, Bernarde et al. 2011, Bernarde and Gomes 2012). Given the great geographical distance and environmental dissimilarity between these two localities, and the overall difficulty in species delimitation due to high intraspecific polymorphism in the species group (Feitosa et al. 2015), a taxonomic revision is required to clarify their status. The specimen from Serra da Mocidade (Fig. 7b) is one of the few documented for the Roraima state (see plate 172 in Campbell and Lamar 2004) and differs slightly in the body colour from patterns described in the literature: it has two light spots on the rostrum, greater extent of white on the head and the white ring after the black nuchal collar is almost imperceptible.

Platemys platycephala melanonota – *Platemys platycephala* (Schneider, 1792) is a solitary and nocturnal chelid, which inhabits shallow temporary pools within Amazonian

lowland rainforests (Vogt 2008). Several years after their original description, a melanistic colour form was described as a distinct subspecies, possessing a large amount of black pigmentation in the carapace and head and some differences in head scalation in comparison to nominal subspecies (Mendes-Pinto et al. 2012). As this subspecies is more rarely recorded, the total geographical distribution is unknown, but there are records from Peru, Ecuador and Brazil (Mendes-Pinto et al. 2012, van Dijk et al. 2014), which suggest a wide distribution and low abundances throughout the range. The specimen from Serra da Mocidade (Fig. 7g) is the first record of the subspecies in the Roraima state, more than 900 km from the nearest known location (Mendes-Pinto et al. 2012).

Discussion

Several remarkable herpetofaunal records were found during the first large biological expedition conducted at the Serra da Mocidade mountain range. Based on our results, it is evident that the herpetofauna inhabitant of this mountain range has a greater biotic affinity with lowlands from the Amazon region, but some elements typical of the uplands from Guiana Shield highlands region occurs above 900 m asl.

However, the local species diversity is certainly underestimated in our results, especially at higher altitudinal zones, as this mountain range has an extensive unexplored area of upland forests, which may harbour populations of undescribed amphibians and reptiles typical of the Guiana Shield highlands region. Additionally, the sampling period covered the dry season in the region. This, linked to the fact that the strong El Niño event of 2015–2016 produced higher temperatures throughout the year (Varotsos et al. 2016), may have potentially limited encounter rates of some herpetological groups.

Integrative approaches are increasingly being used in biological inventories (e.g., Vieites et al. 2009, Jansen et al. 2011, Paz and Crawford 2012, Moraes et al. 2016), and are based on several proposed methods (e.g., Padial et al. 2010). The integrative identification approach used here to reveal the species diversity at Serra da Mocidade illustrates the relevance of using different evolutionary data sources to identify taxa from remote and unexplored Amazonian areas. Replication of this method for future Amazonian biodiversity inventories will certainly contribute to a more precise evaluation of species diversity and distribution, as well as the origin, diversification drivers and conservation status of such species.

With the molecular approach, based on reciprocal monophyly, high nodal support and genetic distances of mtDNA, we detected additional samples and extended the distribution of known lineages (*A. apiau*, *R. martyi*, and *T. oriximinensis*, with genetic distances less than 2%), discovered putative divergent lineages of known species (*H. aff. taylori*, *P. aff. vilarsi*, *V. ritae*, and *D. parviceps*, with genetic distances between 3–6%), as well as candidate new species (*Stefania* sp., *Epicrionops* sp. and *Brasilotyphlus* sp., with genetic distances between 10–17%). The taxonomic status of the putative new species detected in this study needs to be confirmed using a broader and more

detailed analyses of data sources, which may increase the known species diversity at Serra da Mocidade.

Several attempts have been made to define biogeographical sub-regions within Guiana Shield highlands, mainly based on assemblage similarities among isolated mountain ranges (e.g., Mayr and Phelps 1967, Huber 1988a, 1995, McDiarmid and Donnelly 2005). Despite differences in their overall boundaries, all such studies seem to agree on the existence of two main sub-biogeographical regions with high similarity in species composition: the western and eastern Guiana Shield highlands (Mayr and Phelps 1967). This distinction is also observed in the geological origin of regions, as each sub-region is distinct in age and landscape history (Santos et al. 2003). Western Guiana Shield highlands may have experienced a greater faunal exchange during Pleistocene glacial events because the mountains involved lie on a higher basement matrix than Eastern Guiana Shield highlands (Mayr and Phelps 1967, Cook 1974, Cracraft 1985, Kok et al. 2017). At Serra da Mocidade, the herpetofauna composition at highest altitudes was predominantly composed of widespread and altitudinal generalists, with greater similarity to the western sub-region. Occurrence of upland species known to occur in other Guiana Shield highlands mountain ranges (e.g., *A. apiau*, *A. riveroi*) and species closely related to other Guiana Shield highlands endemics (e.g., *Stefania* sp., *Epicrionops* sp.) reinforce the postulated recent high connectivity between highland assemblages of distinct mountain ranges in this region (Kok et al. 2012, Salerno et al. 2012, 2015). Increased gene flow may have occurred during Pleistocene glacial events (Noonan and Gaucher 2005, Lötters et al. 2010, Kok et al. 2012) which made the lowland matrix more permeable, leading to recent events of colonization and speciation. Phylogeographical studies and more extensive sampling are required to address these possibilities more explicitly.

Some species that are often altitudinal-generalists were only found on the Serra da Mocidade at altitudes higher than 900 m (e.g., *D. minutus*, *D. parviceps*, *B. xerophylla*, *A. punctatus*, *B. b. bilineatus*). The Serra da Mocidade mountain range has a complex hydrologic mosaic, with streams that vary in their basin origins and amounts of dissolved sediments (Barbosa 2005, Ministério do Meio Ambiente 2016), which generates high habitat heterogeneity. The absence of some altitudinal generalists at lower altitudes (<900 m asl) may be related to a balance between physiological tolerance and habitat conditions, or to sampling bias. Long-term sampling would be necessary to fully elucidate species distribution patterns along these altitudinal gradients.

The results from this short-term multidisciplinary expedition (see other scientific results in Bastos et al. 2016, Neto et al. 2016, Dantas and Hamada 2017, Fraga et al. 2017, Lourenço 2017, Raimundi et al. 2017, and the documentary associated with the expedition at <http://www.grifafilmes.com/en/new-species>) highlight our poor knowledge of the Brazilian Guiana Shield highlands region. Our study can be used as primary data source for future biodiversity, biogeography, and conservation assessments that consider Guiana Shield highlands on a larger scale. We encourage additional initiatives to enable costly and logistically difficult expeditions to remote Amazonian areas, to fill-in basic knowledge gaps of biological diversity in remote areas, and investigate the processes that led to the currently observed biodiversity patterns.

Acknowledgments

The Expedition “Biodiversity of the Serra da Mocidade” was the result of a collaboration between the Instituto Nacional de Pesquisas da Amazônia (INPA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Comando Militar da Amazônia (CMA), and Grifa Filmes. We are grateful to R. Ferreira for assistance and sharing of data regarding the conservation unit, T. Laranjeiras, H. Palo Jr., M. Amend and R. Melinski for contribution with landscape and specimen photographs, members of Thematic Laboratory of Molecular Biology (INPA) for help during sequencing process and A. Fouquet, P. Passos, P. Nunes, T. Mott, R. MacCulloch and O. Entiauspe for help in species identification. Adrian Barnett helped with the English. Specimens were collected under the permission issued by ICMBio (processes 52206-1 and 44832-1). RF, LJCLM and APA thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Amazonas (FAPEAM) for scholarship. FPW thanks financial support from CNPq (475559/2013-4), FAPEAM (062.00665/2015), Partnerships for Enhanced Engagement in Research from the U.S. National Academy of Sciences and U.S. Agency of International Development (PEER NAS/USAID PGA-2000005316), and L’Oréal-Unesco For Women in Science Program.

References

- Acosta-Galvis A (1999) Distribución, variación y estatus taxonómico de las poblaciones del complejo *Rana palmipes* (Amphibia: Anura: Ranidae) en Colombia. *Revista de la Academia Colombiana de Ciencias* 23: 215–224.
- Aleixo A, Rossetti DF (2007) Avian gene trees, landscape evolution, and geology: towards a modern synthesis of Amazonian historical biogeography? *Journal of Ornithology* 148: 443–453. <https://doi.org/10.1007/s10336-007-0168-7>
- Alvares CA, Stape, JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Koppen’s climate classification map for Brazil. *Meteorologische Zeitschrift* 22: 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Aubrecht R, Barrio-Amorós CL, Breure ASH, Brewer-Carías C, Derka T, Fuentes-Ramos OA, Gregor M, Kodada J, Kováčik L, Lánzos T, Lee NM, Liščák P, Schlögl J, Šmída B, Vlček L (2012) Venezuelan tepuis: their caves and biota. *Acta Geologica Slovaca, Monograph. Comenius University, Bratislava*, 168 pp.
- Ávila-Pires TCS (1995) Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen* 299: 1–706.
- Ávila-Pires TCS, Hoogmoed MS, Rocha WA (2010) Notes on the vertebrates of northern Pará, Brazil: a forgotten part of the Guiana Region, I. Herpetofauna. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* 5: 13–112.
- Ayarzagüena J (1983) Una nueva especie de *Dischidodactylus* Lynch (Amphibia, Leptodactylidae) en la cumbre del Tepui Marahuaca, Territorio Federal Amazonas, Venezuela. *Memoria de la Sociedad de Ciencias Naturales La Salle* 43: 215–220.

- Ayarzagüena J, Señaris JC (1993) Dos nuevas especies de *Hyla* (Anura, Hylidae) para las cumbreras tepuyanas del Estado Amazonas, Venezuela. *Memoria de la Sociedad de Ciencias Naturales La Salle* 53: 127–146.
- Ayarzagüena J, Señaris JC, Gorzula S (1992) El grupo *Osteocephalus rodriguezi* de las tierras altas de la Guayana venezolana: descripción de cinco nuevas especies. *Memoria de la Sociedad de Ciencias Naturales La Salle* 52: 113–142.
- Barbosa RI (2005) Ecopaisagens do Parque Nacional “Serra da Mocidade” (primeira aproximação): Ministério de Ciência e Tecnologia, Instituto Nacional de Pesquisas da Amazônia. Boa Vista, Roraima.
- Barrio-Amorós C, Molina C (2006) A new *Eleutherodactylus* (Anura, Brachycephalidae) from the Venezuelan Guayana, and redescription of *Eleutherodactylus vilarsi* (Melin). *Zootaxa* 1302: 1–20. <https://doi.org/10.11646/zootaxa.1302.1.1>
- Barrio-Amorós CL, Brewer-Carias C (2008) Herpetological results of the 2002 expedition to Sarisariñama, a tepui in Venezuelan Guayana, with the description of five new species. *Zootaxa* 1942: 1–68.
- Barrio-Amorós CL, Duellman WE (2009) Herpetofauna de la Sierra de Lema, Estado Bolívar, Venezuela. *Boletín RAP de Evaluación Ecológica* 55: 137–155.
- Bastos CJP, Sierra AM, Zartman CE (2016) Three new species of *Cheilolejeunea* (Spruce) Steph. (Marchantiophyta, Lejeuneaceae) from northern Brazil. *Phytotaxa* 277: 36–46. <https://doi.org/10.11646/phytotaxa.277.1.3>
- Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayes EW (2014) GenBank. *Nucleic Acids Research* 41: D36–D42. <https://doi.org/10.1093/nar/gkt1030>
- Bergmann PJ, Russell AP (2007) Systematics and biogeography of the widespread Neotropical gekkonid genus *Thecadactylus* (Squamata), with the description of a new cryptic species. *Zoological Journal of the Linnean Society* 149: 339–370. <https://doi.org/10.1111/zoj.2007.149.issue-3>
- Bernarde PS, Gomes JO (2012) Serpentes peçonhentas e ofidismo em Cruzeiro do Sul, Alto Juruá, Estado do Acre, Brasil. *Acta Amazonica* 42: 65–72. <https://doi.org/10.1590/S0044-59672012000100008>
- Bernarde PS, Machado RA, Turci LCB (2011) Herpetofauna da área do Igarapé Esperança na Reserva Extrativista Riozinho da Liberdade, Acre–Brasil. *Biota Neotropica* 11: 117–144. <https://doi.org/10.1590/S1676-06032011000300010>
- Bonaccorso E, Guayasamin JM (2013) On the origin of Pantepui montane biotas: A perspective based on the phylogeny of *Aulacorhynchus* toucanets. *PLoS One* 8: 1–10. <https://doi.org/10.1371/journal.pone.0067321>
- Boulenger GA (1895a) Description of a new batrachian (*Oreophryne quelchii*) discovered by Messrs. J.J. Quelch and F. McConnell on the summit of Mount Roraima. *Annals and Magazine of Natural History, Series 6* 15: 521–522.
- Boulenger GA (1895b) Correction to p. 521 (“Annals”, June 1895). *Annals and Magazine of Natural History, Series 6* 16: 125.
- Boulenger GA (1900) Batrachians. In: Lankester ER (Ed.) Report on a collection made by Messrs. F.V. McConnell and J.J. Quelch at Mount Roraima in British Guiana. *Linnean Society of London, Transactions, Series 2, Zoology* 8: 55–56. <https://doi.org/10.1111/j.1096-3642.1900.tb00312.x>

- Boulenger EG (1911) On a new tree-frog from Trinidad, living in the Society's gardens. Proceedings of the Zoological Society of London: 1082–1083.
- Burt CE, Burt MD (1931) South American lizards in the collection of the American Museum of Natural History. Bulletin of the American Museum of Natural History 61: 227–395.
- Campbell HW, Christman SP (1982) Field techniques for herpetofaunal community analyses. In: Scott Jr NJ (Ed.) Herpetological communities: a Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League. Fish Wildlife Service, USA, Washington, 193–200.
- Campbell JA, Lamar WW (2004) The Venomous Reptiles of the Western Hemisphere. 2 Volumes. Cornell University Press, Ithaca, 976 pp.
- Caramaschi U, Niemeyer H (2005) Geographic distribution: *Stefania tamacuvarina*. Herpetological Review 36: 77.
- Cardoso AJ, Haddad CFB (1984) Variabilidade acústica em diferentes populações e interações agressivas de *Hyla minuta* (Amphibia, Anura). Ciência e Cultura 36: 1393–1399.
- Carvalho VT, MacCulloch RD, Bonora L, Vogt RC (2010) New Species of *Stefania* (Anura: Cryptobatrachidae) from Northern Amazonas, Brazil. Journal of Herpetology 44: 229–235. <https://doi.org/10.1670/07-169.1>
- Castroviejo-Fisher S, Vilà C, Ayarzagüena J, Blanc M, Ernst R (2011) Species diversity of *Hyalinobatrachium* glassfrogs (Amphibia: Centrolenidae) from the Guiana Shield, with the description of two new species. Zootaxa 3132: 1–55.
- Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45–67. <https://doi.org/10.1890/13-0133.1>
- Cisneros-Heredia DF (2013) *Centrolene ritae* Lutz is a senior synonym of *Cochranella oyampiensis* Lescure and *Cochranella ametarsia* Flores (Anura: Centrolenidae). Avances en Ciencias e Ingenierías. Sección B. Quito 5: B1–B4. <https://doi.org/10.18272/aci.v5i2.132>
- Cook RE (1974) Origin of the highland avifauna of southern Venezuela. Systematic Biology 23: 257–264. <https://doi.org/10.1093/sysbio/23.2.257>
- Cole CJ, Townsend CR, Reynolds RP, Macculloch RD, Lathrop A (2013) Amphibians and reptiles of Guyana, South America: illustrated keys, annotated species accounts, and a biogeographic synopsis. Proceedings of the Biological Society of Washington 125: 317–578. <http://doi.org/10.2988/0006-324X-125.4.317>
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Cracraft J (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithological Monographs 36: 49–84. <https://doi.org/10.2307/40168278>
- Dantas GPS, Hamada N (2017) Three new species of *Nilothauma* Kieffer (Diptera: Chironomidae) from Brazil. Zootaxa 4282: 350–360. <https://doi.org/10.11646/zootaxa.4282.2.8>
- Désamoré A, Vanderpoorten A, Laenen B, Gradstein G, Kok PJR (2014) Biogeography of the Lost World (Pantepui region, northeastern South America): insights from bryophytes. Phytotaxa 9: 254–265. <https://doi.org/10.11646/phytotaxa.9.1.14>

- Dewynter M, Marty C, Courtois EA, Blanc M, Fouquet A (2016a) L'identification des rainettes du genre *Dendropsophus* (Hylidae: Dendropsophinae) en Guyane. Les cahiers de la fondation Biotope 6: 1–15.
- Dewynter M, Marty C, Courtois EA, Blanc M, Gaucher P, Martinez Q, Fouquet A (2016b) L'identification des rainettes des genres *Osteocephalus* et *Trachycephalus* (Hylidae: Lophophyllinae) en Guyane. Les cahiers de la fondation Biotope 7: 1–16.
- Dewynter M, Marty C, Blanc M (2016c) L'identification des caïmans de Guyane (*Caiman*, *Melanosuchus* & *Paleosuchus*). Les cahiers de la fondation Biotope 2: 1–10.
- Dewynter M, Marty C, Courtois EA, Blanc M, Fouquet A (2016d) L'identification des rainettes du genre *Hypsiboas* (Hylidae: Cophomantinae) en Guyane. Les cahiers de la fondation Biotope 9: 1–20.
- Dixon JR, Wiest JA, Cei JM (1993) Revision of the Neotropical snake genus *Chironius* Fitzinger (Serpentes, Colubridae). Museo Regionale Di Scienze Naturali Monografie 13: 1–280.
- Donnelly MA, Myers CW (1991) Herpetological results of the 1990 Venezuelan Expedition to the summit of Cerro Guaiquinima, with new tepui reptiles. American Museum Novitates 3017: 1–54.
- Donnelly MA, McDiarmid RW, Myers CW (1992) A new lizard of the genus *Arthrosaura* (Teiidae) from Southern Venezuela. Proceedings of the Biological Society of Washington 105: 821–833.
- dos Santos SP, Ibáñez R, Ron SR (2015) Systematics of the *Rhinella margaritifera* complex (Anura: Bufonidae) from western Ecuador and Panama with insights in the biogeography of *Rhinella alata*. ZooKeys 501: 109–145. <https://doi.org/10.3897/zookeys.501.8604>
- Duellmann WE (1979) The South American Herpetofauna: Its Origin, Evolution, and Dispersal. Kansas University Press, Kansas, 504 pp.
- Duellman WE (1999) Distribution Patterns of Amphibians in South America. In: Duellman WE (Ed.) Patterns of Distribution of Amphibians. The Johns Hopkins University Press, Baltimore and London, 255–328.
- Duellman WE (2015) Marsupial Frogs. *Gastrotheca* & Allied Genera. The Johns Hopkins University Press, Baltimore, 432 pp.
- Duellman WE, Hoogmoed MS (1984) The taxonomy and phylogenetic relationships of the hyloid frog genus *Stefania*. Miscellaneous Publication, Museum of Natural History 75: 1–39. <https://doi.org/10.5962/bhl.title.16293>
- Faivovich J, Haddad CFB, Garcia PCA, Frost DR, Campbell JA, Wheeler WC (2005) Systematic review of the frog family Hylidae, with special reference to Hyalinae: a phylogenetic analyses and taxonomic revision. Bulletin of the American Museum of Natural History 294: 1–240. [https://doi.org/10.1206/0003-0090\(2005\)294\[0001:SROTFF\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2005)294[0001:SROTFF]2.0.CO;2)
- Feitosa DT, Silva NJ Jr, Pires MG, Zaher H, Prudente ALC (2015) A new species of monadal coral snake of the genus *Micrurus* (Serpentes, Elapidae) from western Amazon. Zootaxa 3974: 538–554. <https://doi.org/10.11646/zootaxa.3974.4.5>
- Ferreira RB, Santos IA, Fujisaki ET, Dipogenes A, Azevedo RB, Souza JM, Schutz R, Flores AS, Grigio O, Perdiz R, Azarak P, Machado V, Plaskiewicz A, Almeida R (2014) Relatório Técnico: Expedição Terra Incógnita. Instituto Chico Mendes de Conservação da Biodiversidade.
- Fouquet A, Vences M, Salducci MD, Meyer A, Marty C, Blanc M, Gilles A (2007a) Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax*

- ruber* and *Rhinella margaritifera* species groups. Molecular Phylogenetics and Evolution 43: 567–582. <https://doi.org/10.1016/j.ympev.2006.12.006>
- Fouquet A, Gaucher P, Blanc M, Vélez-Rodríguez CM (2007b) Description of two new species of *Rhinella* (Anura: Bufonidae) from the lowlands of the Guiana Shield. Zootaxa 1663: 17–32.
- Fouquet A, Gilles A, Vences M, Marty C (2007c) Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. PLoS ONE 2: e1109. <https://doi.org/10.1371/journal.pone.0001109>
- Fouquet A, Noonan BP, Blanc M, Orrico VGD (2011) Phylogenetic position of *Dendropsophus gaucheri* (Lescure and Marty 2000) highlights the need for an in-depth investigation of the phylogenetic relationships of *Dendropsophus* (Anura: Hylidae). Zootaxa 3035: 59–67.
- Fouquet A, Cassini C, Haddad CFB, Pech N, Rodrigues MT (2014) Species delimitation, patterns of diversification and historical biogeography of a Neotropical frog genus *Adenomera* (Anura, Leptodactylidae). Journal of Biogeography 41: 855–870. <https://doi.org/10.1111/jbi.12250>
- Fouquet A, Souza SM, Nunes PMS, Kok PJR, Curcio FF, de Carvalho CM, Grant T, Rodrigues MT (2015a) Two new endangered species of *Anomaloglossus* (Anura: Aromobatidae) from Roraima state, northern Brazil. Zootaxa 3926: 191–210. <https://doi.org/10.11646/zootaxa.3926.2.2>
- Fouquet A, Orrico VGD, Ernst R, Blanc M, Martinez Q, Vacher JP, Rodrigues MT, Ouboter PE, Jairam R, Ron SR (2015b) A new *Dendropsophus* Fitzinger, 1843 (Anura: Hylidae) of the *parviceps* group from the lowlands of the Guiana Shield. Zootaxa 4052: 39–64. <https://doi.org/10.11646/zootaxa.4052.1.2>
- Fraga R, Almeida AP, Moraes LJCL, Gordo M, Pirani R, Zamora RR, Carvalho VT, Passos P, Werneck F (2017) Narrow endemism or insufficient sampling? Geographical range extension and morphological variation of the poorly known *Atractus riveroi* Roze, 1961 (Serpentes: Dipsadidae). Herpetological Review 48: 281–284.
- Frost DR (2017) Amphibian Species of the World: an online reference. Version 6.0. <http://research.amnh.org/herpetology/amphibia/index.html>
- Fuentes O, Barrio-Amorós CL (2004) A new *Eleutherodactylus* (Anura, Leptodactylidae) from Marahuaka tepui, Amazonas, Venezuela. Revista Colombiana de Ciencias 28: 285–290.
- Gehara M, Crawford AJ, Orrico VGD, Rodríguez A, Lötters S, Fouquet A, Baldo D, Barrientos LS, Brusquetti F, Castroviejo-Fisher S, de la Riva I, Ernst R, Faivovich J, Urrutia GG, Glaw F, Guayasamin J, Hölting M, Jansen M, Kok PJR, Kwet A, Lingnau R, Lyra M, Moravec J, Padial JM, Pombal Jr J, Rojas-Runjaic FJM, Schulze A, Señaris JC, Solé M, Rodrigues MT, Twomey E, Haddad CFB, Vences M, Köhler J (2014) High levels of diversity uncovered in a widespread nominal taxon: continental phylogeography of the Neotropical tree frog *Dendropsophus minutus*. PLoS ONE 9: 1–12. <https://doi.org/10.1371/journal.pone.0103958>
- Geurgas SR, Rodrigues MT (2010) The hidden diversity of *Coleodactylus amazonicus* (Sphaerodactylidae, Gekkota) revealed by molecular data. Molecular Phylogenetics and Evolution 54: 583–593. <https://doi.org/10.1016/j.ympev.2009.10.004>
- Gibbs AK, Barron CN (1993) The geology of the Guiana Shield. Oxford University Press, New York, 246 pp.

- Gordo M, Azarak P, Carvalho VT (2014) Relatório de Herpetologia. Diagnóstico ambiental do Parque Nacional Serra da Mocidade e Estação Ecológica Niquiá. Instituto Chico Mendes de Conservação da Biodiversidade.
- Gorzula S (1992) La herpetofauna del macizo del Chimantá. In: Huber O (Ed) Chimantá. Escudo de Guayana, Venezuela. Un Ensayo Ecológico Tepuyano. Oscar Todtmann Editores, Caracas, 267–280.
- Gorzula S, Señaris JC (1999) Contribution to the herpetofauna of the Venezuelan Guayana. I. a data base. *Scientia Guianae* 8: 267.
- Guarnizo CE, Paz A, Muñoz-Ortiz S, Flechas SV, Méndez-Narváes J, Crawford AJ (2016) DNA barcoding survey of anurans across the Eastern Cordillera of Colombia and the impact of the Andes on cryptic diversity. *PLoS ONE* 10: 1–20. <https://doi.org/10.1371/journal.pone.0127312>
- Guayasamin JM, Cisneros-Heredia DF, Castroviejo-Fisher S (2008) Taxonomic identity of *Cochranella petersi* Goin, 1961 and *Centrolenella ametarsia* Flores, 1987. *Zootaxa* 1815: 25–34.
- Guayasamin JM, Castroviejo-Fisher S, Trueb L, Ayarzagüena J, Rada M, Vilà C (2009) Phylogenetic systematics of Glassfrogs (Amphibia: Centrolenidae) and their sister taxon *Allophryne ruthveni*. *Zootaxa* 2100: 1–97.
- Harvey MB (2008) New and poorly known *Dipsas* (Serpentes: Colubridae) from northern South America. *Herpetologica* 64: 422–451. <https://doi.org/10.1655/07-068R1.1>
- Haslett JR (1997) Mountain ecology: organism responses to environmental change, an introduction. *Global Ecology and Biogeography* 6: 3–6. <https://doi.org/10.2307/2997522>
- Hawkins MA, Sites JW Jr, Noonan BP (2007) *Dendropsophus minutus* (Anura: Hylidae) of the Guiana Shield: using DNA barcodes to assess identity and diversity. *Zootaxa* 1540: 61–7.
- Hedges SB, Conn CE (2012) A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). *Zootaxa* 3288: 1–244.
- Hershkovitz P (1969) The recent mammals of the Neotropical region: a zoogeographical and ecological review. *Quarterly Review of Biology* 44: 1–70. <https://doi.org/10.1086/405975>
- Heyer WR (1970) Studies on the frogs of the genus *Leptodactylus* (Amphibia: Leptodactylidae): VI. Biosystematics of the *melanonotus* group. *Contributions in Science, Museum of Natural History of Los Angeles* 191: 1–48.
- Heyer WR (1994) Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* 546: 1–124. <https://doi.org/10.5479/si.00810282.546.i>
- Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS (1994) Measuring and monitoring biological diversity: Standard methods for amphibians. Washington: Smithsonian Institution Press, Washington, 384 pp.
- Hollis JL (2006) Phylogenetics of the genus *Chironius* Fitzinger 1826 (Serpentes, Colubridae) based on morphology. *Herpetologica* 62: 435–452. [https://doi.org/10.1655/0018-0831\(2006\)62\[435:POTGCF\]2.0.CO;2](https://doi.org/10.1655/0018-0831(2006)62[435:POTGCF]2.0.CO;2)
- Hoogmoed MS (1979) The herpetofauna of the Guiana region. In: Duellman WE (Ed.) *The South American Herpetofauna: its origin, evolution and dispersal*. Kansas University Press, Kansas, 241–279.

- Hoogmoed MS (1990) Resurrection of *Hyla wavrini* Parker (Amphibia: Anura: Hylidae), a gladiator frog from northern South America. *Zoologische Mededelingen* 64: 71–93.
- Hollowell T, Reynolds RP (2005) Checklist of the terrestrial vertebrates of the Guiana Shield. *Bulletin of the Biological Society of Washington, USA*, 98 pp.
- Hoorn C, Mosbrugger V, Mulch A, Antonelli A (2013) Biodiversity from mountain building. *Nature Geoscience* 6: 154. <https://doi.org/10.1038/ngeo1742>
- Hoorn MC, Wesselingh FP (2010) Amazonia, Landscape and Species Evolution: a look into the past. Wiley-Blackwell, Oxford, 464 pp.
- Huber O (1988a) Vegetacion y flora de Pantepui, region Guayana. *Acta Botanica Brasilica* 1: 41–52. <https://doi.org/10.1590/S0102-33061987000300005>
- Huber O (1988b) Guiana Shield highlands versus Guayana lowlands, a reappraisal. *Taxon* 37: 595–614. <https://doi.org/10.2307/1221102>
- Huber O (1995) Geographical and physical features. In: Berry PE, Holst BK, Yatskievych K (Eds) *Flora of the Venezuelan Guayana*, I. Introduction. Missouri Botanical Garden Press, St. Louis, 1–61.
- IBAMA (2014) LT 500 Kv Manaus–Boa Vista e subestações associadas. Estudo de Impacto Ambiental - EIA.
- ICMBio (2014) Parque Nacional do Viruá: Plano de Manejo. Boa Vista, RR, Brazil. <http://icmbio.gov.br/portal/unidadesdeconservacao/biomas-brasileiros>
- INPA (2016) Inpa realiza expedição para a Serra da Mocidade em parceria com o CMA, Ufam e ICMBio. <http://portal.inpa.gov.br/index.php/ultimas-noticias/2375-expedicao-serra-mocidade2>
- International Union for Conservation of Nature (2016) The IUCN Red List of Threatened Species. <http://www.iucnredlist.org/>
- Jansen M, Bloch R, Schulze A, Pfenninger M (2011) Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. *Zoologica Scripta* 40: 567–83. <https://doi.org/10.1111/j.1463-6409.2011.00498.x>
- Jungfer KH, Faivovich J, Padial JM, Castroviejo-Fisher S, Lyra M, Berneck BM, Iglesias P, Kok PJR, MacCulloch RD, Rodrigues MT, Verdade VK, Torres-Gastello CP, Chaparro JC, Valdujo PH, Reichle S, Moravec J, Gvozdik V, Gagliardi-Urruti G, Ernst R, de la Riva I, Means DB, Lima AP, Señaris JC, Wheelers W, Haddad CFB (2013) Haddad Systematics of spiny-backed treefrogs (Hylidae: *Osteocephalus*): an Amazonian puzzle. *Zoologica Scripta* 42: 351–80. <https://doi.org/10.1111/zsc.12015>
- Karin BR, Metallinou M, Weinell JL, Jackman TR, Bauer AM (2016) Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): an out-of-Asia diversification. *Molecular Phylogenetics and Evolution* 102, 220–232. <https://doi.org/10.1016/j.ympev.2016.05.033>
- Köhler J, Jansen M, Rodríguez A, Kok PJR, Toledo LF, Emmrich M, Glaw F, Haddad CFB, Rödel MO, Vences M (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. *Zootaxa* 4251:1–124. <https://doi.org/10.11646/zootaxa.4251.1.1>
- Körner C, Jetz W, Paulsen J, Payne D, Rudmann-Maurer K, Spehn EM (2017) A global inventory of mountains for bio-geographical applications. *Alpine Botany* 127: 1–15. <https://doi.org/10.1007/s00035-016-0182-6>

- Kok PJR (2008) A new highland species of *Arthrosaura* Boulenger, 1885 (Squamata: Gymnophthalmidae) from Maringma tepui on the border of Guyana and Brazil. *Zootaxa* 1909: 1–15.
- Kok PJR (2009a) A new species of *Oreophrynella* (Anura: Bufonidae) from the Pantepui region of Guyana, with notes on *O. macconnelli* Boulenger, 1900. *Zootaxa* 2071: 35–49.
- Kok PJR (2009b) Lizard in the clouds: a new highland genus and species of Gymnophthalmidae (Reptilia: Squamata) from Maringma tepui, western Guyana. *Zootaxa* 1992: 53–67.
- Kok PJR (2010) A new species of *Chironius* Fitzinger, 1826 (Squamata: Colubridae) from the Pantepui region, northeastern South America. *Zootaxa* 2611: 31–44.
- Kok PJR (2013a) Islands in the sky: species diversity, evolutionary history, and patterns of endemism of the Pantepui Herpetofauna. PhD Thesis, Leiden University, The Netherlands.
- Kok PJR (2013b) Two new charismatic *Pristimantis* species (Anura: Craugastoridae) from the tepuis of “The Lost World” (Pantepui region, South America). *European Journal of Taxonomy* 60: 1–24. <https://doi.org/10.5852/ejt.2013.60>
- Kok PJR (2015) A new species of the Pantepui endemic genus *Riolama* (Squamata: Gymnophthalmidae) from the summit of Murisipán-tepui, with the erection of a new gymnophthalmid subfamily. *Zoological Journal of the Linnean Society* 174: 500–518. <https://doi.org/10.1111/zoj.12241>
- Kok PJR, Castroviejo-Fisher S (2008) Glassfrogs (Anura: Centrolenidae) of Kaiteur National Park, Guyana, with notes on the distribution and taxonomy of some species of the family in the Guiana Shield. *Zootaxa* 1680: 25–53.
- Kok PJR, Rivas GA (2011) A new species of *Anadia* (Reptilia, Squamata) from the Venezuelan “Lost World”, northern South America. *European Journal of Taxonomy* 3: 1–18. <https://doi.org/10.5852/ejt.2011.3>
- Kok PJR, MacCulloch RD, Lathrop A, Willaert B, Bossuyt F (2010) A new species of *Anomaloglossus* (Anura: Aromobatidae) from the Pakaraima Mountains of Guyana. *Zootaxa* 2660: 18–32.
- Kok PJR, Means DB, Bossuyt F (2011) A new highland species of *Pristimantis* Jiménez de la Espada, 1871 (Anura: Strabomantidae) from the Pantepui region, northern South America. *Zootaxa* 2934: 1–19.
- Kok PJR, MacCulloch RD, Means DB, Roelants K, Van Bocxlaer I, Bossuyt F (2012) Low genetic diversity in tepui summit vertebrates. *Current Biology* 22: 589–590. <https://doi.org/10.1016/j.cub.2012.06.034>
- Kok PJR, Ratz S, Tegelaar M, Aubret F, Means DB (2015) Out of taxonomic limbo: a name for the species of *Tepuihyla* (Anura: Hylidae) from the Chimantá Massif, Pantepui region, northern South America. *Salamandra* 51: 283–314.
- Kok PJR, Russo VG, Ratz S, Aubret F (2016) On the distribution and conservation of two “Lost World” tepui summit endemic frogs, *Stefania ginesi* Rivero, 1968 and *S. satelles* Señaris, Ayarzagüena, and Gorzula, 1997. *Amphibian and Reptile Conservation* 10: 5–12.
- Kok PJR, Russo VG, Ratz S, Means DB, MacCulloch RD, Lathrop A, Aubret F, Bossuyt F (2017) Evolution in the South American ‘Lost World’: insights from multilocus phylogeography of stefanias (Anura, Hemiphractidae, *Stefania*). *Journal of Biogeography* 44: 170–181. <https://doi.org/10.1111/jbi.12860>
- La Marca E, Azevedo-Ramos C, Coloma LA, Ron S, Hardy J (2010) *Lithobates palmipes*. The IUCN Red List of Threatened Species. <http://www.iucnredlist.org/details/58689/0>

- Lancini AR (1968) El género *Euspondylus* (Sauria: Teiidae) en Venezuela. Publicaciones Ocasionales del Museum de las Ciencias Naturales, Caracas 12: 1–8.
- Lavilla EO, Caramaschi U, Langone JA, Pombal Jr JP, Sá RO (2013) The identity of *Rana margaritifera* Laurenti, 1768 (Anura, Bufonidae). Zootaxa 3646: 251–264. <https://doi.org/10.11646/zootaxa.3646.3.4>
- Lavilla EO, Langone JA, Caramaschi U, Pombal Jr. JP, de Sá RO (2017) Comments on the neotype of *Rana margaritifera* Laurenti, 1768 (Anura, Bufonidae). Zootaxa 4286: 113–114. <https://doi.org/10.11646/zootaxa.4286.1.5>
- Lescure J, Marty C (2000) Atlas des Amphibiens de Guyane. Collections Patrimoines Naturels, Paris.
- Lima AC, Prudente ALC (2009) Morphological variation and systematics of *Dipsas catesbyi* (Sentzen, 1796) and *Dipsas pavonina* Schlegel, 1837 (Serpentes: Dipsadinae). Zootaxa 2203: 31–48.
- Lomolino MARK (2001) Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10: 3–13. <https://doi.org/10.1046/j.1466-822x.2001.00229.x>
- Lötters S, van der Meijden A, Rödder D, Koester TE, Kraus T, La Marca E, Haddad CFB, Veith M (2010) Reinforcing and expanding the predictions of the disturbance vicariance hypothesis in Amazonian harlequin frogs: A molecular phylogenetic and climate envelope modelling approach. Biodiversity Conservation 19: 2125–2146. <https://doi.org/10.1007/s10531-010-9869-y>
- Lourenço WR (2017) Scorpions from Brazilian Amazonia, with a description of two new species from ‘Serra da Mocidade’ National Park in the State of Roraima (Scorpiones: Buthidae, Chactidae). Arachnida. Rivista Aracnologica Italiana 12: 2–17.
- Lutz B (1973) Brazilian Species of *Hyla*. University of Texas Press, Austin, 260 pp.
- MacCulloch RD, Lathrop A (2002) Exceptional diversity of *Stefania* (Anura: Hylidae) on Mount Ayanganna, Guyana: three new species and new distribution records. Herpetologica 57: 327–346. [https://doi.org/10.1655/0018-0831\(2002\)058\[0327:EDOSAH\]2.0.CO;2](https://doi.org/10.1655/0018-0831(2002)058[0327:EDOSAH]2.0.CO;2)
- MacCulloch RD, Lathrop A (2009) Herpetofauna of Mount Ayanganna, Guyana: Results of the Royal Ontario Museum Ayanganna Expedition 2000. Contributions in Science, Royal Ontario Museum 4: 1–35.
- MacCulloch RD, Reynolds B (2013) Baseline Inventory of Amphibians and Reptiles in the Vicinity of Kurupukari, Guyana. Check List 9: 1378–1382. <https://doi.org/10.15560/9.6.1378>
- MacCulloch RD, Lathrop A, Reynolds B, Señaris JC, Schneider G (2007) Herpetofauna of Mount Roraima, Guiana Shield Region, northeastern South America. Herpetological Review 38: 24–30.
- Maciel AO, Mott T, Hoogmoed MS (2009) A second species of *Brasilotyphlus* (Amphibia: Gymnophiona: Caeciliidae) from Brazilian Amazonia. Zootaxa 2226: 19–27.
- Maciel AO, Hoogmoed MS (2011) Taxonomy and distribution of caecilian amphibians (Gymnophiona) of Brazilian Amazonia, with a key to their identification. Zootaxa 2984: 1–53.
- Mägdefrau H, Mägdefrau K, Schlüter A (1991) Herpetologische Daten vom Guaiquinimatepui, Venezuela. Herpetofauna 13: 13–26.

- Magnusson WE, Campos Z (2010) Schneider's Smooth-fronted Caiman *Paleosuchus trigonatus*. In: Manolis SC, Stevenson C (Eds) Crocodiles. Status Survey and Conservation Action Plan. Third Edition. Crocodile Specialist Group, Darwin, Australia, 43–45.
- Mannion PD, Upchurch P, Benson RBJ, Goswami A (2014) The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution* 29: 42–50. <https://doi.org/10.1016/j.tree.2013.09.012>
- Martinelli G (2007) Mountain biodiversity in Brazil. *Brazilian Journal of Botany* 30: 587–597. <https://doi.org/10.1590/S0100-84042007000400005>
- Martins M (1998) The frogs of the Ilha de Maracá (Cap. 14). In: Milliken W, Ratter JA (Eds) Maracá: The biodiversity and environment of an Amazonian rainforest. John Wiley & Sons, Chichester, England, 285–306.
- Martins M, Oliveira ME (1988) Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6: 78–150.
- Mayr E, Phelps WH (1967) The origin of the bird fauna of the south Venezuelan highlands. *Bulletin of the American Museum of Natural History* 136: 273–327.
- McDiarmid RW, Paolillo A (1988) Herpetological collections: Cerro de la Neblina. In: Brewer-Carias C (Ed.) Cerro de la Neblina. Resultados de la expedición 1983–1987. FUDECI, Caracas, Venezuela, 667–670.
- McDiarmid RW, Donnelly MA (2005) The herpetofauna of the Guiana Shield highlands: amphibians and reptiles of the Lost World. In: Donnelly MA, Crother BI, Guyer C, Wake MH, White ME (Eds) Ecology and Evolution in the Tropics: A Herpetological Perspective. University of Chicago Press, Chicago, 461–560.
- Mendes-Pinto TJ, Souza SM, Vogt RC, Bernhard R (2012) First record of *Platemys platycephala melanonota* Ernst, 1984 (Reptilia, Testudines, Chelidae) for the Brazilian Amazon. *Revista de Ciências Ambientais* 5: 103–107. <https://doi.org/10.18316/264>
- Miralles A, Carranza S (2010) Systematics and biogeography of the Neotropical genus *Mabuya*, with special emphasis on the Amazonian skink *Mabuya nigropunctata* (Reptilia, Scincidae). *Molecular Phylogenetics and Evolution* 54: 857–869. <http://doi.org/10.1016/j.ympev.2009.10.016>
- Miralles A, Rivas G, Barrio-Amorós CL (2005) Taxonomy of the genus *Mabuya* (Reptilia, Squamata, Scincidae) in Venezuela. *Zoosystema* 27: 825–837.
- Ministério do Meio Ambiente (2016) Ministério do Meio Ambiente. Relatório Parametrizado - Unidade de Conservação: Parque Nacional Serra da Mocidade. Cadastro Nacional de Unidade de Conservação. <http://www.icmbio.gov.br>
- Moraes LJCL, Pavan D, Barros MC, Ribas CC (2016) The combined influence of riverine barriers and flooding gradients on biogeographical patterns for amphibians and squamates in south-eastern Amazonia. *Journal of Biogeography* 43: 2113–2124. doi: <http://doi.org/10.1111/jbi.12756>
- Morais AR, Batista VG, Gambale PG, Signorelli L, Bastos RP (2012) Acoustic communication in a Neotropical frog (*Dendropsophus minutus*): vocal repertoire, variability and individual discrimination. *Herpetological Journal* 22: 249–257.
- Morrone JJ (2014) Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782: 1–110. doi: <http://10.11646/zootaxa.3782.1.1>

- Motta AP, Castroviejo-Fisher S, Venegas PJ, Orrico VGD, Padial JM (2012) A new species of the *Dendropsophus parviceps* group from the western Amazon Basin (Amphibia: Anura: Hylidae). *Zootaxa* 3249: 18–30.
- Murphy JC, Jowers MJ (2013) Treerunners, cryptic lizards of the *Plica plica* group (Squamata, Sauria, Tropiduridae) of northern South America. *ZooKeys* 355: 49–77. <https://doi.org/10.3897/zookeys.355.5868>
- Myers CW (1997) Preliminary remarks on the summit herpetofauna of Auyantepui, eastern Venezuela. *Acta Terramaris* 10: 1–8.
- Myers CW, Williams EE, McDiarmid RW (1993) A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. *American Museum Novitates* 3070: 1–15.
- Myers CW, Donnelly MA (1996) A New Herpetofauna from Cerro Yaví, Venezuela: First results of the Robert G. Goelet American-Terramar Expedition to the Northwestern Tepuis. *American Museum Novitates* 3172: 1–56.
- Myers CW, Donnelly MA (1997) A tepui herpetofauna on a granitic mountain (Tamacuari) in the borderland between Venezuela and Brazil: Report from the Phipps Tapirapecó Expedition. *American Museum Novitates* 3213: 1–71.
- Myers CW, Donnelly MA (2001) Herpetofauna of the Yutajé-Corocoro Massif, Venezuela: second report from the Robert G. Goelet American Museum-Terramar Expedition to the Northwestern Tepuis. *Bulletin of the American Museum of Natural History* 261: 1–85.
- Myers CW, Donnelly MA (2008) The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet American Museum-Terramar Expedition. *Bulletin of the American Museum of Natural History* 308: 1–147. <https://doi.org/10.1206/308.1>
- Neto AMS, Aldrete ANG, Rafael JA (2016) A new species of *Timnewia* García Aldrete (Psocodea: 'Psocoptera': Ptiloneuridae), from Brazil. *Zootaxa* 4173: 489–495. <https://doi.org/10.11646/zootaxa.4173.5.6>
- Nogué S, Rull V, Vegas-Villarúbia T (2013) Elevational gradients in the neotropical table mountains: patterns of endemism and implications for conservation. *Diversity and Distributions* 19: 676–687. <https://doi.org/10.1111/ddi.12017>
- Nogué S, Rull V, Vegas-Villarúbia T (2009) Modeling biodiversity loss by global warming on Pantepui, northern South America: projected upward migration and potential habitat loss. *Climatic change* 94: 77–85. <https://doi.org/10.1007/s10584-009-9554-x>
- Noonan BP, Gaucher P (2005) Phylogeography and demography of Guiana harlequin toads (*Atelopus*): Diversification within a refuge. *Molecular Ecology* 14: 3017–3031. <https://doi.org/10.1111/j.1365-294X.2005.02624.x>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2017) *vegan*: Community Ecology Package. R package version 2.4-3. <https://CRAN.R-project.org/package=vegan>
- Oliveira DP, Carvalho VT, Hrbek T (2016) Cryptic diversity in the lizard genus *Plica* (Squamata): phylogenetic diversity and Amazonian biogeography. *Zoologica Scripta* 45: 630–641. <https://doi.org/10.1111/zsc.12172>
- Orrico VGD, Nunes I, Mattedi C, Fouquet A, Lemos AW, Rivera-Correa M, Lyra ML, Loebmann D, Pimenta BVS, Caramaschi U, Rodrigues MT, Haddad CFB (2017) Integrative

- taxonomy supports the existence of two distinct species within *Hypsiboas crepitans* (Anura: Hylidae). *Salamandra* 53: 99–113.
- O'Shea M (1989) The herpetofauna of Ilha de Maracá, state of Roraima, northern Brazil. In: Doote J (Ed.) Reptiles. Proceedings of the 1988 U.K. Herpetological Societies, Symposium on captive breeding. British Herpetological Society, London, 51–72.
- O'Shea MT, Stimson AF (1993) An aberrant specimen of *Drymobius rhombifer* (Colubridae: colubrinae): a new generic record for Brazil. *Herpetological Journal* 3: 70–71.
- O'Shea MT (1998) The reptilian herpetofauna of the Ilha de Maracá (Cap. 12). In: Milliken W, Ratter JA (Eds) Maracá: The biodiversity and environment of an Amazonian rainforest. John Wiley & Sons, Chichester, England, 231–262.
- Ouboter PE, Jairam R, You KWT (2007) Additional records of amphibians and reptiles from Nassau Mountain, Suriname. In: Alonso LE, Mol JH (Eds) A Rapid Biological Assessment of the Lely and Nassau Plateaus, Suriname (with additional information on the Brownsberg Plateau). RAP Bulletin of Biological Assessment, 126–129.
- Ouboter PE, Jairam R (2012) Amphibians of Suriname. Brill, Leiden, 388 pp.
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7: 16. <https://doi.org/10.1186/1742-9994-7-16>
- Padial JM, Grant T, Frost DR (2014) Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. *Zootaxa* 3825: 1–132. <https://doi.org/10.11646/zootaxa.3825.1.1>
- Palumbi SR, Martin A, Romano S, Mcmillan WO, Stice L, Grabowski G (1991) The Simple Fool's Guide to PCR. University of Hawaii, Honolulu, 94 pp.
- Passos P, Kok PJR, Albuquerque NR, Rivas G (2013) Groundsnakes of the Lost World: A Review of *Atractus* (Serpentes: Dipsadidae) from the Pantepui region, northern South America. *Herpetological Monographs* 27: 52–86. <https://doi.org/10.1655/HERPMON-OGRAHS-D-12-00001R2.1>
- Paz A, Crawford AJ (2012) Molecular-based rapid inventories of sympatric diversity: a comparison of DNA barcode clustering methods applied to geography-based vs clade-based sampling of amphibians. *Journal of Biosciences* 37: 887–896. <https://doi.org/10.1007/s12038-012-9255-x>
- Peters JA, Donoso-Barros R (1986) Catalogue of the Neotropical Squamata. Smithsonian Institution Press, Washington DC, 640 pp.
- Pinto-Sánchez NR, Calderón-Espinosa ML, Miralles A, Crawford AJ, Ramírez-Pinilla MP (2015) Molecular phylogenetics and biogeography of the Neotropical skink genus *Mabuya* Fitzinger (Squamata: Scincidae) with emphasis on Colombian populations. *Molecular Phylogenetics and Evolution* 93: 188–211. doi: <http://doi.org/10.1016/j.ympev.2015.07.016>
- Pyron RA, Wiens JJ (2011) A large-scale phylogeny of Amphibia with over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61: 543–583. <https://doi.org/10.1016/j.ympev.2011.06.012>
- Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 1–53. <https://doi.org/10.1186/1471-2148-13-93>
- Raimundi EA, Nascimento JMC, Barroso PCS, Hamada N, Boldrini R (2017) Three new species of *Miroculis* from the Serra da Mocidade National Park, Roraima State, Brazil,

- with new records and checklist of the Leptophlebiidae (Ephemeroptera). Zootaxa 4317: 573–583. <https://doi.org/10.11646/zootaxa.4317.3.8>
- Ramalho WP, Viana L, Benevides R, Silva EP, Alves-Silva R (2011) First record of *Lithobates palmipes* (Spix, 1824) (Anura, Ranidae) for the state of Piauí, Northeastern Brazil. Herpetology Notes 4: 249–251.
- Rebouças-Spieker R, Vanzolini PE (1990) *Mabuya carvalhoi*, especie nova do estado de Roraima, Brasil (Sauria, Scincidae). Revista Brasileira de Biologia 50: 377–386.
- Ribeiro-Júnior MA (2015a) Catalogue of distribution of lizards (Reptilia: Squamata) from the Brazilian Amazonia. I. Dactyloidae, Hoplocercidae, Iguanidae, Leiosauridae, Polychrotidae, Tropicuridae. Zootaxa 3983: 1–110. <https://doi.org/10.11646/zootaxa.3983.1.1>
- Ribeiro-Júnior MA (2015b) Catalogue of distribution of lizards (Reptilia: Squamata) from the Brazilian Amazonia. II. Gekkonidae, Phyllodactylidae, Sphaerodactylidae. Zootaxa 3981: 1–55. <https://doi.org/10.11646/zootaxa.3981.1.1>
- Ribeiro-Júnior MA, Amaral S (2016) Catalogue of distribution of lizards (Reptilia: Squamata) from the Brazilian Amazonia. III. Anguidae, Scincidae, Teiidae. Zootaxa 4205: 401–430. <https://doi.org/10.11646/zootaxa.4205.5.1>
- Ribeiro-Júnior MA, Amaral S (2017) Catalogue of distribution of lizards (Reptilia: Squamata) from the Brazilian Amazonia. IV. Alopoglossidae, Gymnophthalmidae. Zootaxa 4269: 151–196. <https://doi.org/10.11646/zootaxa.4269.2.1>
- Rivas GA, Molina CR, Ugueto GN, Barros TR, Barrio-Amorós CL, Kok PJR (2012) Reptiles of Venezuela: an updated and commented checklist. Zootaxa 3211: 1–64.
- Rivero JA (1961) Salientia of Venezuela. Bulletin of the Museum of Comparative Zoology 126: 1–207.
- Rivero JA (1966) Notes on the genus *Cryptobatrachus* (Amphibia: Salientia) with the description of a new race and four new species of a new genus of hylid frogs. Caribbean Journal of Science 6: 137–149.
- Rivero JA (1970) On the origin, endemism and distribution of the genus *Stefania* Rivero (Amphibia, Salientia) with a description of a new species from southeastern Venezuela. Boletín Sociedad Venezolana de Ciencias Naturales 28: 456–481.
- Robinson M (1989) Comentarios sobre una colección de anfibios y reptiles hecha en los alrededores del río Cunucunuma al norte del Cerro Duida y en la cima del Cerro Marahuaca, Territorio Federal Amazonas. Acta Terramaris 1: 59–64.
- Rodrigues DJ, Barros AB, Noronha JC, Almeida EJ (2013) New record and distribution map of *Lithobates palmipes* (Spix, 1824) (Anura, Ranidae) in the state of Mato Grosso, Brazil. Herpetology Notes 6: 391–393.
- Rojas-Runjaic FJM, Camargo-Siliet E, Carvalho VT, La Marca E (2017) New record and range extension of the Horned Toad, *Rhinella ceratophrys* (Boulenger, 1882) (Anura: Bufonidae), in Venezuela, and confirmation of its presence in Brazil. Check List 13: 1–6. <https://doi.org/10.15560/13.1.2035>
- Roze JA (1958a) Los reptiles del Auyantepui, Venezuela. Acta Biologica Venezuelica 2: 243–269.
- Roze JA (1958b) Los reptiles de Chimantá tepui (Estado Bolívar, Venezuela) colectados por la expedición botánica del Chicago Natural History Museum. Acta Biologica Venezuelica 2: 299–314.

- Roze JA (1961) El genero *Atractus* (Serpentes: Colubridae) en Venezuela. *Acta Biologica Venezuelica* 3: 103–19.
- Roze JA (1987) Summary of coral snakes (Elapidae) from Cerro de la Neblina, Venezuela, with description of a new subspecies. *Revue Française de Aquariologie Herpetologie* 14: 109–112.
- Rull V (2005) Biotic diversification in the Guiana Shield highlands: a proposal. *Journal of Biogeography* 32: 921–927. <https://doi.org/10.1111/j.1365-2699.2005.01252.x>
- Rull V, Vegas-Vilarrúbia T, Safont E (2016) The Lost World's pristinity at risk. *Diversity and Distributions* 22: 995–999. <https://doi.org/10.1111/ddi.12469>
- Sá RO, Grant T, Camargo A, Heyer WR, Ponssa ML, Stanley E (2014) Systematics of the Neotropical genus *Leptodactylus* Fitzinger, 1826 (Anura: Leptodactylidae): Phylogeny, the relevance of non-molecular evidence, and species accounts. *South American Journal of Herpetology* 9: S1–S100. doi: <http://doi.org/10.2994/SAJH-D-13-00022.1>
- Salerno PE, Ron SR, Señaris JC, Rojas-Runjaic FJM, Noonan BP, Cannatella DC (2012) Ancient tepui summits harbor young rather than old lineages of endemic frogs. *Evolution* 66: 3000–3013. doi: <http://doi.org/10.1111/j.1558-5646.2012.01666.x>
- Salerno PE, Señaris JC, Rojas-Runjaic FJM, Cannatella DC (2015) Recent evolutionary history of Lost World endemics: population genetics, species delimitation, and phylogeography of sky-island treefrogs. *Molecular Phylogenetics and Evolution* 82: 314–323. <https://doi.org/10.1016/j.ympev.2014.10.020>
- San Mauro D, Gower DJ, Müller H, Loader SP, Zardoya R, Nussbaum RA, Wilkinson M (2014) Life-history evolution and mitogenomic phylogeny of caecilian amphibians. *Molecular Phylogenetics and Evolution* 73: 177–189. <https://doi.org/10.1016/j.ympev.2014.01.009>
- Santos JOS, Potter PE, Reis NJ, Hartmann LA, Fletcher IR, McNaughton NJ (2003) Age, source, and regional stratigraphy of the Roraima Supergroup and Roraima-like outliers in northern South America based on U-Pb geochronology. *Geological Society of America Bulletin* 115: 331–348. [https://doi.org/10.1130/0016-7606\(2003\)115<0331:ASARSO>2.0.CO;2](https://doi.org/10.1130/0016-7606(2003)115<0331:ASARSO>2.0.CO;2)
- Schubert C, Briceño H (1987) Origen de la topografía tepuyana: una hipótesis. *Pantepuy* 1: 11–14.
- Schlüter A, Mägdefrau K (1991) First record of *Hyla parviceps* on the lower step of a central Venezuelan table mountain. *Amphibia-Reptilia* 12: 217–219. <https://doi.org/10.1163/156853891X00202>
- Señaris JC, Ayarzagüena J (1993) Una nueva especie de *Centrolenella* (Anura: Centrolenidae) del Auyan-Tepui, Edo. Bolívar, Venezuela. *Memoria de la Sociedad de Ciencias Naturales La Salle* 53: 121–126.
- Señaris JC, Ayarzagüena J, Gorzula S (1994) Los sapos de la familia Bufonidae (Amphibia: Anura) de las tierras altas de la Guayana venezolana: Descripción de un nuevo género y tres especies. *Publicaciones de la Asociación Amigos de Doñana* 3: 1–37.
- Señaris JC, Ayarzagüena J (2005) Revisión taxonómica de la Familia Centrolenidae (Amphibia: Anura) de Venezuela. *Publicaciones del Comité Español del Programa Hombre y Biosfera. Red IberoMaB de la UNESCO, Sevilla* 7.
- Señaris JC, Margarita L, Rojas-Runjaic F, Barrio-Amorós CL (2014) Guía ilustrada de los anfibios del Parque Nacional Canaima, Venezuela. Ediciones IVIC, Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela, 264 pp.

- Silva FRS (2016) Sistemática e história natural de anfíbios anuros das nascentes dos rios Samã e Miang em áreas de altitude do Escudo da Guiana em Roraima (Amphibia, Anura). Masters' Dissertation. Instituto Nacional de Pesquisas da Amazônia. Boa Vista, Roraima, Brazil.
- Sombroek W (2001) Spatial and temporal patterns of Amazon rainfall - Consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* 30: 388–396. <http://doi.org/10.1579/0044-7447-30.7.388>
- Stafford PJ, Castro F (2010) *Drymobius rhombifer*. The IUCN Red List of Threatened Species. <http://www.iucnredlist.org/details/176799/0>
- Steyermark JA (1986) Speciation and endemism in the flora of Venezuelan tepuis. In: Vuilleumier F, Monasterio M (Eds) High altitude tropical biogeography. Oxford University Press, New York, 317–373.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analyses Version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Uetz P, Hošek J (2017) The Reptile Database. <http://www.reptile-database.org>
- Vacher JP, Kok PJR, Rodrigues MT, Lima JD, Lorenzini A, Martinez Q, Fallet M, Courtois EA, Blanc M, Gaucher P, Dewynter M, Jairam R, Ouboter P, Thébaud C, Fouquet A (2017) Cryptic diversity in Amazonian frogs: Integrative taxonomy of the genus *Anomaloglossus* (Amphibia: Anura: Aromobatidae) reveals a unique case of diversification within the Guiana Shield. *Molecular Phylogenetics and Evolution* 112: 158–173. <https://doi.org/10.1016/j.ympev.2017.04.017>
- Van Dijk PP, Iverson JB, Rhodin AGJ, Shaffer HB, Bour R (2014) Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. In: Rhodin AGJ, Pritchard PCH, van Dijk PP, Saumure RA, Buhlmann KA, Iverson JB, Mittermeier RA (Eds) Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5: 000.329–000.479. <https://doi.org/10.3854/crm.5.000.checklist.v7.2014>
- Varotsos CA, Tzanis CG, Sarlis NV (2016) On the progress of the 2015–2016 El Niño event. *Atmospheric Chemistry and Physics* 16: 2007–2011. <https://doi.org/10.5194/acp-16-2007-2016>
- Vences M, Nagy ZT, Sonet G, Verheyen E (2012) DNA barcoding amphibians and reptiles. In: Lopez I, Erickson DL (Eds) DNA barcodes: methods and protocols. Springer Protocols Methods in Molecular Biology, 79–107. https://doi.org/10.1007/978-1-61779-591-6_5
- Vences M, Thomas M, Bonett RM, Vieites DR (2005) Deciphering amphibian diversity through DNA barcoding: chances and challenges. *Philosophical Transactions of the Royal Society London, Series B, Biological Sciences* 360: 1859–1868. <https://doi.org/10.1098/rstb.2005.1717>
- Vences M, Wake DB (2007) Speciation, species boundaries and phylogeography of amphibians. In: Heatwole HH, Tyler M (Eds) Amphibian Biology, Vol. 6, Systematics. Surrey Beatty & Sons, Chipping Norton, Australia, 2613–2669.
- Vial J, Jimenez-Porras J (1967) The Ecogeography of the Bushmaster, *Lachesis muta*, in Central America. *American Midland Naturalist* 78: 182–187. <https://doi.org/10.2307/2423378>

- Vieites D, Wollenberg KC, Andreone F, Koehler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences* 106: 8267–8272. <https://doi.org/10.1073/pnas.0810821106>
- Vogt RC (2008) Tartarugas da Amazônia. Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil, 104 pp.
- Watling JI, Ngadino LF (2007) A preliminary survey of amphibians and reptiles on the Nassau and Lely plateaus Eastern Suriname. In: Alonso LE, Mol JH (Eds) *A Rapid Biological Assessment of the Lely and Nassau Plateaus, Suriname (with additional information on the Brownsberg Plateau)*. RAP Bulletin of Biological Assessment, 119–125.
- Wallach V, Williams KL, Boundy J (2014) *Snakes of the world: a catalogue of living and extinct species*. CRC Press, Boca Raton, Florida, 1237 pp. <https://doi.org/10.1201/b16901>
- Wilkinson M, O'Connor A, Nussbaum RA (2013) Taxonomic status of the Neotropical caecilian genera *Brasilotyphlus* Taylor, 1968, *Microcaecilia* Taylor, 1968 and *Parvicaecilia* Taylor, 1968 (Amphibia: Gymnophiona: Siphonopidae). *Occasional Papers of the Museum of Zoology, University of Michigan* 744: 1–12.
- Williams EE, Praderio MJ, Gorzula S (1996) A phenacosaur from Chimanté tepui, Venezuela. *Breviora* 506: 1–15.
- Zweifel RG (1986) A new genus and species of microhylid frog from the Cerro de la Neblina region of Venezuela and a discussion of relationships among New World microhylid genera. *American Museum Novitates* 2847: 1–24.

Supplementary material I

Specimens examined

Authors: Leandro J.C.L. Moraes, Alexandre P. de Almeida, Rafael de Fraga, Rommel R. Rojas, Renata M. Pirani, Ariane A.A. Silva, Vinícius T. de Carvalho, Marcelo Gordo, Fernanda P. Werneck

Data type: (measurement/occurrence/multimedia/etc.)

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.715.20288.suppl1>

