

***Elisesione*, a new name for *Wesenbergia* Hartman, 1955, and the description of a new species (Annelida, Hesionidae)**

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Academic editor: *C. Glasby* | Received 22 June 2016 | Accepted 28 October 2016 | Published 16 November 2016

<http://zoobank.org/51170AC7-78FF-4093-A5C0-EBA609A83FDB>

Citation: Salazar-Vallejo SI (2016) *Elisesione*, a new name for *Wesenbergia* Hartman, 1955, and the description of a new species (Annelida, Hesionidae). *ZooKeys* 632: 1–12. doi: 10.3897/zookeys.632.9652

Abstract

Wesenbergia Hartman, 1955 (Annelida, Hesionidae) is both preoccupied and a junior homonym of *Wesenbergia* Kryger, 1943 (Hymenoptera, Pteromalidae), and must be renamed. *Elisesione* **nom. n.** is proposed as a replacement name, derived from the combination of the first name of the discoverer, Elise Wesenberg-Lund, and *Hesione* Savigny in Lamarck, 1818. *Elisesione mezianei* **sp. n.**, is described from the Wallis and Futuna islands (southwest Pacific). A key to separate *E. mezianei* **sp. n.** from its congener *E. problematica* (Wesenberg-Lund, 1950) is included; further, the record of *E. problematica* for Japan should be regarded as a distinct species because it has palps shorter than antennae (subequal in the type species), and shorter neurochaetal blades (7–9 times longer than wide *vs* 8–12 times longer than wide in the type species).

Keywords

Acicular lobe, *Hesione*, Iceland, polychaetes, simple palps, Wallis and Futuna

Introduction

Hesionid polychaetes are usually colorful polychaetes which are striking because the number of body segments is inversely related to body size. For example, species of *Hesione* Savigny in Lamarck, 1818 only have 16 chaetigers during their benthic life, but, are one of the largest representatives in the family with a length of up to 70 mm long in

preserved specimens (pers. obs.), although they have been reported to reach 120 mm (Salazar-Vallejo and Rizzo 2009). On the contrary, several genera have smaller species with numerous segments, but they have fragile bodies that break easily; consequently, finding complete specimens is difficult. For example, careful studies have shown that complete specimens with about 30 segments are only 5 mm long (Pleijel et al. 2009).

The phylogenetic affinities among the Hesionidae were assessed by Pleijel (1998). His results indicated two subfamilies (Hesioninae Grube, 1850 and Ophiodrominae Pleijel, 1998), and that Hesioninae includes two tribes: Psamathini Pleijel, 1998 and Hesionini Grube, 1850. Hesionini includes *Hesione*, *Leocrates* Kinberg, 1866, *Leocratides* Ehlers, 1908, *Wesenbergia* Hartman, 1955, and *Dalhousiella* McIntosh, 1901. Pleijel (1998: 114) regarded *Dalhousiella* as *incertae sedis* within Hesionini because he could not study the type specimen, which became lost in the mail. However, *Dalhousiella* is a distinct genus that resembles *Leocratides* because they have biarticulate palps and uniramous parapodia, but they differ because there are no jaws in *Dalhousiella* whereas they are present in *Leocratides*, as indicated elsewhere (McIntosh 1908: 134, 135; Fauvel 1923: 234).

According to Pleijel (1998:107) Hesionini includes species with 21 segments, eight pairs of anterior cirri, bidentate neurochaetae, and pharynx without marginal papillae. The included genera can be separated by the presence of bi-articulated palps [(*Dalhousiella*, *Leocrates*, and *Leocratides*), with biramous (*Leocrates*) or uniramous parapodia (*Dalhousiella* and *Leocratides*), and by the presence of jaws (*Leocratides*), or their absence (*Dalhousiella*)], simple palps (*Wesenbergia*), or the lack of palps (*Hesione*) (Rizzo and Salazar-Vallejo 2014).

Wesenberg-Lund (1950) reported, in one of her many contributions to the Danish Ingolf-Expedition series (Thorson 1969), finding an unusual hesionid polychaete collected in sediments at 550 m depth off Southwest Iceland. The single specimen was damaged but the possession of four appendages on the anterior prostomial margin, separated it from *Hesione* which has only two appendages, and she proposed *Hesionella problematica* as a new genus and new species.

Wesenberg-Lund overlooked a previous publication by Hartman (1939) who had proposed the same genus-group name for another hesionid polychaete, *Hesionella mccullochae*, a small species occurring within the burrows of a lumbrinerid. The homonymy was recognized by Hartman (1955: 41), and she proposed *Wesenbergia* as a replacement name for *Hesionella* Wesenberg-Lund, 1950. Some years later a second replacement name was required for *Hesionella* Friedrich, 1956; Hartmann-Schröder (1959: 74) proposed *Fridericiella* as the replacement, which subsequently became a junior synonym of *Microphthalmus* Mecznirow, 1865 (Westheide (2013), as indicated in WoRMS).

Wesenbergia Hartman, 1955 has been recorded for Japan (Imajima 2003) and included in large monographic works (Fauchald 1977, Pleijel 1998), and in keys to hesionid genera (Salazar-Vallejo and Orensanz 2007, Rizzo and Salazar-Vallejo 2014). However, *Wesenbergia* Hartman, 1955 is both preoccupied and a junior homonym of *Wesenbergia* Kryger, 1943, a group of parasitic hymenopterans, and must be replaced.

It must be emphasized that detecting such a homonymy could not have been possible even if one had access to the full edition of Neave (1939–1940, *cit.* Evenhuis 2016), but this task is now made easier by consulting the online *Nomenclator Zoologicus* (<http://uiio.mbl.edu/NomenclatorZoologicus/>).

As part of an on-going revision of *Hesione*, materials from several different collections from European, American and Mexican museums or institutions have been examined by the author. In the collections of the Muséum National d'Histoire Naturelle, Paris, a remarkable specimen provided with antennae and simple palps was found, belonging to an undescribed species corresponding to *Wesenbergia*. In this contribution, the new species is described, and because *Wesenbergia* is a junior homonym, a new replacement name is proposed, together with a key to the known species of the genus.

Material and methods

The holotype was collected during the Musorstom Expedition 7: Wallis and Futuna Islands (Richer de Forges and Menou 1993); it has been deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN). The holotype was photographed with a Canon PowerShot G6 digital camera and a microscope adapter; plates were prepared by compressing a series of photos for each image using Helicon Focus. Immersion of the specimen for 30 sec in an oversaturated methyl-green solution improved the contrast.

Results

Hesionidae Grube, 1850

Hesioninae Grube, 1850

Hesionini Grube, 1850

Elisione nomen novum

Hesionella Wesenberg-Lund, 1950: 14.

Wesenbergia Hartman, 1955: 41; Fauchald 1977: 77; Pleijel 1998: 112, 163 (*non* Kryger 1943).

Type species. *Hesionella problematica* Wesenberg-Lund, 1950, by monotypy.

Etymology. The name is a combination of the first name of the late Elise Wesenberg-Lund, and *Hesione*, which is the type genus for the family, but in order to make it more euphonic, the first two letters of the genus-group name are suppressed; the new name emphasizes the similarities between these two genera. Gender feminine.

Diagnosis (emended). Hesionini with two antennae; palps simple, lateral to antennae. Eight pairs of tentacular cirri. Dorsal cirri with short or long cirrophores. Notochaetae absent. Aciculae colorless or blackish. Acicular lobes single or double.

Neurochaetae with blades bidentate, guards approaching subdistal tooth, or absent. Prepygidial segment with dorsal cirri about 10 times longer than ventral cirri.

Remarks. *Wesenbergia* Kryger, 1943 was proposed for a group of chalcid hymenoptera, but the name was overlooked by Hartman (1955) when she proposed the same genus-group name for hesionid polychaetes. Despite *Wesenbergia* Kryger, 1943 being considered a synonym of *Macromesus* Walker, 1848 within Hymenoptera, the name still cannot be made available (ICZN 1999, Art. 23, Principle of Priority).

Homonymies are not allowed in Zoological Nomenclature (ICZN 1999, Chap. 12) and junior homonyms must be replaced (Art. 60). Further, the Code of Ethics includes (ICZN 1999, Point 3) a recommendation for the procedure, especially if the author(s) involved are alive. There are no junior synonyms available and this explains why a new name must be proposed, and both authors involved are deceased.

As indicated above, *Wesenbergia* Hartman, 1955 is a junior homonym and must be replaced, even though the senior homonym is regarded as a junior synonym (Heqvist 1960). In naming *Wesenbergia*, Hartman used the first word in the compound last name of Elise Wesenberg-Lund. Using this same principle, the new name, *Elisesione*, is derived from the first name of the author.

Elisesione nom. n. is closely related to *Hesione* as shown by Ruta et al. (2007). They differ, however, not only by the presence of simple palps in the former, but because the body is more or less cylindrical, not widened medially or posteriorly as in *Hesione* species. In fact, the lateral cushions, which are typically divided into 2-3 sections and can vary on their degree of lateral expansion in *Hesione*, are rather solid, undivided and projected anteriorly in *Elisesione* nom. n. This feature was noted in the original description when the body was characterized as scolopendriiform (Wesenberg-Lund 1950: 14). Further, the anterior eyes of *Wesenbergia* (only recorded for the shallow water species), are half-moon shaped and about three times larger than posterior ones; this is another feature not recorded for any *Hesione* species.

Savigny (1822: 39) included four anterior appendages in the generic diagnosis of *Hesione*, but because they were not included in the description (Savigny 1822: 40), nor in the corresponding illustration (his plate 3, figure 3), they were regarded as a mistake. Grube (1867: 65) corrected this and later Chamberlin (1919: 185) used this in his key to genera. However, by regarding *Hesione* as having four antennae and eight pairs of tentacular cirri, de Quatrefages (1866) proposed *Fallacia* for species having two antennae: *H. pantherina* Risso, 1826 and *H. proctochona* Schmarida, 1861, whereas Claparède (1868: 541) proposed *Telamone* for species having two antennae and six pairs of tentacular cirri with *H. sicula* delle Chiaje, 1822 as its only species. *Fallacia* and *Telamone* are junior synonyms of *Hesione* (Fauvel 1911: 374, Chamberlin 1919: 186, Pleijel 1998: 107), and *H. sicula* and *H. pantherina* have been regarded as synonyms (Fauvel 1923: 233).

Distribution. The two known species in the genus have been found in different ecological conditions and geographical regions. The type species, *E. problematica*, was found in the North Atlantic, off Iceland, in sediments taken at 550 m depth, and the new species, *E. mezzianei* sp. n., was collected in the Western South Pacific, in hard substrates in shallow water (35 m), in the Wallis and Futuna Islands. Another species,

previously recorded as *E. problematica* from Japan (Imajima 2003) differs from the nominal form in several features. For example, in the Japanese specimens palps are half as long as antennae (rather than about equal-sized), and ventral cirri extend beyond chaetal lobe (rather than short of it); pigmentation also differs because the Japanese specimens are brownish with dorsal cirrostyles banded, whereas the Icelandic specimens are pale yellowish.

Key to species of *Elisesione* nomen novum

- 1 Acicular lobe single; parapodia with dorsal ceratophores about twice longer than wide; neurochaetal blades with guards **2**
- Acicular lobe double; parapodia with dorsal ceratophores 4–5 times longer than wide; neurochaetal blades 1–3 times longer than wide, without guards (palps about 2/3 as long as antennae)..... ***E. mezianei* sp. n.**
- 2 Neurochaetal blades 8–12 times longer than wide; palps as long as antennae ***E. problematica* (Wesenberg-Lund, 1950)**
- Neurochaetal blades 7–9 times longer than wide; palps half as long as antennae..... ***E. problematica sensu* Imajima, 2003**

Elisesione mezianei sp. n.

<http://zoobank.org/09A8C65D-DBE4-43AB-9AF7-F3029BF64C7A>

Figs 1, 2

Type material. Holotype (MNHN 1777), Musorstom Expedition 7, Wallis & Futuna Islands, Sta. 536 (12°30.8'S, 176°41'W), Waren Dredge, Waterwitch Bank, 128 km NW off Wallis Island, 27–37 m, coralline rocks, crinoids, crabs, 16 May 1992, B. Richer, coll.

Etymology. This species is named to honor Dr. Tarik Meziane, Curator of Polychaeta in the Muséum National d'Histoire Naturelle, Paris, as an appreciation of his efforts and support to my research activities during many years. The epithet is a noun in apposition.

Description. Holotype (MNHN 1777) complete, subcylindrical, slightly damaged, bent ventrally, many neurochaetal blades broken; 28 mm long, 3 mm wide, 16 chaetigers (right parapodium of chaetiger 7 removed for observation, now kept in plastic vial with holotype).

Body with parallel sides (Fig. 1A), barely tapered posteriorly; pigmentation brownish, with abundant irregular spots variably fused into transverse or longitudinal lines, leaving a mid-dorsal, irregular, wider than long pale area in each segment (Fig. 1B); pigment intensity and definition progressively reduced posteriorly. Lateral and ventral surfaces pale.

Prostomium slightly wider than long, anterior margin with a shallow depression, lateral margins rounded, wider medially, posterior margin with a shallow depression,

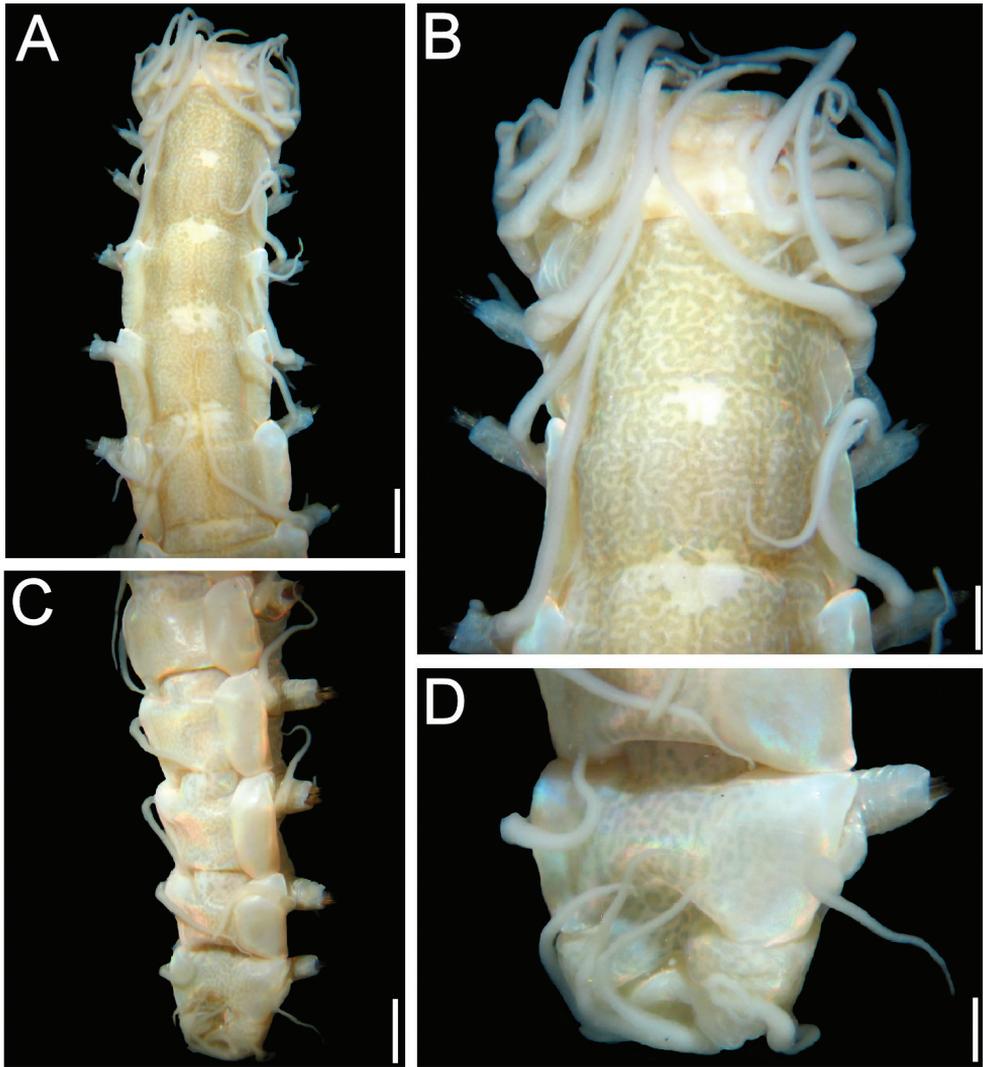


Figure 1. *Elisesione mezianei* sp. n. Holotype (MNHN 1777). **A** Anterior region, dorsal view **B** Anterior end, dorsal view **C** Posterior region, slightly oblique dorsal view **D** Pygidium. Scale bars **A** 1.6 mm, **B** 0.5 mm, **C** 1.2 mm, **D** 0.4 mm.

as long as $1/6$ prostomial length. Antennae digitate, longer than interocular distance. Palps simple, blunt, $2/3$ as long as antennae, positioned at the same level, external to antennae. Eyes blackish, anterior ones half-moon shaped, three times as large as posterior rounded ones (Fig. 2A, B).

Enlarged cirri long, thick, longest one reaches chaetiger 5. Lateral cushions low, projected anteriorly, slightly projected laterally, undivided.

Parapodia with chaetal lobes cylindrical, truncate, longer than wide; dorsal cirri thick with cirrophores cylindrical, 4–5 times longer than wide (Fig. 2C), cirrostyle

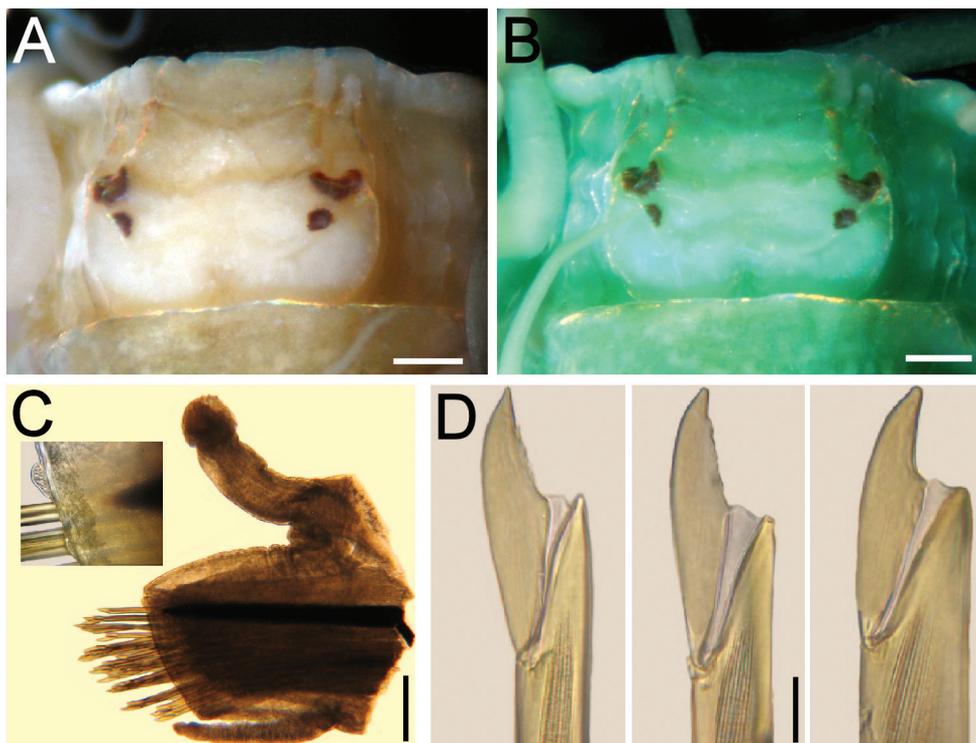


Figure 2. *Elisesione mezianei* sp. n. Holotype (MNHN 1777). **A** Prostomium, dorsal view **B** Same, after methyl-green staining **C** Chaetiger 7, right parapodium, anterior view, dorsal cirrostyle removed, only base left on cirrophore (inset: close-up showing tips of double acicular lobe) **D** Chaetiger 7, neurochaetal blades, variably eroded; the one on the right has a wider handle due to optical interference, not really wider than the others. Scale bars **A, B** 0.27 mm, **C** 0.3 mm, **D** 20 μ m.

basally cylindrical, smooth, medially annulated, distally articulated, shorter than body width (without parapodia). Ventral cirri basally smooth, rugose medially and distally, surpassing chaetal lobes.

Acicula black, tapered; acicular lobe double, each lobe blunt, of similar size, barely visible because of chaetal lobe contraction (Fig. 2C, inset). Neurochaetae about 30 per bundle, handle and blade brownish, blade unidentate but some chaetae with subdistal tooth remains, probably eroded; guards not seen (Fig. 2D).

Posterior end tapered into a blunt cone (Fig. 1C); prepygidial segment with asymmetrical cirri, dorsal ones over 10 times longer than ventral ones; pygidium smooth, depressed (Fig. 1D); anus dorso-terminal, open, about 9 anal papillae.

Pharynx not exposed. Oocytes not seen.

Remarks. As indicated in the key above, *Elisesione mezianei* sp. n. differs from both the Icelandic and the Japanese *E. problematica* in parapodial and chaetal features. In *E. mezianei* dorsal ceratophores are long (4–5 \times longer than wide), the acicular lobe is double, and neurochaetal blades are short (1–3 times longer than wide),

whereas in *E. problematica* dorsal ceratophores are short (2× longer than wide), the acicular lobe is single, and neurochaetal blades are long (8–12× longer than wide). Based upon the observation of other similar hesionid specimens, it is clear that these morphological differences are not the result of preservation methods, or prolonged storage in ethanol.

On the contrary, pigmentation patterns can be modified by dissolution in ethanol, because of photo-oxidation, or both, and despite the striking contrast between the two species, they could not be employed as diagnostic features. The pigmentation of *E. mezzianei* is long-lasting since it has been in ethanol for at least 16 years, when it was initially sorted-out as part of the Musorstom materials (Salazar-Vallejo 1999). Although they might be regarded of as having a little diagnostic relevance, the dorsal anastomosing thin brownish lines together with the shape and large size of the anterior eyes, are quite remarkable and unique for the genus, and, it must be added, not apparent in any *Hesion*e species.

Distribution. *Elisesione mezzianei* sp. n. is the second species in a previous monotypic genus and it is apparently rare along its distribution in rocky, shallow water substrates (35 m) in the Southwestern Pacific. The distribution for the genus is rather interesting and difficult to explain. The type species, *E. problematica* (Wesenberg-Lund, 1950) thrives in very cold waters in Iceland, and was also recorded in Japan in sediments at 150–320 m depth (Imajima 2003), whereas the new species, *E. mezzianei*, was found in shallow environments in a single locality in the tropical Pacific.

Discussion

Solving a problem of homonymy in zoological nomenclature is not a remarkable contribution *per se*, especially after 2004 when the *Nomenclator Zoologicus* was available online (Remsen et al. 2006). In fact, during a research visit in Rio de Janeiro, Brazil in 2012, Alexandra Rizzo (Rio de Janeiro State University), and I became aware of this homonymy but decided to wait to gather more information, and especially, to find some means to make more than a mere proposal for a replacement name. In fact, the Wikipedia entry for Hesionidae (<https://en.wikipedia.org/wiki/Hesionidae>) has an indication that *Wesenbergia* Hartman, 1955 is a junior homonym. The present proposal for a replacement name together with the description of a new species will hopefully be regarded as a better means to solve the problem.

In any case, solving this homonymy problem is by no means a derogatory remark on the impressive publication output of either Elise Wesenberg-Lund or Olga Hartman. They were extremely productive, often published large monographs or revisions, and the former also dealt with a wide variety of invertebrate groups. It was a mistake, a small one, and being related to a formerly monotypic genus, with apparently a single record, this name replacement would not imply a large impact on polychaete taxonomy or benthic ecology, faunal listings or similar efforts.

Acknowledgments

This contribution was made possible by funding from El Colegio de la Frontera Sur, and the Muséum National d'Histoire Naturelle, through the generous support of Tarik Meziane in Paris, and by the generous support of my direct bosses in Chetumal: Luis F. Carrera-Parra (Group Leader), and Laura Carrillo (Head of Department). The preliminary sorting out of the Musorstom materials was made possible because Fredrik Pleijel, then in the MNHN, and Alain Crosnier invited me to process the polychaetes. They were certainly expecting more and better results and they deserve more, but I'm just too slow and sloppy. Some parts of this research were made during a research stay in the Université Catholique de l'Ouest, in Angers, thanks to the kind support of Patrick Gillet. Lars Vilhelmsen, Natural History Museum of Denmark, kindly sent the Gunnar Thorson's obituary of Dr. Elise Wesenberg-Lund. Leslie Harris from the Los Angeles County Museum of Natural History, and Jerry D. Kudenov, from the University of Alaska, Anchorage, kindly read an earlier draft and helped a lot to improve it. The critical reading by Alexandra Rizzo and Chris Glasby resulted in this final form.

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Rowlandius dimitrescoae species group: new diagnosis, key and description of new cave-dwelling species from Brazil (Schizomida, Hubbardiidae)

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Academic editor: *P. Stoev* | Received 25 May 2016 | Accepted 20 October 2016 | Published 16 November 2016

<http://zoobank.org/C384D6F4-13F3-4AD8-BFC9-845957671FED>

Citation: Giupponi APL, Miranda GS, Villarreal OM (2016) *Rowlandius dimitrescoae* species group: new diagnosis, key and description of new cave-dwelling species from Brazil (Schizomida, Hubbardiidae). ZooKeys 632: 13–34. doi: 10.3897/zookeys.632.9337

Abstract

The *Rowlandius dimitrescoae* species group is reviewed and rediagnosed, and its composition is revised. The group now includes *R. cousinensis*, *R. decui*, *R. dimitrescoae*, *R. insignis*, *R. linsduarte*, *R. monensis*, *R. peckorum*, *R. potiguar*, *R. sul*, *R. ubajara*, and *R. pedrosoi* **sp. n.** A new species is described from a cave in northeast Brazil (Santa Quitéria, Ceará). Identification keys and distributional maps are provided for the species of the group. Sixteen species of Schizomida, including five of *Rowlandius*, are currently recognized from Brazil.

Keywords

Diversity, Hubbardiinae, Neotropics, Schizomids, Short-tailed whipscorpion, taxonomy

Introduction

Rowlandius Reddell & Cokendolpher, 1995, is the most diverse Neotropical genus of Schizomida with 63 described species (Reddell and Cokendolpher 1995; Teruel 2012; Teruel et al. 2012; Delgado-Santa and Armas 2013; Santos et al. 2013). Reddell and Cokendolpher (1995) proposed the genus with a broad concept, using characters that could also fit other genera, and was redefined by Teruel (2004). Reddell and Cokendolpher (1995) assumed *Rowlandius* as monophyletic, but this has never been tested in a phylogenetic analysis; on the contrary, the presence of several variable characters within the genus (e.g., the number of setae on the propeltidium and the shape of the spermathecae) indicates the opposite (Teruel et al. 2012). Within *Rowlandius*, the *biconourus* species group was also proposed as monophyletic, but this hypothesis has not been tested either (Teruel et al. 2012).

The species that compose *Rowlandius* were recognized as a species group long before the genus was erected, when almost all species of Schizomida were placed in *Schizomus* Cook, 1899 (the historical “trash can” of the order). The first attempt to subdivide *Schizomus* into species groups was made by Rowland and Reddell (1979a) who proposed seven; one of them, the *dumitrescoae* group, was divided in three complexes: *dumitrescoae*, *primibiconourus* and *viridis* complex. All *Schizomus* species of these complexes were transferred to *Rowlandius* by Reddell and Cokendolpher (1995). Later, new endeavors to detect and define groups within *Rowlandius* were made by Armas (2002), Teruel (2012) and Teruel et al. (2012), but these included only Cuban species and did not cover all morphological variation within the genus.

Almost 80% of *Rowlandius* species with a known male have striking secondary sexual dimorphism, i.e., the male pedipalp segments are much longer than that of the conspecific females. An interesting case of dimorphism is present in *R. gracilis* Teruel, 2004 and *R. potiguar* Santos, Ferreira & Buzzato, 2013, where the same population has both heteromorphic males with long pedipalp articles and homeomorphic males with shorter, female-sized pedipalp articles (Teruel 2004; Teruel et al. 2012; Santos et al. 2013; Oliveira and Ferreira 2014).

Rowlandius has an extensive geographic distribution, occurring from Cuba to Brazil. A major radiation of the genus seems to have occurred in the Greater Antilles, where the vast majority of the known species are found (Harvey 2003). In contrast, only five species have been described so far from continental South America (*R. arduus* Armas, Villarreal & Colmenares-García, 2009, *R. linsduarte* Santos, Dias, Brescovit & Santos, 2008, *R. potiguar* Santos, Ferreira & Buzzato, 2013, *R. sul* Cokendolpher & Reddell, 2000 and *R. ubajara* Santos, Ferreira & Buzzato, 2013). The genus has been recorded from different biomes, including the Brazilian Amazonia, the Brazilian Atlantic forest, and the Venezuelan cloud forest (Santos et al. 2008; Armas et al. 2009). Recently, some species were discovered inhabiting caves or patches of forest inserted in dry areas of Brazil, the Caatinga (Santos et al. 2008; Santos et al. 2013).

In the present article, a new species of *Rowlandius* is described and illustrated from the state of Ceará, northeast Brazil. Additionally, the *Rowlandius dumitrescoae* group is rediagnosed, an identification key to its species is provided, and the relationships of the new species are discussed.

Material and methods

The material studied is deposited in Museu Nacional, Universidade Federal de Rio de Janeiro (MNRJ) and FIOCRUZ, Instituto Oswaldo Cruz (CAVAISC). Terminology of pedipalps, legs and spermathecae follows Reddell and Cokendolpher (1995) and Moreno-González et al. (2014); flagellum setation follows terminology of Harvey (1992), modified by Cokendolpher and Reddell (1992), Villarreal et al. (2014), Moreno-González et al. (2014) and Monjaraz-Ruedas et al. (2016); cheliceral setation terminology is based on Lawrence (1969) modified by Villarreal et al. (2016). Description format follows Villarreal et al. (2016). The terms α - and β -males are used here for the two different sizes of heteromorphs. Those with extremely long palp segments are α -heteromorphic males, and those with palp lengths intermediate between those of females and those of α -males are called β -heteromorphic males.

The keys were built based on the material analyzed and the original descriptions (in the case of species with no specimens available for examination). Males are unknown for *Rowlandius sul* and this species was not included in the male key. The preparation and illustrations of the spermathecae follow Villarreal et al. (2016). Dorsal, ventral, and lateral photos were made with a Leica MZ16 microscope attached to a FujiFilm X10 camera. Pictures of live specimens (courtesy of Denis Rafael Pedroso; Fig. 8) were taken with a Canon PowerShot SX130 IS. To generate the SEM images, the specimens were critical point dried and mounted on stubs using an adhesive copper aluminum tape. The mounted stubs were then coated with platinum-palladium and scanned with a JEOL JSM-6390 LV.

Acronyms used:

- AMN** anterior median notch of the chitinized arch;
- Dm** dorso-median setae of abdomen and flagellum;
- DL** dorso-lateral setae of the abdomen and flagellum;
- LL** lateral lobe of spermathecae;
- ML** median lobe of spermathecae;
- Msp** microsetae patch of the male flagellum;
- VL** ventro-lateral setae of the abdomen and flagellum.

Additional material examined

Rowlandius ubajara Santos, Ferreira & Buzzato, 2013: BRAZIL, Ceará, Ubajara, Ubajara National Park, 11–14.i.2013, 3°50'24.42"S 40°54'3.96"W, 869m a.s.l., Carlos

Frankl Sperber, Thiago Gechel Kloss, Fabiene Maria de Jesus and Gabriel de Oliveira Lobregart *leg.* (1 male, MNRJ 4270).

Rowlandius potiguar Santos, Ferreira & Buzzato, 2013: BRAZIL, Rio Grande do Norte, Martins, 6°5'7.87"S 37°55'6.62"W, 319m a.s.l., C. Fukushima and A. Giupponi *leg.* (8 females, MNRJ 4269).

Taxonomy

Hubbardiidae Cook, 1899

Hubbardiinae Cook, 1899

***Rowlandius* Reddell & Cokendolpher, 1995**

***Rowlandius dumistrocae* species group**

Diagnosis. Male pedipalps of some species sexually dimorphic, with femur and patella extremely elongated, and femur strongly bent proximally (Figs 3D–E, 4A, B). Male flagellum lanceolate (as in *R. cousinensis* (Rowland & Reddell, 1979), *R. dumitrescoae* (Rowland & Reddell, 1979), *R. insignis* (Hansen in Hansen & Sorensen, 1905), *R. monensis* (Rowland & Reddell, 1979) and *R. pedrosoi* sp. n.), subquadrate (as in *R. linsduarte* and *R. potiguar*) or ovoid (as in *R. peckorum* (Rowland & Reddell, 1979) and *R. ubajara*); male flagellum with rounded dorsal projections (with exception of *R. dumitrescoae*), never surpassing the lateral borders; male flagellum with posterior border surface (between setae *Dl3*) elevated or flat (more rare). Spermathecae with four lobes, lateral pair long with a curved stalk and a terminal enlarged bulb; median lobes short and digitiform or subconical (Figs 7A, B). Chitinized arch very short (relation width/length = 3.7) with acute lateral tips (*R. cousinensis*, *R. linsduarteae*, *R. monensis*, *R. pedrosoi* sp. n., *R. potiguar* and *R. ubajara*) or rounded lateral tip (*R. dumitrescoae*, *R. insignis*, *R. peckorum* and *R. sul*); anteromedian notch contacting the posterior branch in some species. Gonopod absent. The species included in this group can be checked in Table 4.

Distribution. Brazil, Costa Rica, Cuba, Jamaica, Martinique (Windward Islands) and Puerto Rico (Fig. 9).

***Rowlandius pedrosoi* sp. n.**

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Figures 1–8, Tables 3 and 4

Diagnosis. Large specimens, male body total length 4.01mm, females 3.85mm (chelicerae and flagellum not included). Spermathecae similar to *R. potiguar*, but stalk of LL thicker and curved in the apical third; *R. pedrosoi* sp. n. with stalk of LL and ML with several glandular pores. Lateral tip of chitinized arch “V-shaped”, with obtuse angle,

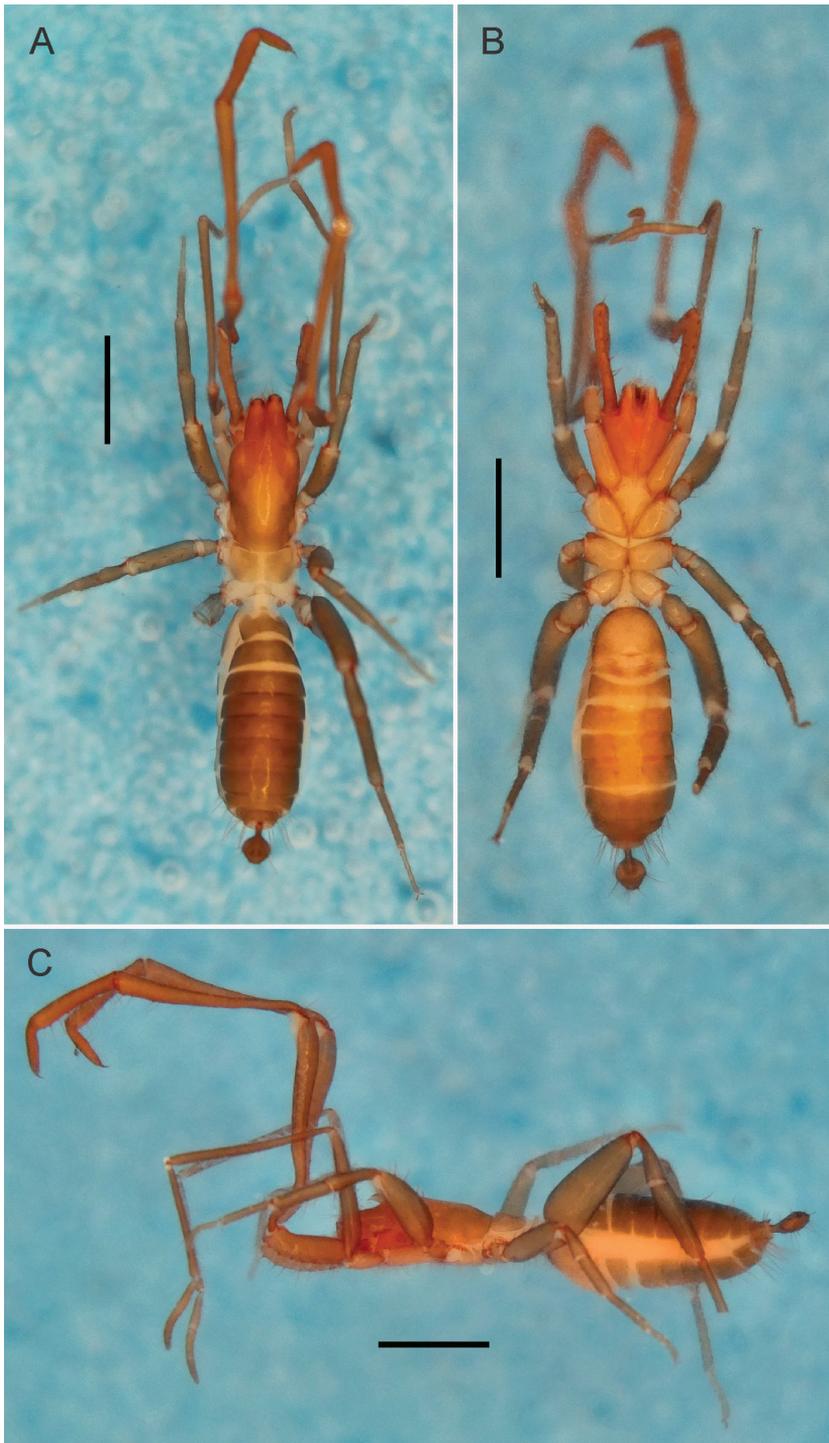


Figure 1. Habitus of an α -heteromorphic male of *Rowlandius pedrosoi* sp. n. (MNRJ 04266). **A** Dorsal view **B** Ventral view **C** Lateral view. Scale bars 1 mm.

greater than 150°, which distinguishes *R. pedrosoi* sp. n. from *R. potiguar* and *R. linsduarte*. Heteromorphic males present, with α (long pedipalps) and β (shorter pedipalps, but longer than those of females) heteromorphics, similar to *R. potiguar*. Male flagellum with setae *Dm1* exactly between the main globose area of the flagellum and the stalk, such as in *R. linsduarte* and differently from *R. potiguar* and *R. ubajara*.

Type material. Holotype: BRAZIL, Ceará, Santa Quitéria, Gruta P-08, 41529 mE / 9495881 mN SAD'69S, 15–21.vii.2014, Pellegatti and Pedroso *leg.* (1 male, MNRJ 04266). **Paratypes:** same data as holotype (1 male, 7 females and 10 juveniles, MNRJ 04267); same data as holotype (1 female and 1 juvenile, CAVAISC-ARAC 0008); same data as holotype, 03–13.ii.2014 (4 females and 8 juveniles, MNRJ 04268).

Etymology. The species name is in honor of arachnologist Denis Rafael Pedroso, friend and collector of the type series (of this and many other new species of arachnids).

Description. *Male holotype.* Color (Fig. 8E–F): live animals with abdominal tergites and sternites olive-brown; pleura white. Pedipalps reddish-brown; legs light brown with the extremities dark-brown. Prosoma light brown; ventral region lighter than the dorsal. Alcohol preserved specimens (Fig. 1) with propeltidium and chelicerae reddish-brown, meso and metapeltidium yellowish-brown (lighter than the chelicerae and propeltidium), legs light brown, abdominal tergites brown and sternites yellowish-brown, flagellum medium-brown. Ventrally coxae I–IV and sternal region yellowish. All body setation light reddish-brown.

Prosoma (Fig. 1). Anterior process of propeltidium with two setae (one behind the other) followed by two pairs of dorsosubmedian transversally oriented setae; eye-spot suboval; metapeltidium divided. Anterior sternum with 11+2 setae and posterior sternum with 5 setae. Anterior process as wide as long, with a wide base, narrowing abruptly, forming an almost right triangle; the tip of the process is curved downwards.

Opisthosoma (Fig. 1). Setae: Tergite I with two pairs of anterior microsetae and one pair of large *Dm* setae. Tergite II with three pairs of anterior microsetae parallel to each other, and one large pair of *Dm* setae. Tergites III–IX and XII each with one pair of large *Dm* setae; VIII with small *Dl2*; IX without *Dm*, but pairs *Dl1* and *Dl2* present; X without dorsal setae; XI with *Dl1* and without *Dl2*; XII with short rounded posterodorsal process and with setae *Dl1* and *Dl2*. Abdominal apodemes with coloration identical to the rest of the sternites. Sternites I–II with many scattered microsetae. Sternite III with 22 microsetae. Sternite IV with *Vl2*, *Vl1* and *Vm2* plus four *AS* microsetae. Sternite V with *Vl2*, *Vl1A*, *Vl1B* and *Vm2*, plus six *AS*. Sternite VI with *Vm1*, *Vm2*, *Vl1A*, *Vl1B*, *Vl2*, plus six *AS*. Sternite VII with *Vm2*, *Vl1* (A and B), *Vl2*, six *AS* and without *Vm1*. Sternite VIII with *Vm2*, *Vl1*, *Vl2*, plus six *AS*. Sternite IX with *Vm1*, *Vm2*, *Vl1* and *Vl2* plus one pair of supranumeric setae between *Vl1* and *Vm2*. Sternite X with *Vm1*, *Vm2*, *Vl1* and *Vl2*. Sternite XI with *Vm1*, *Vm2* and *Vl1*. Sternite XII with six setae plus four microsetae.

Flagellum (Fig. 2). In dorsal view flagellum diamond shaped, as wide as long, with rounded lateral and apical tips; with three bulges: a pair positioned dorsosubmedian (each bulge seated on opposite sides), without setae, separated by a depression, and one bulge in the central distal region (posteromedian), with the setae *Dm4* on its apex;

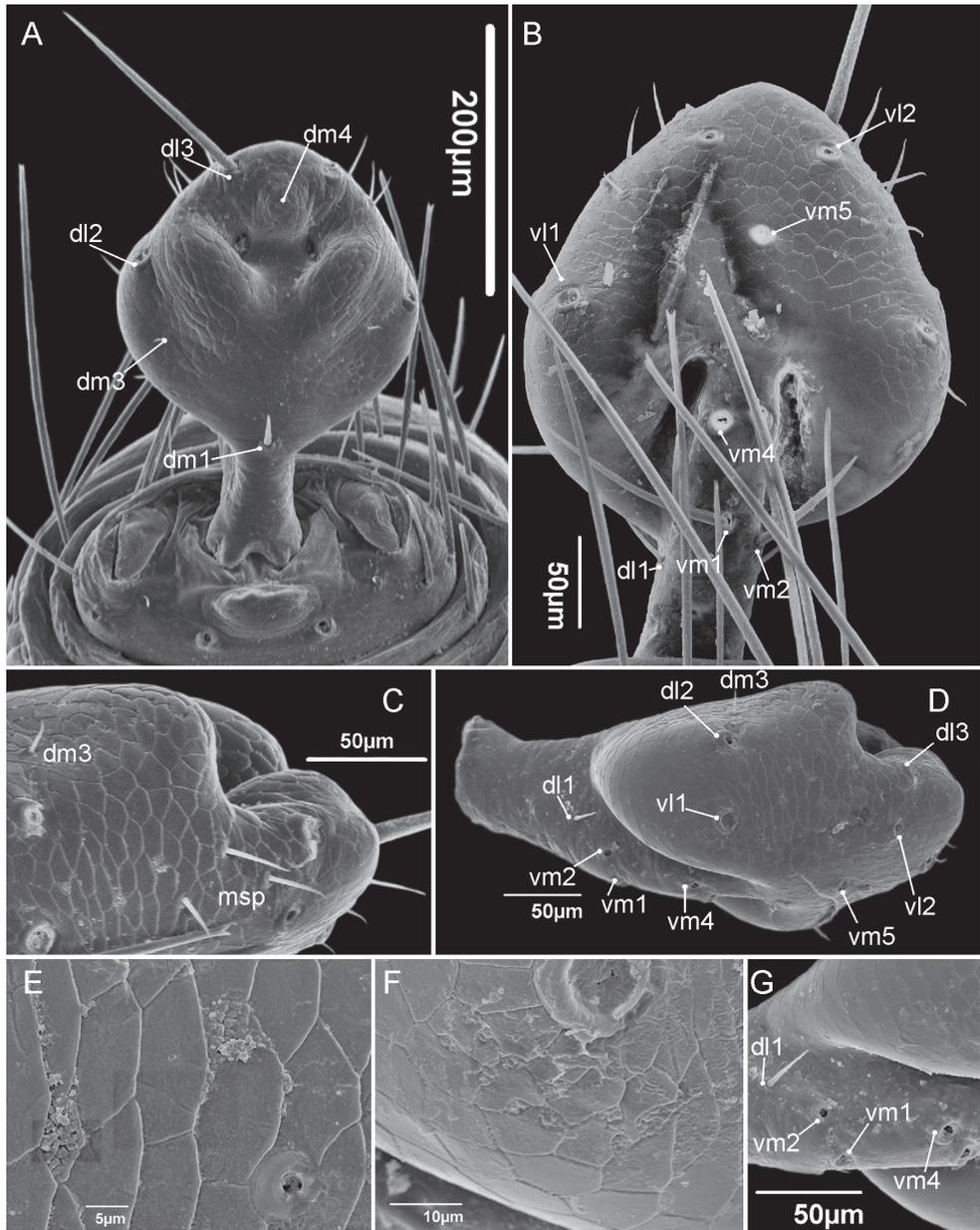


Figure 2. Male flagellum of *Rowlandius pedrosoi* sp. n. (MNRJ 04267). **A** Dorsal view **B** Ventral view **C** Detail in distolateral view **D** Lateral view **E** Uropygi gland opening **F** A set of glands below *VL1* **G** Detail of the position of the proximal ventral and lateral setae.

the central distal bulge is not connected to the lateral ones, with a depression between them. *Dm1* is exactly on the edge between the diamond-shaped part and the stalk. *DL3* is positioned distally in relation to *Dm4*. Ventrally, *Vm5* is closer to *VL2* than to *VL1*

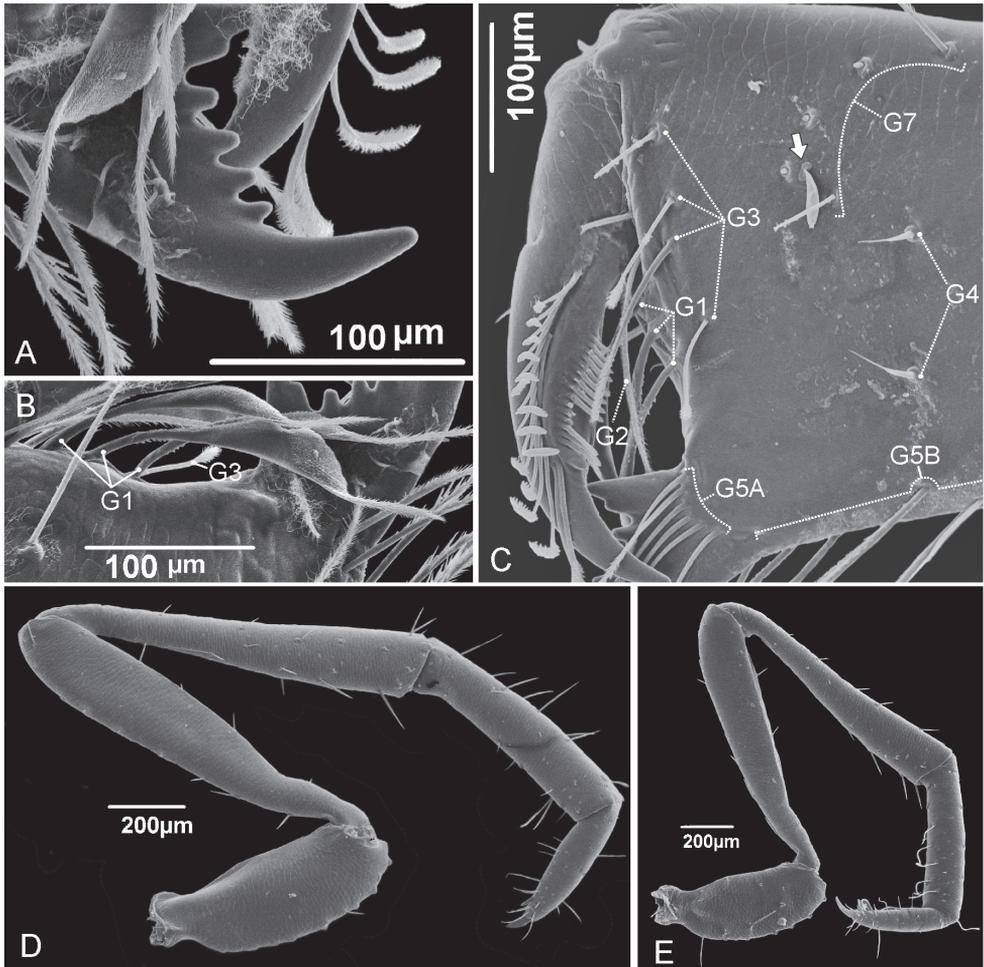


Figure 3. Details of the chelicera and pedipalps of *Rowlandius pedrosoi* sp. n., male (MNRJ 04267). **A** Fixed finger of chelicera **B** Cheliceral setae G1 **C** Mesal view of right chelicera showing setal groups; the arrow indicates the *Basidiobolus* fungus **D** Right pedipalp of a β -heteromorphic, ectal view **E** Left pedipalp of a β -heteromorphic, mesal view.

and *Vm4*. *Vm1* is closer to *Vm4* than to *Vm2*. Three microsetae on the lateral of the flagellum (msp), between the pairs *Dl2/Vl1* and *Dl3/Vl2*, closer to the latter. *Dl1*, *Vl1* and *Vl2* forming a straight line in the frontal axis. *Female flagellum* (Fig. 6A–C) with four flagellomeres (I=II=III>IV), wider between the second and third flagellomeres. Dorsally with a small *Dm1* close to the distal margin of the first flagellomere, placed in the middle line; a pair of larger *Dl1* on the wider portion of flagellum, in the point between the second and third flagellomere; one large *Dm4* in the apical portion of the third flagellomere; a pair of small *Dl4* on the fourth flagellomere in mediolateral position; a pair of large *Dl3* apically on the terminal position of the flagellum. Ventrally with a small basal *Vm1* on the first flagellomere, positioned near the distal border; a pair of median *Vm4* in the second flagellomere; one large medial placed *Vm5* on the

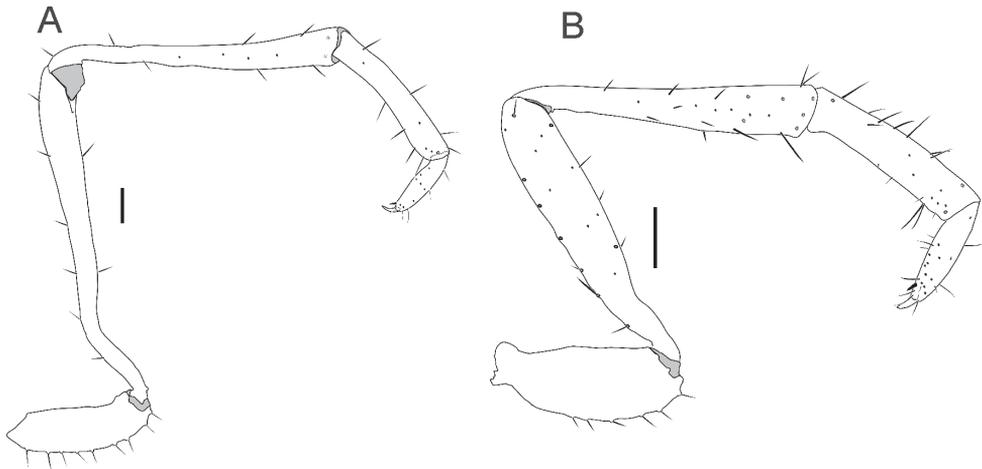


Figure 4. Right pedipalps of heteromorphic males of *Rowlandius pedrosi* sp. n., ectal view (MNRJ 04267). **A** α -heteromorphic **B** β -heteromorphic. Scale bars 0.2 mm.

third flagellomere; a pair of a large *VII* on wider portion of the flagellum, between the second and third flagellomeres; a pair of large *VI2* on the fourth flagellomeres, apically.

Chelicerae (Fig. 3A–C). Movable finger sharp and curved; serrula with 16 hyaline teeth increasing in size towards distal region; guard tooth rounded. Lamella smooth. Fixed finger with bifid basal tooth, followed by four small subequal teeth; last tooth is the biggest, recurved, with an acute apex, subequal to the basal cusp of bifid tooth. Seta-tion: G1 (setae group 1) with 3 spatulate setae; G2 with 4 feathered setae; G3 with 4 setae, all feathered dorsally and with serrated ventral surfaces; G4 with 2 setae, smooth, short and thick with thin apex; G5A with 6 similar sized feathered setae; G5B with 9 setae larger than G5A; G6 with 1 smooth setae longer than half of movable finger length; G7 with 6 setae decreasing in size from proximal to distal, feathered from the middle to its end. Setal group formula: 3–4–4–2–6–9–1–6.

Pedipalp (Figs 3D–E, 4). All segments without spinose setae. **Trochanter**: subcylindrical in α -heteromorphic males (in lateral view), longer than wide, with apical portion curved upward; short trapezoid in β -heteromorphic males and even shorter in females (Fig. 5); without apical spur (frontal projection); one ventral row of eight large setae with an intermediate row of three small setae. **Femur**: subcylindrical, club-shaped, with distal portion two times wider than the basal part; in α -heteromorphic males the femur is longer than the total length of the prosoma (pro-, meso- and metapeltidium together); in α -heteromorphic males the femur is longer than the patella (in β -heteromorphic males the femur and patella are subequal and in females the patella is longer); with few setae, only one ventral and one dorsal row of setae; on the ectal surface only one apical setae; on the mesal surface, one row of three setae. **Patella**: subcylindrical, club-shaped, with distal portion two times wider than the basal part; more setae than the femur, with two dorsal and two ventral rows, and four setae on the ectal surface. **Tibia**: cylindrical, α -heteromorphic males with distal portion slightly wider; shorter than half the length of



Figure 5. Habitus of a female of *Rowlandius pedrosoi* sp. n. (MNRJ 04267). **A** Dorsal view **B** Ventral view **C** Lateral view. Scale bars 1 mm.

the femur and patella; in β -heteromorphic males and females, the tibia, femur and the patella have similar length. The tibia has the largest number of setae on the pedipalps, with some feather-like setae on the ventral region. **Tarsus:** conical, shorter than the tibia, with lots of setae in the distal third, with two dorsolateral and two ventrolateral

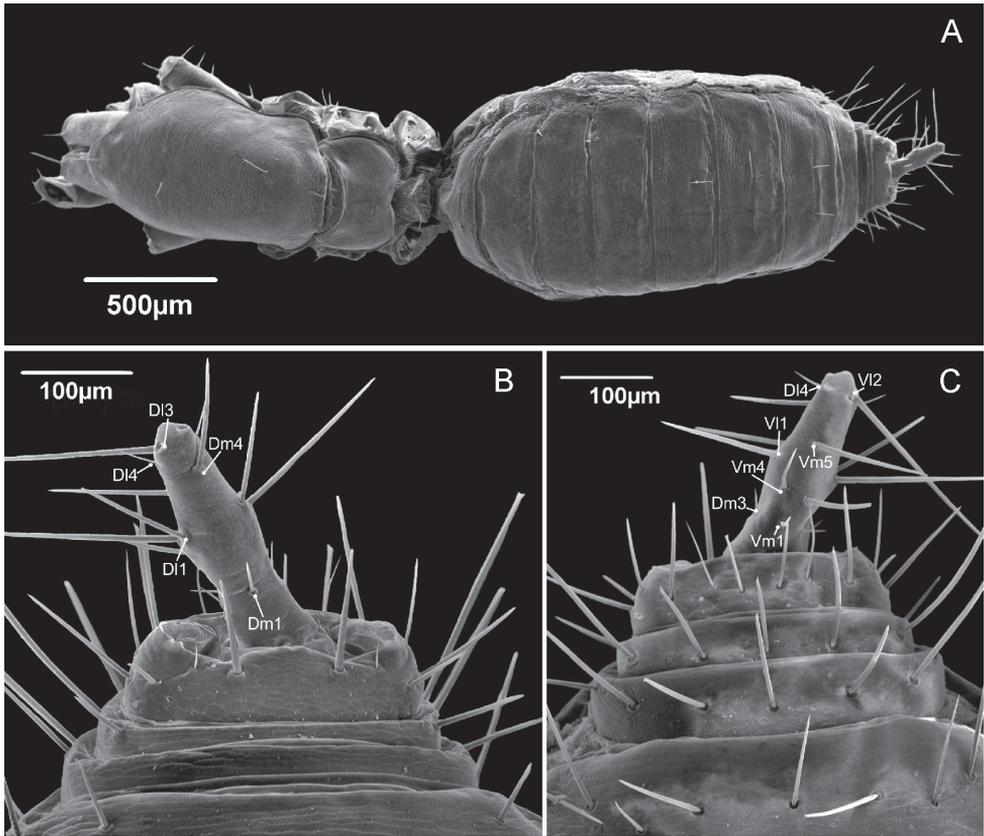


Figure 6. Details of prosoma, opisthosoma and abdomen of a female of *Rowlandius pedrosoi* sp. n. (MNRJ 04267). **A** Dorsal view of prosoma and opisthosoma **B** Dorsal view of female flagellum **C** Ventral view of female flagellum.

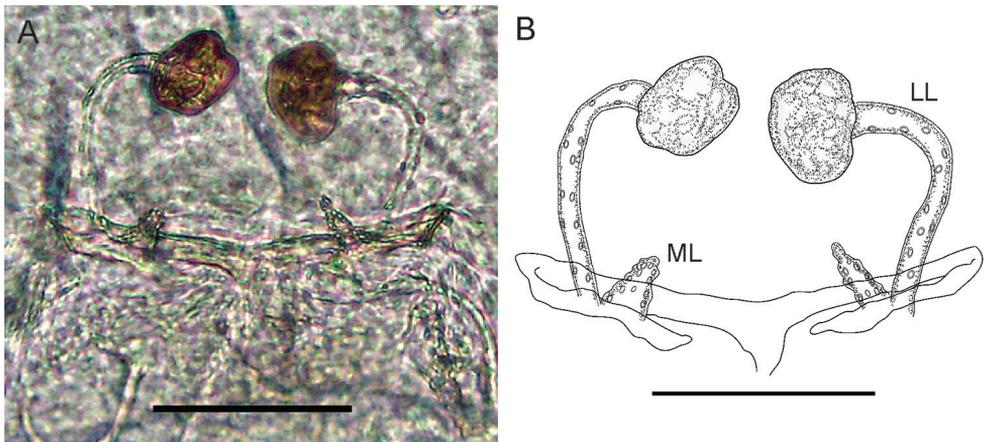


Figure 7. Spermathecae of *Rowlandius pedrosoi* sp. n. (MNRJ 04267). **A** Dorsal view picture **B** Schematic drawing. Scale bars 100 µm.

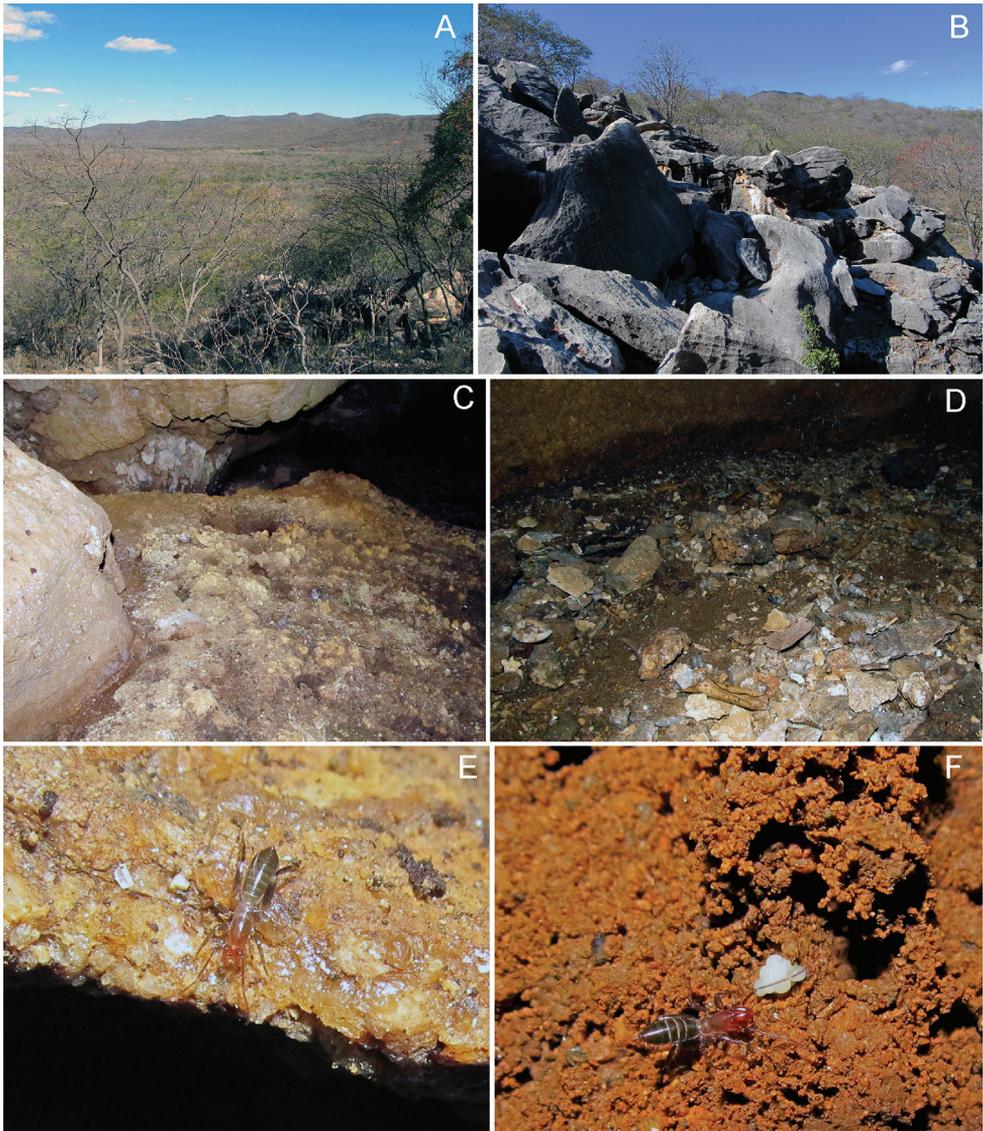


Figure 8. Habitat of *Rowlandius pedrosoi* sp. n. **A** A view of the landscape where the cave is located **B** Entrance of the cave **C–D** Microhabitat inside the cave where the specimens were collected **E** Female wandering on the cave floor **F** Female walking over some eggs.

rows of setae; two ventrodiscal spines pointing forward; tarsal claw sharp and curved, slightly larger than half the tibia length; tarsal spur present.

Spermathecae of paratype (Fig. 7). Two pairs of lobes; stalk of the lateral lobe (LL) long, curved (the tips close to each other) and very light colored (almost transparent); with few granules along the structure. Tip of the LL with a wrinkled, rounded structure (resembling a walnut), brown colored (which means it is sclerotized), of about half width of the

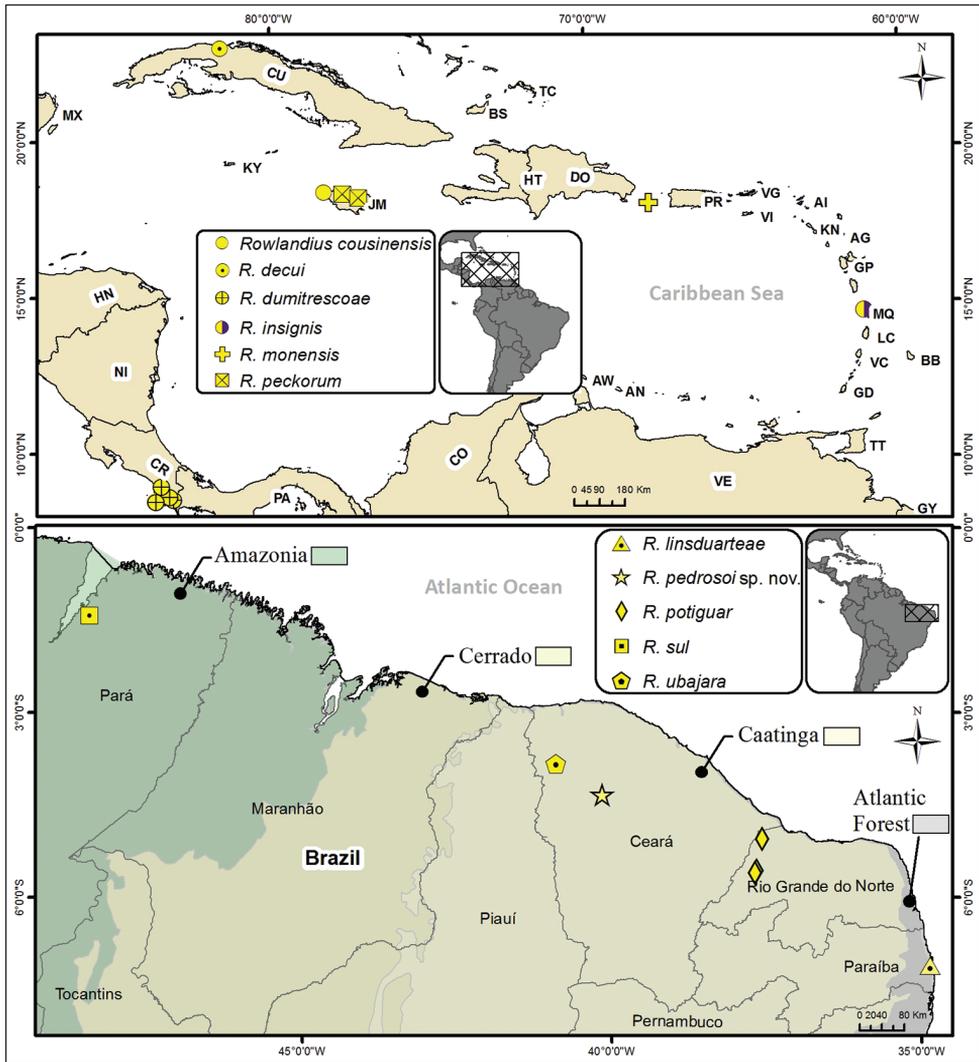


Figure 9. Map showing the distribution of the species of *Rowlandius dumitrescoae* group. The background colors in the Brazilian map represent the biomes.

stalk. The bases of LLs are separated by a distance similar to their lengths. The median lobes (ML) are short, cone-shaped, with a wide base and thin apex; its length is less than a third the size of the LL stalk; the integument is wrinkled with folds on its surface. Bases of the two lobes in contact. The chitinized arch is wider than long, cordiform (or as a “V”, as described by Santos et al. 2013), similar to *R. potiguar*, however, in *R. pedrosoi* sp. n. the arch is strongly flattened. In *R. potiguar*, the vertex of the “V” has about 90–100° (a right angle tending towards the obtuse); in *R. pedrosoi* sp. n. the same vertex is clearly more obtuse than 150°.

Distribution (Fig. 9). Only known from the type locality: Brazil, Ceará, Santa Quitéria.

Natural history. The type locality is the largest cave in the state of Ceará, formed as a sloping crack (Fig. 8A–B) and with no more than seven square meters of floor space. The specimens were found in one of the few spots with some moisture in the ground. The soil was composed of damp earth of fine sediment agglomerated with gravel, small stones, shells of gastropods and bones from small mammals (Fig. 8C–F). When captured, the schizomids were walking on stones, gravel and debris, where the light barely reached (twilight zone).

Noteworthy of mention is a rare find of a secondary capilliconidium of a (probable) *Basidiobolus* sp. fungus among the cheliceral G7 setae (Fig. 3C, arrow; cf Blackwell and Malloch (1989)). The capilliconidium produces an apical droplet of extracellular material that helps the fungus to attach to and disperse with the host (Dykstra and Bradley-Kerr 1994).

Identification keys to the species of the *dumitrescoae* group

Key to the males (*R. sul* male unknown)

- 1 Occurs in Brazil **2**
- Occurs in the Caribbean or Central America **5**
- 2 Male pedipalp trochanter trapezoid in mesal view, with biggest edge facing downwards; apical region of trochanter with a small protrusion that does not touch the articulation of the trochanter-femur; pedipalps showing sexual dimorphism, i.e. larger than those of females; males with heteromorphs; posterodorsal process-XII long **3**
- Male pedipalp trochanter cylindrical in mesal view; apical region of trochanter without a small protrusion (all apical region is the articulation trochanter-femur); males without heteromorphs; pedipalps without sexual dimorphism; posterodorsal process-XII short **4**
- 3 Posterodorsal process on abdominal segment XII with wide base (exceeding the width of the flagellum pedicel), with rhombus apex, almost as wide as the base of the process; flagellum wider in the basal third; in dorsal view, the dorsal projections of the flagellum reach the lateral border of the flagellum (see Santos et al. 2013, fig. 3A) ***R. ubajara*** (state of Ceará)
- Posterodorsal process on abdominal segment XII with narrow base (not exceeding the width of the flagellum pedicel), with thin apex (much narrower than the base); flagellum wider in the median region; in dorsal view the dorsal projections do not reach or surpass the lateral borders of the flagellum (see Santos et al. 2008, fig. 1) ***R. linsduarte*** (state of Paraíba)
- 4 Posterodorsal process on abdominal segment XII wider than long; base of the male flagellum dorsal projections not connected, i.e. with a median projection between them (see Santos et al. 2013, fig. 4A, 5A) ***R. potiguar*** (state of Rio Grande do Norte)

- Posterodorsal process on abdominal segment XII longer than wide (Fig. 6); base of the flagellum dorsal projections connected, i.e. without the median projection between them (Fig. 2) ***R. pedrosoi* sp. n.** (state of Ceará)
- 5 Flagellum with one posteromedian depression **6**
- Flagellum without a posteromedian depression **7**
- 6 Flagellum with dorsal risings in lateral view ***R. decui*** (Cuba)
- Flagellum without dorsal risings in lateral view ... ***R. dumitrescoae*** (Costa Rica)
- 7 Dorsum of flagellum, in lateral view, with big median rising, connected by a parabola-shaped region between lateral and posterior bulge
..... ***R. cousinensis*** (Jamaica)
- Dorsum of flagellum, in lateral view, flat-shaped between lateral and posterior bulge **8**
- 8 Pedipalp dimorphic (elongated segments); flagellum in lateral view with median region and stalk at the same level ***R. insignis*** (Martinique)
- Pedipalp not dimorphic; flagellum in lateral view with median region higher than the level of the stalk **9**
- 9 Flagellum lanceolate; flagellum in lateral view with flat posterior region
..... ***R. monensis*** (Jamaica)
- Flagellum nearly globose; flagellum in lateral view with elevated posterior region ***R. peckorum*** (Puerto Rico)

Key to the females

- 1 Occurs in Brazil **2**
- Occurs in the Caribbean or Central America **6**
- 2 Median lobes of spermathecae long, finger shaped; stalk of lateral lobes slightly curved and without globose structure in the apex (slightly wider than the rest of the stalk); chitinized arch procurved ***R. ubajara*** (state of Ceará)
- Median lobes of spermathecae short, cone shaped; stalk of lateral lobes curved and with globose structure in the apex; chitinized arch cordiform ... **3**
- 3 Chitinized arch of spermathecae with rounded inferior part (posterior branch); median lobes closer to the anterior part of the chitinized arc **4**
- Chitinized arc of spermathecae with “V” shaped inferior part (posterior branch); median lobes closer to the posterior part of the chitinized arc **5**
- 4 Lateral lobes of spermathecae with a winding stalk and a small globose structure at the apex (globe less than twice the width of the base) ***R. sul*** (state of Pará)
- Lateral lobes of spermathecae with an arched stalk and a large globose structure at the apex (globe twice as wide as the base) ***R. linsduarte*** (state of Paraíba)
- 5 Chitinized arch of spermathecae with central region of the anterior part “V” shaped ***R. potiguar*** (state of Rio Grande do Norte)
- Chitinized arch of spermathecae with central region of the anterior part almost straight ***R. pedrosoi* sp. n.** (state of Ceará)

- 6 Median lobes of spermathecae close to the base of the chitinized arch and distant to the base of the lateral lobes; lateral lobes long, stalk curved, apex discoid ***R. dumitrescoae*** (Costa Rica)
- Median lobes of spermathecae distant to the base of the chitinized arch and close to the base of the lateral lobes; lateral lobes long or short, stalk curved or not, and apex rounded or discoid..... **7**
- 7 Lateral lobes of spermathecae short; median and lateral lobes with their bases in the same line (one is not anterior or posterior to the other) ***R. monensis*** (Puerto Rico)
- Lateral lobes of spermathecae long; base of the lateral and median lobes not in the same line..... **8**
- 8 Posterior region of the chitinized arch of spermathecae straight ***R. cousinensis*** (Jamaica)
- Posterior region of the chitinized arch of spermathecae curved **9**
- 9 Lateral and median lobes of spermathecae close to the anterior region of the chitinized arch; median and lateral lobes with their bases in the same line ***R. peckorum*** (Jamaica)
- Lateral and median lobes of spermathecae in the center of the chitinized arch; median lobes positioned anteriorly to lateral lobes .. ***R. insignis*** (Martinique)

Discussion

In general, species groups facilitate comparisons and identifications in speciose genera as they comprise a subset of a genus, and make the process of understanding relationships

Table 1. Species groups and complexes proposed by Rowland and Reddell (1979a) and Reddell and Cokendolpher (1995) to the *dumitrescoae* group (when the species were still in *Schizomus* (R&R79) and after being transferred to *Rowlandius* (R&C95)).

Group	Complex	Species
<i>dumitrescoae</i> group	<i>dumitrescoae</i> complex	<i>R. dumitrescoae</i>
		<i>R. decui</i>
	<i>primibiconourus</i> complex	<i>R. cousinensis</i>
		<i>R. primibiconourus</i>
		<i>R. longipalpus</i>
		<i>R. brevipatellatus</i>
	<i>viridis</i> complex	<i>R. gladiger</i>
		<i>R. monensis</i>
		<i>R. desecho</i>
		<i>R. biconourus</i>
		<i>R. insignis</i>
	<i>R. peckorum</i>	
	<i>R. viridis</i>	

more comprehensible (Passos et al. 2015). Initially, only few genera were recognized in Schizomida and some of these (e.g., *Schizomus* Cook, 1899; *Trithyreus* Kraepelin, 1899) accumulated a number of species, but eventually they were subdivided, first into species groups, some of which were later recognized as new genera (Rowland and Reddell 1979a, b, 1980, 1981). The *dumitrescoae* group is an example of species group that was raised to genus. The group was defined by Rowland and Reddell (1979a) and was later transferred to *Rowlandius* by Reddell and Cokendolpher (1995). At that time, all species were from Central America (see Table 1 and Fig. 9) and were defined by the large body size, carapace with two to four pairs of dorsal and one pair of apical setae, female flagellum with four flagellomeres, spermathecae elongated laterally and reduced in the middle, and a few other characters (Rowland and Reddell 1979a). Afterwards, Armas (2002) proposed other species groups based on Cuban species and defined them using mainly characters of the pedipalp and the spermathecae (Table 2).

Studies on South American Schizomida revealed *Rowlandius* species inhabiting Brazil (Cokendolpher and Reddell 2000; Santos et al. 2008; Santos et al. 2013) and those species have a set of characters shared with some Caribbean (*R. cousinensis*, *R. decui*, *R. insignis*, *R. monensis* and *R. peckorum*) and Central American species (*R. dumitrescoae*), suggesting that the Brazilian *Rowlandius* fauna also belong to the *dumitrescoae* group. The characters present in all these species are: **1)** female spermathecae with long lateral lobes and with a broad distal expansion, **2)** median lobes short, digitiform without distal expansion, **3)** gonopod absent, **4)** chitinized arch with opened anterior branch (without AMN) and posterior branch rounded (*R. cousinensis*, *R. dumitrescoae*, *R. insignis*, *R. monensis* and *R. peckorum*), or anterior branch closed and posterior branch retrocurved (*R. pedrosoi* sp. n. and *R. potiguar*)

Table 2. *Rowlandius* species groups and complexes proposed by Armas (2002).

Groups	Subgroups	Species	Diagnostic character
I		<i>R. biconourus</i>	"Presence of a dorsal spur on the heteromorphic pedipalp trochanter of the male."
		<i>R. ramosi</i>	
		<i>R. recuerdo</i>	
II		<i>R. abeli</i>	"Spermathecae differs significantly from the general pattern present in congeners."
III		<i>R. decui</i>	"Spermathecae with the terminal bulb underdeveloped and short middle lobe."
		<i>R. digitiger</i>	
IV		<i>R. cubanacan</i>	"Long and subequal spermathecae with the terminal bulb underdeveloped."
		<i>R. labarcae</i>	
V	V-1	<i>R. negreai</i>	"Spermathecae with terminal bulbs well developed, with lateral lobes clearly longer and with a larger bulb."
		<i>R. monticola</i>	
	V-2	<i>R. baracoae</i>	
	V-3	<i>R. toledo</i>	
		<i>R. gladiger</i>	
		<i>R. alayoni</i>	
		<i>R. siboney</i>	
	<i>R. terueli</i>		

Table 3. Measurements of *Rowlandius pedrosoi* sp. n. specimens.

Body	Male holotype MNRJ 4266	Female paratype MNRJ 4267
Total body: L	4.01	3.85
Propeltidium: L	1.25	0.98
Propeltidium: W	0.67	0.61
Metapeltidium: L	0.62	0.24
Metapeltidium: W	0.25	0.29
Abdomen: L	2.3	2.00
Abdomen: W	0.9	0.92
Flagellum: L	0.37	0.25
Flagellum: W	0.23	0.07
Pedipalp: L		
trochanter	0.82	0.58
femur	2.06	0.56
patella	1.84	0.62
tibia	0.91	0.53
tarsus + claw	0.54	0.41
Leg: I L		
coxa	0.42	0.61
trochanter	0.33	0.33
femur	1.18	1.23
patella	1.55	1.53
tibia	1.07	0.99
basitarsus	0.33	0.21
telotarsus	0.55	0.3
Leg: IV L		
femur	1.06	1.24
patella	0.51	0.55
tibia	0.82	0.89
basitarsus	0.67	0.67
telotarsus	0.47	0.46

or rounded (*R. linsduarte*, *R. ubajara* and *R. sul*), **5**) males with pedipalp elongated (such as *R. decui*, *R. dumitrescoae*, *R. insignis*, *R. potiguar* and *R. pedrosoi* sp. n.), and **6**) male flagellum never trilobate in dorsal view, but diamond-shaped and with dorsal projection (absent in *R. dumitrescoae* and reduced in *R. decui*). Santos et al. (2008) already noted that *R. linsduarte* and *R. sul* are more closely related to each other than to any other species based on the female genitalia, but did not include them in any group. Here a new composition of the *dumitrescoae* group is proposed based on the above-mentioned characters (see also Table 4).

Some *Rowlandius* illustrated in the literature are potentially part of the *dumitrescoae* group, but are not presently included, once no material was accessible during the preparation of the work. One of them is an undescribed species from Tortuguero,

Table 4. List of species maintained, removed, and added to the *dumitrescoae* group.

Species maintained	Species removed	Species added
<i>R. cousinensis</i>	<i>R. primibiconourus</i> *	<i>R. linsduarte</i>
<i>R. decui</i>	<i>R. longipalpus</i>	<i>R. potiguar</i>
<i>R. dumitrescoae</i>	<i>R. gladiger</i>	<i>R. sul</i>
<i>R. monensis</i>	<i>R. desecho</i>	<i>R. ubajara</i>
<i>R. peckorum</i>	<i>R. biconourus</i>	<i>R. pedrosoi</i> sp. n.
<i>R. insignis</i>	<i>R. viridis</i>	

*This species was removed because its documentation in the literature is insufficient and we had no access to specimen; see discussion for details.

Costa Rica, illustrated by Armas (2009) (see fig. 3D); the spermathecae of the specimen fits the present definition of the *dumitrescoae* group, but as the species was not formally described and the male is not known, the correct relationship of the morphospecies cannot be assured by now. Another species that can potentially be part of the group is *R. viridis*; Rowland and Reddell (1979a) illustrated this species from four localities, and one of them (from Pedro Great Cave, Clarindon Parish) is similar to the standard shape of the *dumitrescoae* group, but since there is a huge variation in the size and shape of the lobes in this species, further studies are needed before reaching a conclusion on those populations.

An interesting character observed in some species of *Rowlandius* (e.g. *R. dumitrescoae*, *R. insignis*, *R. potiguar* and *R. pedrosoi* sp. n.) is the strong sexual dimorphism of the palps. The femur and patella of the pedipalps are extremely long in α -heteromorphic males compared to females and homeomorphic males, as reported by Santos et al. (2013). Other cases of elongated male-dimorphic appendages in arachnids are found in harvestmen (Orrico and Kury 2009; Buzatto et al. 2011; Zatz et al. 2011) and whip spiders (Vasconcelos et al. 2014). It is possible that the elongate pedipalps of *R. pedrosoi* sp. n. evolved due to sexual selection pressures, similarly to that found in *R. potiguar* (Santos et al. 2013).

Rowlandius is the only short-tailed whip scorpion genus found in the dry biome of Caatinga (Santos et al. 2008; Santos et al. 2013). The four schizomid species found in that harsh environment (*R. linsduarte*, *R. pedrosoi* sp. n., *R. potiguar* and *R. ubajara*) are restricted to protected places, such as forests or caves, where the temperature is mild, the humidity is high and the variation these environmental conditions is lower. These species appear to be limited to these hypogean habitats, but they do not have apparent troglomorphisms and their presence in caves may be a recent invasion after climate change in Northeastern Brazil and retraction of the forest (Santos et al. 2007). The small size and the relatively thin cuticle of schizomids makes them sensitive to dehydration and caves serve as a suitable habitat for these animals (Oliveira and Ferreira 2014). The exotic species *Stenochrus portoricensis* Chamberlim, 1922, for example, has already been found in caves in Central Brazil (Gallão et al. 2015).

Acknowledgments

We thank Denis Rafael Pedrosa (MNRJ) and Flávia Pellegatti Franco for collecting the material and providing specimens for description; Henrik Enghoff for helping with the identification of the *Basidiobolus* fungus; Lars Vilhelmsen for checking the English; *Plataforma de Microscopia Eletrônica Rudolf Barth* (FIOCRUZ – IOC) and its technologists and technicians Roger, Wendell and Rômulo for helping with the SEM. We are also grateful to Mario Gatti and Rodolfo Armando da Cunha from *Coleção Micológica Trichocomaceae* (FIOCRUZ – IOC) for making available the microscope for image capture, to José Augusto Martins Roxinol (UFV; SISBIOTA 563360/2010-0) for donating a specimen of *R. ubajara* and Caroline Fukushima (IBSP) and Wilmar Silva (IBSP) for donating specimens of *R. potiguar* (this material was collected in the scope of the project “*Biodiversidade de Aranhas Migalomorfas* (Araneae, Mygalomorphae) *de diferentes formações vegetais do Rio Grande do Norte, Brasil*” (CAPES #23038.00814/2011-83)). We are also grateful to the reviewers James Cokendolpher, Mark Harvey and Jairo A. Moreno-González for the important corrections and comments that helped improve the quality of the article. This study was partly supported by grants from *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES, www.capes.gov.br/) to OVM (process number 5900115 CAPES/PEC-PG) and to GSM (process number 8922-13-6 CAPES/Science Without Borders). GSM is also grateful for the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate (grant number DNRF96).

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A new species of *Lathys* from Turkey (Araneae, Dictynidae)

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Academic editor: *Shuqiang Li* | Received 10 August 2016 | Accepted 28 October 2016 | Published 16 November 2016

<http://zoobank.org/97C54E02-F8C2-4B8C-BF42-02EEEB1EE028>

Citation: Özkütük RS, Marusik YM, Elverici M, Kunt KB (2016) A new species of *Lathys* from Turkey (Araneae, Dictynidae). ZooKeys 632: 35–45. doi: 10.3897/zookeys.632.10130

Abstract

A new species, *Lathys ankaraensis* **sp. n.**, is described based on the material collected in the Central Anatolia. The new species belongs to the *humilis*-group. Habitus, as well as copulatory organs of both sexes, are described and illustrated by means of line drawings and digital and SEM photographs. A key for the four *Lathys* species known in Turkey is also provided.

Keywords

Aranei, Asia, Central Anatolia, meshweb spiders

Introduction

Lathys Simon, 1884 with 45 known species, is one of the largest genera of Dictynidae distributed chiefly in the Holarctic (WSC 2016). So far, three species of *Lathys* have been reported from Turkey: *L. humilis* (Blackwall, 1855), *L. lehtineni* Kovblyuk, Kastrygina & Omelko, 2014, and *L. stigmatisata* (Menge, 1869) (Bayram et al. 2016). All species were recently redescribed in details by Marusik et al. (2006, 2009a,b) and Kovblyuk et al. (2014). Recent field studies focused on litter sampling revealed one more species new to science. It was found in several localities from woodland habitats in Central Anatolia.

The goal of this paper is to provide a description of the new species together with notes comparing the two sibling species.

Material and methods

Examined specimens were collected from the Central Anatolia region of Turkey by using a litter reducer (Fig. 1). The specimens were preserved in 70% ethanol. Digital images of the copulatory organs were taken with a Leica DFC295 digital camera attached to a Leica S8AP0 stereomicroscope and several photographs were taken in different focal planes and combined using auto montage software. SEM microphotographs were made from dried and sputter coated (by gold) organs by use of a Zeiss Ultra Plus SEM device (Anadolu University, Eskişehir). All measurements are in millimeters.

The following abbreviations were used in the text:

Fe	femur,
Me	metatarsus,
Pa	patella,
Ta	tarsus,
Ti	tibia.

Depositories: AUZM, Anadolu University Zoological Museum (Eskişehir, Turkey); ZMMU, Zoological Museum of Moscow University (Moscow, Russia).

Drawings 8–16 and 17–21 are made by M. Kovblyuk and Z. Kastrygina.



Figure 1. Distribution map of four Turkish *Lathys* spiders.

Taxonomy

Lathys ankaraensis sp. n.

<http://zoobank.org/23A710E1-61A5-4415-B5C6-DC256FAB07B2>

Figs 2–5, 8–11, 17–19, 22–28, 31–35, 37–40

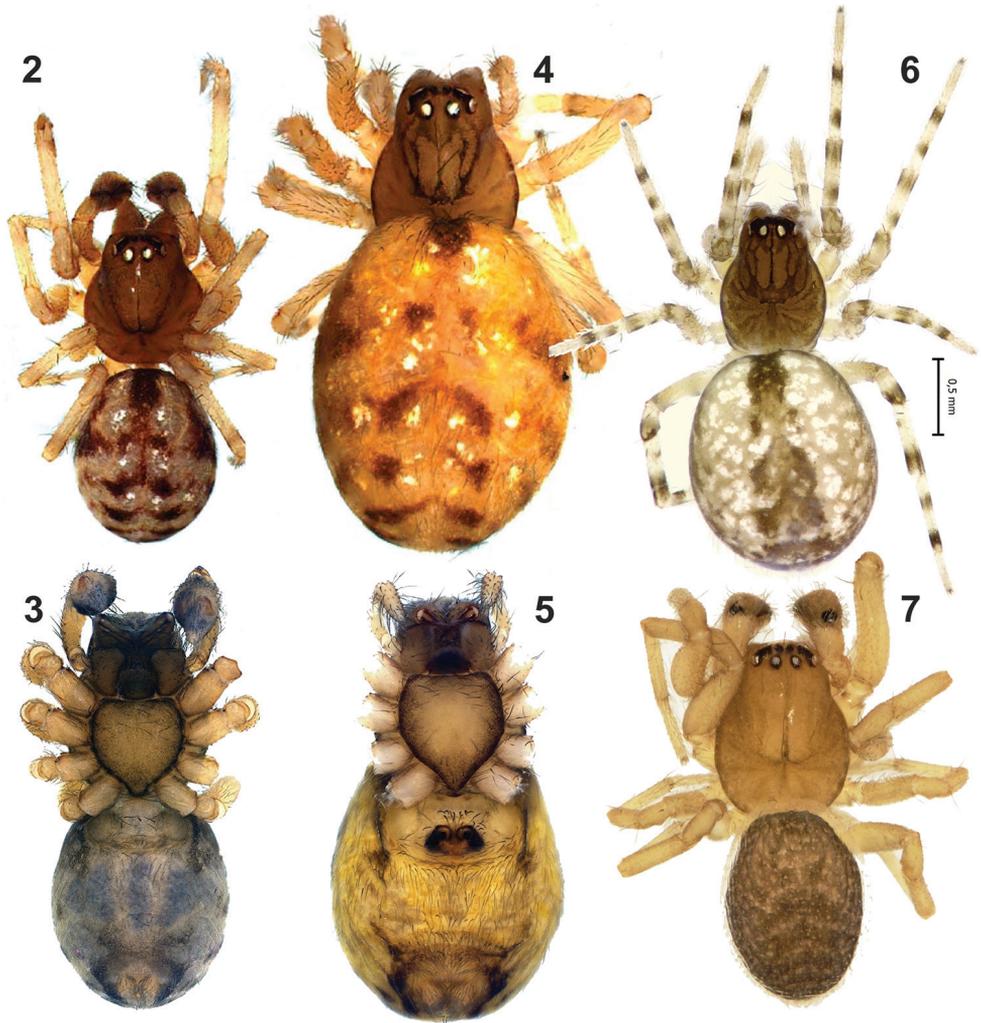
Material examined. Holotype ♂ (AUZM) Ankara Province, Çankaya District, Türkkonut, Dodurga Village (40°0'26.01"N; 32°35'23.78"E), 1090 m, 27 May 2012, M. Elverici leg. Paratypes 6♂, 13♀ (AUZM); ♂, 2♀ (ZMMU) same data as holotype; 5♀ (ZMMU) Eskişehir Province, Centrum, Meşelik Area (39°43'25"N; 30°29'17"E), 980 m, young pine stand with oak shrubs, 26 September 2010, Y.M. Marusik leg.; 2♀ (ZMMU) Eskişehir Province, Çatacak Forests (39°55'54"N; 31°08'22"E), 1190 m, pine stand with few oaks, 27 September 2010, Y.M. Marusik leg.; 2♂ (ZMMU) Ankara Province, Çamlıdere District (40°32'42.54"N; 32°30'0.00"E), 960 m, litter under *Pinus* trees, 28 May 2009, Y.M. Marusik leg.; 2♀ 2 juv. (ZMMU) Ankara Province, Çankaya District, Dodurga Village (39°49'16.20"N; 32°40'5.90"E), 1080 m, shrubby oak stands in steppe, sifting litter, 1 January 2013, Y.M. Marusik leg.; 2♀ (AUZM) Sivas Province, İmranlı District, Yapraklıpınar Village (39°47'52.93"N; 38°5'3.75"E), 1700 m, 14 October 2015, K.B. Kunt leg.; 3♂, 2♀ (AUZM) Sivas Province, Gemerek District, İkizce Village (39°12'52.84"N; 36°10'23.48"E), 1290 m, shrubby oak stands in steppe, 20 November 2015, K.B. Kunt leg.; 2♂, 5♀ (AUZM) Kayseri Province, Pınarbaşı District, Kazancık Village (39°3'41.26"N; 36°33'54.93"E), 1600 m, 29 April 2016, K.B. Kunt leg.

Derivatio nominis. The specific name is a toponym that refers to the type locality, Ankara, capital city of the Republic of Turkey.

Diagnosis. *Lathys ankaraensis* sp. n. belongs to the *humilis* species group represented by two species in the West Palaearctic, *L. humilis* (Blackwall, 1855) and *L. nielsenii* (Schenkel, 1932). It can be distinguished from the congeners by a combination of the following characters: having white guanine spots on dorsum of abdomen (absent in *L. nielsenii*), longer copulatory ducts (*Cd*) with a series of loops (Figs 18, 24, 39) (single loop in the congeners), partially fused atria (*At*, separated in *L. humilis*), wider septum (*Se*) occupying anterior half of fovea (thin and long in *L. humilis*), and straight posterior tip of conductor (*Tc*) (slightly bent in *L. humilis*, cf. Figs 10 and 14).

Description. Measurements. **Male.** Holotype ♂: total length 2.00; carapace 1.00 long, 0.72 wide, 0.38 high; chelicerae 0.53 long. Paratypes ♂ (n=9): total length 1.78–2.36; carapace 0.72–1.20 long, 0.66–0.83 wide; 0.35–0.40 high; chelicerae 0.37–0.54 long.

Carapace dark greenishbrown. Cephalic region higher than thoracic region. Fovea distinct, blackish. Darkly colored crack-like pattern with indistinct borders apparent around fovea, at the corners of thoracic region and at the rear side of PME. Anterior eyes arranged in almost straight line. Chelicera color as carapace. Anterior surface of chelicera with irregularly distributed blackish setae of varying sizes, raised on small pits. Anterior

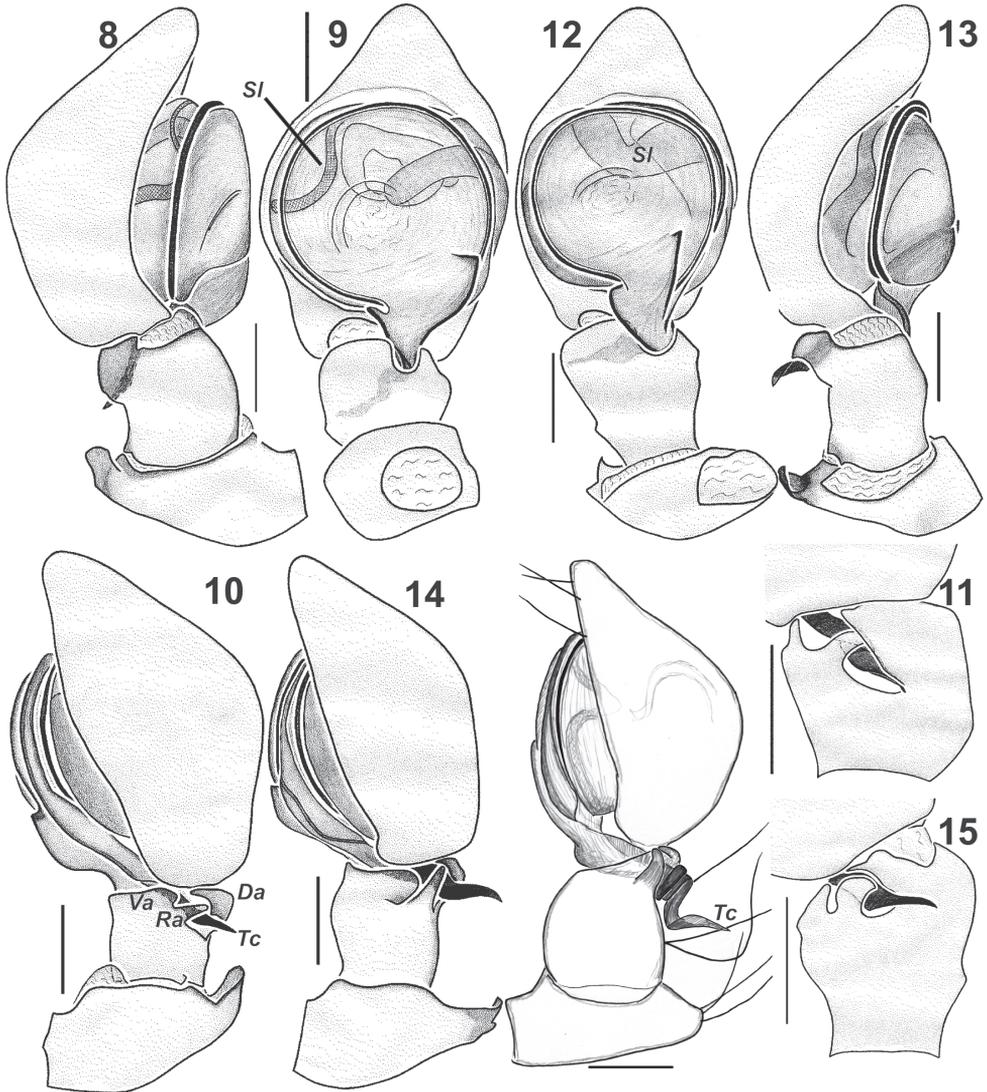


Figures 2–7. Habitus of *Lathys ankaraensis* sp. n. (2–5), *L. humilis* (from Turkey 6) and *L. stigmatisata* (from Crimea 7). 2, 7 male, dorsal 3 male, ventral 4, 6 female, dorsal 5 female, ventral.

margin of the cheliceral groove with four teeth, and posterior margin with three. Teeth on posterior margin smaller than anterior teeth, and almost identical in size to each other. Gnathocoxae yellowish brown, longer than wide, with sparsely distributed tiny, blackish, short setae on the surface. Labium trapezoid, slightly wider than long; darker in color compared to gnathocoxae. Sternum yellowish light brown, dark brown at the edges, with blackish setae on the surface varying in size especially towards the edges. Legs greyish light brown, with blackish setae in all segments, especially intense on ventral surfaces.

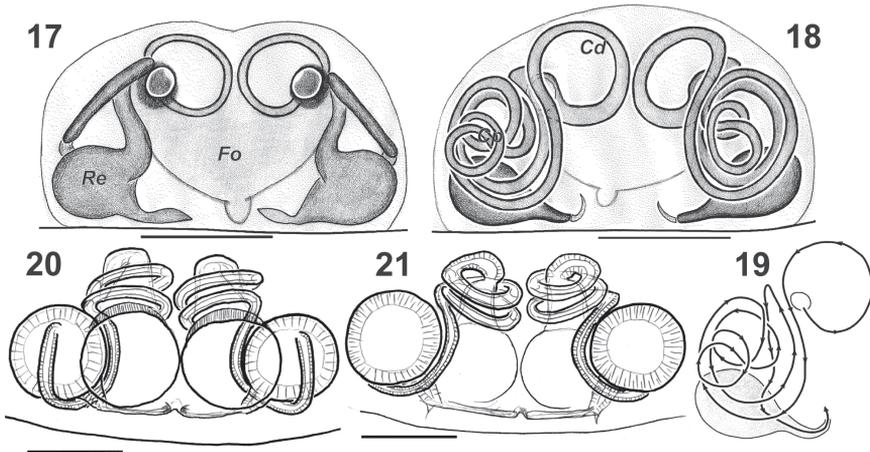
Posterior part of segments with dark rings.

Abdomen oval, with a characteristic pattern. Abdominal pattern forming a blackish-brown longitudinal band starting from the middle of the anterior side, barely reaching

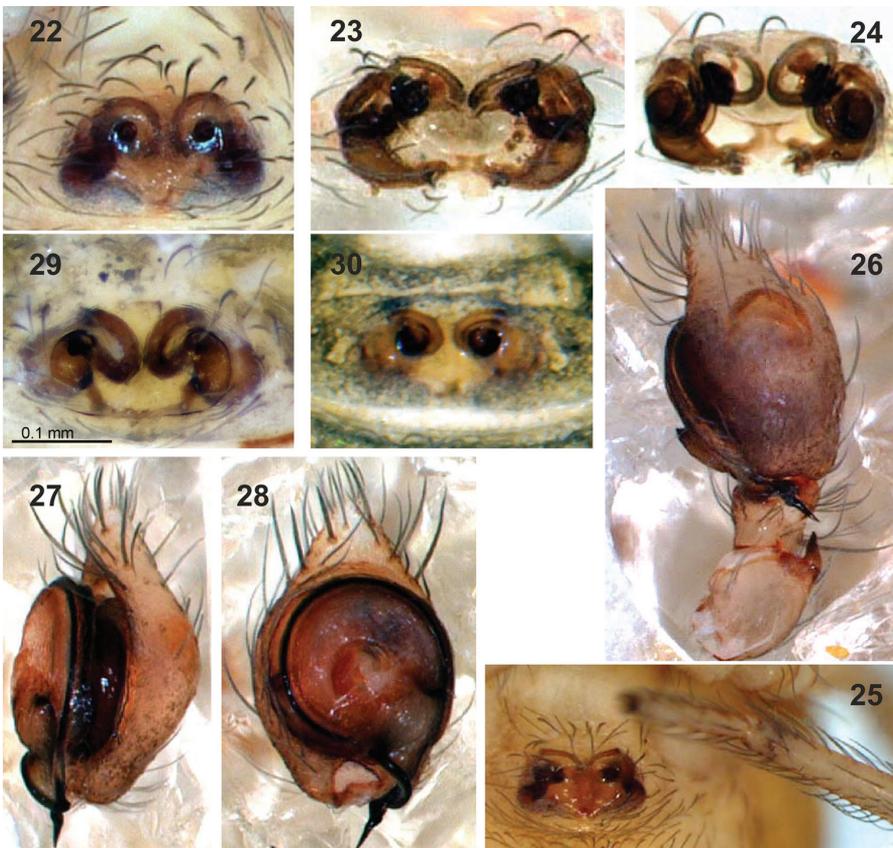


Figures 8–16. Male palps of *Lathys ankaraensis* sp. n. (8–11), *L. humilis* (from Turkey 12–15) and *L. stigmatisata* (from Crimea 16). 8, 13 prolateral 9, 12 ventral 10, 14, 16 retrolateral 11, 15 tibia, tip of conductor and base of cymbium, dorso-retrolateral. Abbreviations: **Da** dorsal apophysis; **Ra** retrolateral apophysis; **SI** loop of seminal duct; **Tc** posterior tip of conductor; **Va** ventral apophysis.

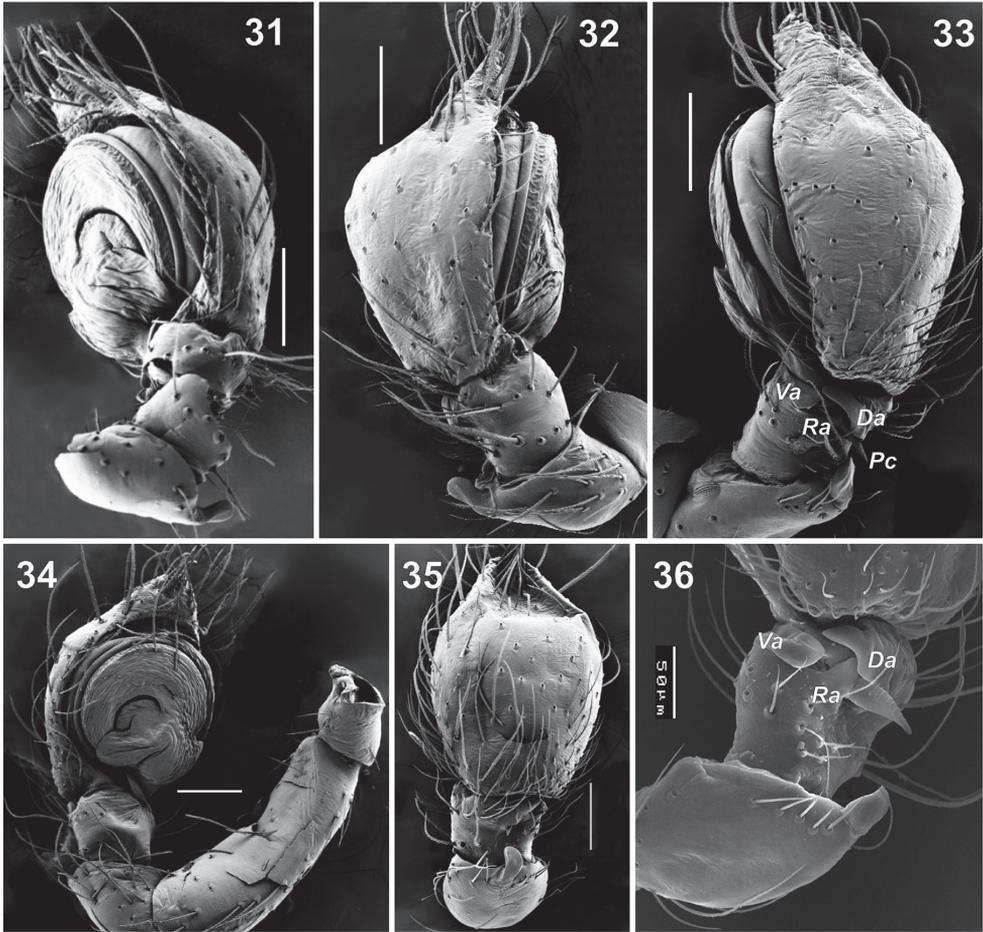
to the middle of abdomen, followed by five chevrons on the posterior. A variable dark colored pattern apparent on sides; tends to join with the first chevron at the anterior half. Apart from the specified patterns, dorsal side of abdomen grayish light brown, with variably distributed bright white spots. Ventral side of abdomen generally light in color, usually grayish, brown in some specimens.



Figures 17–21. Epigynes of *Lathys ankaraensis* sp. n. (17–19) and *L. stigmatisata* (from Crimea 20–21). 17, 20 ventral 18, 21 dorsal 19 schematic drawing of insemination duct. Abbreviations: **Cd** copulatory ducts; **Cp** other coils; **Fo** fovea; **Re** Reseptacle.



Figures 22–30. Copulatory organs of *Lathys ankaraensis* sp. n. (22–28), *L. humilis* (from Turkey 29) and *L. nielsenii* (from Finland 30).

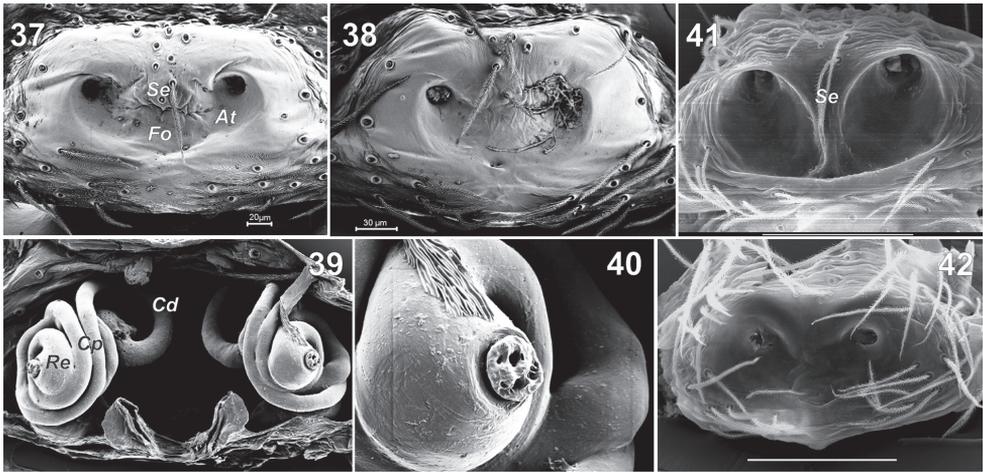


Figures 31–36. Male palps of *Lathys ankaranaensis* sp. n. (**31–35**) and *L. stigmatisata* (from Crimea **36**). **31** posterior-retrolateral **32** prolateral **33, 36** dorso-retrolateral **34** ventral **35** dorsal. Abbreviations: **Da** dorsal apophysis; **Pc** posterior arm of conductor; **Ra** retrolateral apophysis; **Va** ventral apophysis.

Palp as in Figs 8–11, 26–28, 31–35; patella with flat dorsal apophysis located on conical dorsal extension; tibia with three apophyses: ventral (*Va*), retrolateral (*Ra*) and dorsal (*Da*); cymbium conical, its height subequal to half of the length; posterior arm of conductor (*Pc*) with almost straight tip locked by three tibial apophyses and cymbium; sperm duct makes a loop (*Sl*) at approximately the 10 o'clock position (Fig. 9).

Female. Paratypes ♀ (n=10). Total length 1.90–2.60; carapace 0.54–0.80 long, 0.52–0.56 wide, 0.29–0.40 high; chelicerae 0.25–0.36 long.

Females slightly lighter than males. Crack-like blackish pattern on carapace much more distinct in females. Dorsal pattern on abdomen distinct but usually duller in color compared to males. Calamistrum with eight setae, slightly longer than half of metatarsus. Spines lower in number compared to males. For leg measurements see Table 1.



Figures 37–42. Epigynes of *Lathys ankaraisensis* sp. n. (37–40), *L. humilis* (from Crimea 41) and *L. nielsenii* (from Finland 42). 37–38, 41–42 ventral 39 dorsal 40 receptacle with gland; dorsal. Abbreviations: **At** atrium; **Cd** copulatory ducts; **Cp** posterior coils; **Fo** fovea; **Re** Receptacle; **Se** septum.

Table I. Leg measurements of *Lathys ankaraisensis* sp. n.

Legs	Fe	Pa	Ti	Me	Ta	Total
♂ / ♀						
I	0.83 / 0.66	0.33 / 0.27	0.75 / 0.52	0.63 / 0.43	0.33 / 0.29	2.87 / 2.15
II	0.70 / 0.59	0.30 / 0.24	0.62 / 0.44	0.54 / 0.36	0.32 / 0.26	2.48 / 1.88
III	0.61 / 0.50	0.26 / 0.22	0.40 / 0.32	0.48 / 0.32	0.30 / 0.22	2.05 / 1.55
IV	0.67 / 0.63	0.27 / 0.25	0.58 / 0.47	0.51 / 0.46	0.30 / 0.26	2.33 / 2.04

Epigyne as in Figs 17–19, 22–25, 37–40; fovea (*Fo*) wide, twice as wide than long, with two partly fused atria (*At*), septum (*Se*) located in anterior half of fovea, wide, covered with few setae. Endogyne with small receptacles (*Re*) and long copulatory ducts forming several coils in two plains, anterior part with one coil (*Cl*) almost parallel to the epigynal plate, and other coils (*Cp*) make several loops around receptacles.

Natural history. It seems that adult specimens of the new species can be found throughout the whole year. *Lathys ankaraisensis* sp. n. was found exclusively in the litter under pine trees or oak bushes (Fig. 43).

Comments. The first record of the genus *Lathys* from Turkey has been provided with *L. humilis* from the Marmara region (Tekirdağ province; European part of Turkey; van Helsdingen 2013). Subsequent records were presented more recently as *L. lehtinenii* and *L. stigmatisata* respectively from the Aegean (Aydın Province, Danışman et al. 2014) and Central Anatolia (Koçyiğit et al. 2016) regions.

With description of *L. ankaraisensis*, the number of *Lathys* species known from Turkey has increased to four and number of dictynid species to twenty (Bayram et al. 2016). These numbers are expected to increase in near future as there are species known from the close vicinity such as *L. cambridgei* (Simon, 1874), *L. spasskyi*

- 3 Palpal patella with dorsal conical outgrowth (Fig. 16), tip of conductor coiled with terminal loop wider than conductor.....*L. stigmatisata*
 – Palpal patella without dorsal conical outgrowth, the terminal loop of conductor not wider than other loops *L. lehtineni*

Females

- 1 Abdomen with white guanine spots, epigyne with one atrium, copulatory openings widely spaced.....**2**
 – Abdomen without white guanine spots, epigyne without atrium, but with two separate openings**3**
 2 Atrium with a septum (Fig. 41), insemination ducts short, not encircling receptacle..... *L. humilis*
 – Atrium without septum (Figs 37–38), insemination ducts long, encircling receptacles (Fig. 18, 24, 39) *L. ankaraensis* sp. n.
 3 Copulatory openings small, spaced by approx. 1/2 diameters..... *L. lehtineni*
 – Copulatory openings large, separated by thin septum (Fig. 20)*L. stigmatisata*

Acknowledgements

This work was supported by the Research Foundation of Anadolu University (Project Number: 1503F093). We are deeply indebted to Dr. Müjdat Çağlar (Eskişehir, Turkey) for providing assistance during SEM photography. All drawings presented in this paper were made by Dr. Mykola Kovblyuk and Mrs. Zoya Kastrygina (Simferopol, Ukraine). The English of an earlier draft was corrected by Dr. Terry Howell (Ankara, Turkey).

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A new genus and species of Tettigarctidae from the Mesozoic of northeastern China (Insecta, Hemiptera, Cicadoidea)

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Academic editor: B. Price | Received 3 August 2016 | Accepted 26 October 2016 | Published 16 November 2016

<http://zoobank.org/FF0FA369-9E8A-4813-A7B9-FF0232B1F889>

Citation: Zheng Y, Jun Chen J, Wang X (2016) A new genus and species of Tettigarctidae from the Mesozoic of northeastern China (Insecta, Hemiptera, Cicadoidea). ZooKeys 632: 47–55. doi: 10.3897/zookeys.632.10076

Abstract

A new genus *Maculaprosbole* of Tettigarctidae with a new species *M. zhengi* is described based on a complete fossil forewing from the Mesozoic of northeastern China. Due to its broad costal area and clavus, *Maculaprosbole zhengi* **gen. et sp. n.** can be attributed to the subfamily Cicadoprosbolinae. This genus is similar to the genera *Sanmai* and *Hirtaprosbole* in coloration pattern and forewing venation, respectively. However, it differs from *Hirtaprosbole* in crossvein r-m absent and apical CuA section strongly curved, running along the nodal line for a distance, and *Sanmai* in transverse coloration mainly focusing on the postnodal area. Herein, the prominent coloration pattern of this new taxon is discussed.

Keywords

Coloration pattern, Daohugou, Tettigarctidae, taxonomy

Introduction

Tettigarctidae, the most primitive family of Cicadoidea, is now relict with only two modern species attributed into one genus (Moulds 1990, 2012, Shcherbakov 2009). The taxonomy of the Tettigarctidae is based mainly on the fore- and hindwing venation (Shcherbakov 2009, Li et al. 2012), and this family is divided into two subfamilies

based on forewing features: Cicadoprosobolinae Evans, 1956 and Tettigarctinae Distant, 1905 (Wang B and Zhang 2009, Li et al. 2012). The fossils records of the Mesozoic Tettigarctidae are rather diverse (Nel 1996, Nel et al. 1998, Dietrich 2002, Menon 2005, Moulds 2005, Wang B and Zhang 2009, Wang B et al. 2013). The earliest Tettigarctidae appeared in the earliest Jurassic and terminal Triassic (ca. 200 Myr) of Eurasia (Shcherbakov 2009). The *Paratettigarcta zealandica* at around 23 ~ 16 Ma is known as the youngest Tettigarctidae fossil (Kaulfuss and Moulds 2015). Up to now, 27 genera and 40 extinct species (Liu et al. 2015, Kaulfuss and Moulds 2015, Chen and Wang B 2016, Chen et al. 2016) of Tettigarctidae have been reported from all over the world, ranging from the Late Triassic to the Eocene, and are distributed from Northern Hemisphere to Southern Hemisphere, Eurasia, Australia, Africa, and England, etc (Shcherbakov and Popov 2002, Martins-Neto et al. 2003, Wappler 2003, Shcherbakov 2009). Beyond that, two living species within one genus of Tettigarctidae are restricted to high altitude habitat in continental South Australia and Tasmania (Carver et al. 1992, Moulds 1990, Moulds 2005, Li et al. 2012, Liu et al. 2016).

A large number of fossils, especially the highly diverse array of insects, have been well-known and described from Daohugou based on the exceptionally well-preserved materials, showing sharp details of morphology, taxonomy and evolution (Rasnitsyn et al. 2006, Pott et al. 2012, Wang B et al. 2013, Chen et al. 2014, Wang H et al. 2015). To date, 25 insect orders have been reported from the Daohugou Biota (Huang 2010, Li et al. 2010, 2013, Wang B et al. 2013). In Tettigarctidae, eleven species within seven genera had been described from Daohugou to date (Wang B and Zhang 2009, Li et al. 2012, Chen et al. 2014, Chen et al. 2016, Chen and Wang B 2016, this study). The Tettigarctidae, in fact, is a particular group which is known to be much more rich in Daohugou than in any other fauna (Wang B and Zhang 2009, Wang B et al. 2013, Chen et al. 2016). However, their systematic position is still not very clear (Wang B and Zhang 2009, Li et al. 2012, Liu et al. 2016).

In this paper, a new fossil genus is confirmed and described, with a new species of the Tettigarctidae from Daohugou in northeast China.

Material and methods

The fossil specimen studied herein was collected from the Middle Jurassic Daohugou deposits (41°18.31'N; 119°13.18'E) in Ningcheng Country, Chifeng City, Inner Mongolia of China. Very recently some studies indicate Daohugou is enjoyed a humid and warm-temperate climate in the Middle Jurassic based on the palaeoenvironmental reconstructions (Ren and Krzeminski 2002, Wang B et al. 2013, Na et al. 2015). This type fossil is preserved as impressions on the surface of grey tuffaceous siltstones. The material described in this paper is deposited in Shandong Tianyu Museum of Nature at Pingyi, Shandong province, China.

The fossil was examined and then photographed with the Nikon D800 digital camera and the Photomicrographs were taken with a Nikon SMZ1000 stereomicro-

scope. The line drawing was created using Adobe Illustrator CS3 and Adobe Photoshop CS5. The quantitatively measure of forewing used NIH ImageJ software (<http://rsb.info.nih.gov/ij/>). The terminologies of wing venation and cell nomenclature used in herein are modified after Chen et al. (2015). Venation symbols: main longitudinal veins are SC, ScP, RA, RP, M, CuA, CuP and A; crossveins are ir, im, m-cu; cells are a1 ~ a11. The norms of measurements for the wing were following: the wing length measured from the base to the apex and the width measured at the widest part (Li et al. 2012).

Systematic paleontology

Order Hemiptera L., 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cicadoidea Latreille, 1802

Family Tettigarctidae Distant, 1905

Subfamily Cicadoprosobolinae Evans, 1956

Maculaprosbole gen. n.

<http://zoobank.org/947E0D09-5577-417A-A191-5E12A3A9CBE0>

Type species. *Maculaprosbole zhengi* new species, designated herein (Fig 1). No other species are currently included in the genus.

Etymology. The generic name is a composition of the Latin “macula”, meaning spots and stripes, and the suffix of the genus of *Cicadoprosobole* Becker-Migdisova, 1947.

Diagnosis. Forewing large-sized, relatively wide and with oblique apical margin. Wing membrane with distinct color patterns. Clavus and costal area long. Nodal line at the middle of wing. Nodus distinct. RA with three branches; crossvein ir halfway from nodal line to wing tip; vein RP single and extended upward along the nodal line; vein M four-branched; M_{1+2} branched beyond M_{3+4} ; M_{1+2} fork into M_1 and M_2 with a right angle, and M_1 fused with RP for a distance, then nearly parallel to M_2 ; crossvein r-m absent; crossvein m nearly straight, almost perpendicular to M_2 ; vein CuA strongly downward along nodal line, branching into CuA_1 and CuA_2 just after nodal line; vein CuP almost straight, ending at about 2/5 of wing.

Remarks. The new genus undoubtedly belongs to the family Tettigarctidae based on the following diagnostic characteristics of the forewing: nodal line clearly visible; vein RA three-branched; intercostal area widest beyond nodal line; vein RP single and strongly bowed; vein M four-branched. The stem of M is shorter than ScP+R. *Maculaprosbole* gen. n. is assigned to the subfamily Cicadoprosobolinae based on the forewing features: costal area broad, basal cell narrow; clavus arched; branch CuA_2 long, sinuous and near S-shaped. This genus is most similar in coloration pattern of forewing (such as dark or light speckles, longitudinal stripes) with *Sanmai* Chen, Zhang & Wang B 2016, but differs from *Sanmai* in the transverse coloration mainly focusing on the

postnodal area. *Maculaprosbole* shares some features in forewing venation with that of *Hirtaprosbole* Liu, Li & Yao, 2015: nodal line at middle of forewing, RA three-branched; stem ScP+R longer than stem M; CuP straight; cell a6 nearly quadrate; cell a8 subequal to cell a10 in length. However, it differs from *Hirtaprosbole* in the following characters: stem ScP+RA separated at the nodal line, ScP ending beyond the middle of anterior margin M_1 fused with RP for a distance and crossvein r-m absent (vs. r-m is located between M_1 and RP); apical CuA section strongly curved, running along nodal line for a distance (vs. CuA slightly sigmoidal, not along nodal line).

***Maculaprosbole zhengi* sp. n.**

<http://zoobank.org/F16A76A5-C78B-40C4-AC9A-3169B02046CF>

Fig. 1

Diagnosis. As for genus.

Description. Forewing long and elongate apically and relatively wide, with oblique apical margin, near triangular in the tip, with distinctly dark or gray pigmented transverse bands, irregular speckles and longitudinal stripes, mainly behind the nodal line and postnodal area. Length about 34.04 mm, width about 14.54 mm, with the ratio of length/width approximately 2.34; costal margin broad, length about 21.36 mm; clavus arched, small and broad (length 15.06 mm, maximum width 4.55 mm), with conspicuous light pigmented bands. Nodal line situated in the middle of forewing. Crossvein r-m absent; branched into ScP+R and M at basal 0.17 wing length. Stem ScP+R bifurcated into ScP+RA and RP at basal 0.47 wing length; vein ScP forked with RA at nodal line, and terminating at nodus; RA with three branches, RA_1 short and nearly straight, RA_2 and RA_3 long and slightly sinuous, RA_2 parallel to RA_3 ; branch RA_3 connected with vein RP by the crossvein ir. Crossvein ir at the middle of nodal line and outer margin. Vein RP strongly curved, running along the nodal line for a distance; vein M_1 strongly curved and fused with RP for a distance, then subparallel to M_2 ; stem ScP+R relatively shorter than stem M. Stem M forked into M_{1+2} and M_{3+4} at basal 0.15 wing length, and at different level. M_{1+2} branched into M_1 and M_2 at basal 0.33 wing length; M_{3+4} bifurcated into M_3 and M_4 at basal 0.21 wing length; stem CuA long and initially sinuous, fusing with nodal line and running along with nodal line for a distance, then branched into CuA_1 and CuA_2 just beyond nodal line. CuA_1 long and relatively straight; CuA_2 short and obviously sinuous; CuP long and straight. A_1 sinuous. A_2 short and strongly curved; eleven apical cells.

Etymology. The species name refers to Prof. Xiaoting Zheng, who is the founder of Shandong Tianyu Museum of Nature and donated the type material.

Type specimen. Holotype STMN48-1813, complete forewing; housed in Shandong Tianyu Museum of Nature.

Locality and age. Middle Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

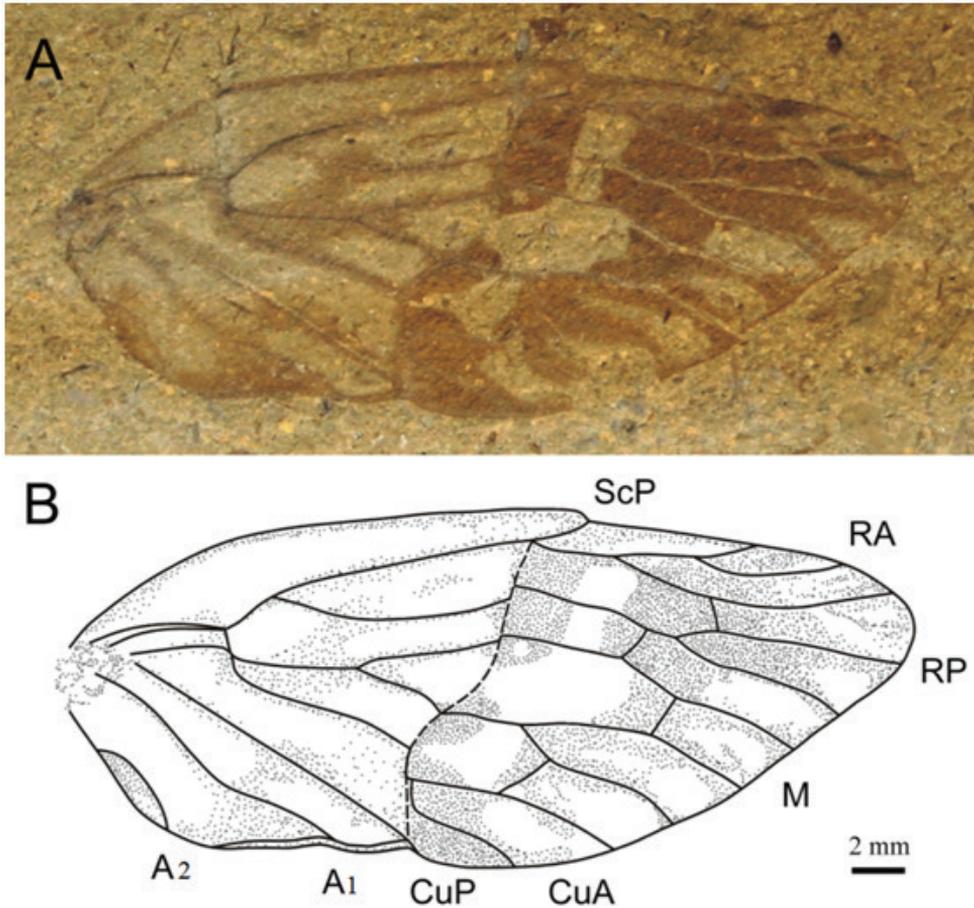


Figure 1. Holotype of *Maculaprosbole zhengi* gen. et sp. n. **A** Photograph **B** Line drawing.

Discussion

The Daohugou palaeolake was a low-energy preservational environment (Wang B et al. 2009, Chen et al. 2014, 2016). A large number of insect fossils have been found with well-preserved body structure and wing impression in the fossil beds (Ren et al. 2002, Wang B et al. 2013). Wang B et al. (2013) reported approximately 9% Mesozoic cicadomorph fossils designated as Jurassic tettigarctids. Tettigarctidae is quite abundant and morphologically diversified in the Daohugou area (Wang B and Zhang 2009, Chen et al. 2016, Chen and Wang B 2016). To date, one species within the genus *Sunotettigarcta* of the subfamily Tettigarctinae and nine species within five genera (*Macrotettigarcta*, *Shuraboprosbole*, *Tianyuprosbole*, *Hirtaprosbole* and *Sanmai*) assigned to the subfamily Cicadoprosbolinae have been described and illustrated (Wang B and Zhang 2009, Li et al. 2012, Chen et al. 2014, 2016, Chen and Wang B 2016). Those fossils provide new insights into the evolution, ecology, and behavior of tettigarctids.

We herein attribute a new genus *Maculaprosbole* to the family Tettigarctidae. Material of *Maculaprosbole* is undoubtedly identified as a new taxon and distinctly differs from other tettigarctids in possessing these forewing characters: nodal line at the middle of wing; vein RA divided into three branches; vein RP running along the nodal line for a distance and fused with M_1 for a long distance; CuA strongly curved, fused with nodal line for a distance and forked into CuA_1 and CuA_2 just beyond it. This study brings new insights to improve our knowledge of the biodiversity and wing structure diversification of the Mesozoic Tettigarctidae.

Nowadays, the prominent color pattern on wings, with dark or light stripes and conspicuous transverse longitudinal bands, is a topic that has been known in many insect fossils (Cott 1940, Wang Y et al. 2010, Chen et al. 2016). The color patterns on wings provide camouflage by strongly contrasting markings such as spots or stripes to hide themselves or frighten predators (Stevens et al. 2006; Stevens and Merilaita 2009; Seymoure and Aiello 2015), and are also attributed to sexual selection on visual signals (Wang B et al. 2006, Punzalan et al. 2008, Hilfert-Rüppell and Rüppell 2013).

In Mesozoic tettigarctids, eight species with four genera (*Sanmai*, *Protabanus*, *Liassocicada* and *Shuraboprosbole*) have been reported possessing a color pattern with dark or light stripes and irregularly colored bands (Hong 1982, Nel 1996, Wang B and Zhang 2009, Kaulfuss and Moulds 2015, Chen et al. 2016). The disruptive coloration of the forewing seems to be an autapomorphy of *Maculaprosbole*. The new fossil has prominent disruptive coloration of the type with dark or light speckles and longitudinal stripes on the forewing membrane, which is remarkably different from most Mesozoic tettigarctids. However, this disruptive coloration pattern seems to be similar to *Sanmai* in the Daohugou beds. The stripes and spots on the forewings of *Sanmai* and *Maculaprosbole* might be effective color camouflage and break up the body outline as well as the surface (Cuthill et al. 2005, Schaefer and Stobbe 2006, Chen et al. 2016).

Acknowledgements

We express our sincere thanks to Dr. Junqiang Zhang and Prof. Yameng Li for their constructive comments on our manuscript. In addition, we are grateful to Prof. Xiaoting Zheng donated the holotype of *Maculaprosbole zhengi*. This research is supported by grants from the National Natural Science Foundation of China (41502007), the Scientific Foundation of Shandong Province (ZR2013DQ017) and China Postdoctoral Science Foundation funded project (2015M580480).

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Two new species of the megadiverse lentic diving-beetle genus *Hydrovatus* (Coleoptera, Dytiscidae) described from NE Thailand

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Academic editor: M. Michat | Received 13 September 2016 | Accepted 26 October 2016 | Published 16 November 2016

<http://zoobank.org/0F28B33D-1F61-4113-A4BF-707A420C554D>

Citation: Biström O, Bergsten J (2016) Two new species of the megadiverse lentic diving-beetle genus *Hydrovatus* (Coleoptera, Dytiscidae) described from NE Thailand. ZooKeys 632: 57–66. doi: 10.3897/zookeys.632.10483

Abstract

Here we describe two new *Hydrovatus* species (Coleoptera: Dytiscidae: Hydroporinae: Hydrovatini) from the province of Khon Kaen, Isan region in NE Thailand. *Hydrovatus* is the third most species rich genus of diving beetles (Dytiscidae). It occurs on all continents except Antarctica and now numbers 210 currently recognized species. Both new species, *H. diversipunctatus* **sp. n.** and *H. globosus* **sp. n.**, were collected at lights and are only known from the type locality “Khon Kaen” (a city and province). Diagnoses based on morphology for the separation from closely related species are given together with illustrations of male genitalia and habitus photos. We provide a determination key to Old World species of the *pustulatus* species group and to Oriental species of the *oblongipennis* species group.

Keywords

Hydrovatus, Coleoptera, Dytiscidae, taxonomy, new species, keys to species, Thailand

Introduction

Hydrovatus in the subfamily Hydroporinae together with *Copelatus* (Copelatinae) and *Laccophilus* (Laccophilinae) are the only three genera of diving beetles (Dytiscidae) with more than 200 species (Nilsson 2016; Miller and Bergsten 2016). As genera they

* Contribution to the study of Dytiscidae 87.

also share the characteristics of having a cosmopolitan distribution existing on all continents except Antarctica (Miller and Bergsten 2016). A good dispersal ability is probably part of this colonization success as witnessed by them all having common species that regularly come flying to lights (Miller and Bergsten 2016). Good dispersal ability in aquatic insects is commonly associated with inhabiting lentic waters (Ribera and Vogler 2000; Ribera et al. 2003; Hof et al. 2006; Hjalmarsson et al. 2015), and all three genera have lentic representatives. *Hydrovatus* however stands out in that lotic species are largely lacking (Balke 2005). This genus is truly characteristic of standing swamps and ponds rich in vegetation. It is surprising that a strictly lentic diving beetle genus has become megadiverse since the characteristic of good dispersal ability generally is linked with larger distribution ranges and, according to theory, a lower speciation rate (Ribera et al. 2001; Hjalmarsson et al. 2015; but see Letsch et al. 2016). Finally, while all three ‘megagenera’ may be considered difficult due to their diversity, *Hydrovatus* in contrast to *Copelatus* and *Laccophilus* have received a modern world monographic revision and is therefore more accessible on a global level (Biström 1997).

In terms of morphology *Hydrovatus* has a characteristic body shape with acuminate elytral apices and some males have modified antenna, both features rather uncommon in diving beetles. Further *Hydrovatus* have deeply incised metacoxal processes with long, slender metacoxal lobes and female gonocoxae are fused into a knife-like ovipositor (Miller and Bergsten 2016). As in the species-poor sister genus *Queda*, also in Hydrovatini, the apex of the prosternal process is broad and triangular (Miller and Bergsten 2014). Currently there are 208 species recognized in the genus (Nilsson 2016). Following the global monograph on the genus (Biström 1997), only a handful of new species have been described, mainly from western Africa (Bilardo and Rocchi 1999, 2008; Schizzerotto and Pederzani 2015), but also from the Oriental region (Biström 1999; Manivannan and Madani 2011).

Unsorted, unidentified, accession material in museum collections around the world are “gold mines” with likely tens of thousands of undescribed species waiting to be discovered (Balke et al. 2013). During a recent visit to Budapest in Hungary the senior author of this article had a chance to study the insect collection in the Hungarian Natural History Museum (HNHM). Among the unsorted diving beetles material in the collection two series of specimens from Khon Kaen in NE Thailand with peculiar body shapes were discovered. After examination under a dissection microscope both proved to belong to undescribed species, which we here describe. Referring to the revision of the genus *Hydrovatus* (Biström 1997) one of the new species belongs to the species group *pustulatus* (group 3) and the other, to the species group *oblongipennis* (group 11).

Material and methods

The type material of both species is kept in the Hungarian Natural History Museum, Budapest, Hungary (HNHM), the Finnish Museum of Natural History, Helsinki, Finland (FMNH) and the Swedish Museum of Natural History, Stockholm, Sweden

(NHRS). Habitus photographs were produced using a Canon EOS 5D Mark II DSLR camera with an MP-E 65mm f/2.8 1–5× macro lens mounted on a Stackshot (Cognisys) motorized rail. For light source the macro twin-head flash MT-24EX (Canon) was used with a home-made light diffusor. A Z-stack of 15–35 photos was taken by operating the Stackshot rail through the software Zerene stacker (Zerene Systems) and stacking the images in the same software to produce an image with focus throughout the globular body. Black and white line drawings of genitalia were produced using a Wild M11 dissection microscope with a camera lucida.

Results

Hydrovatus diversipunctatus sp. n.

<http://zoobank.org/112B3346-2DF9-49A3-8A7E-8CF204324ED6>

Type locality. Thailand: Khon-Kaen [city and province in the region of Isan, NE Thailand].

Type material 8 exs. (1 male, 7 females). Holotype, male: “Nordost-Thailand Khon-Kaen ad lucem / Dr. Sastri Saowakontha leg. 28.4.1980” (HNHM). - Paratypes: Same data as holotype (1 ex. FMNH); same data as holotype but “25.IV.1980” (1 ex. HNHM, 1 ex. NHRS); same data as holotype but “22.IV.1980” (2 exs. HNHM, 1 ex. FMNH); same data as holotype but “20.5.1980” (1 ex. HNHM).

Diagnosis. The new species is undoubtedly closest to *H. subrotundatus* Motschulsky. These two species share the characteristics of having the lateral elytral margin clearly visible from above (Fig. 1a–b, compare with Fig. 1c–d). The two species are distinguished by clear difference in body size and shape; *H. diversipunctatus* is larger and less rounded-globular than *H. subrotundatus*. Moreover, *H. diversipunctatus* deviates by having much coarser pronotal punctures in comparison with general punctuation of elytra (diameter of pronotal punctures about 4× larger than general punctures of elytra). Additionally, head between eyes has complete frontal margin in *H. subrotundatus*, while frontal margin in *H. diversipunctatus* fades away close to eyes. Shape of male genitalia is quite similar in the two species. Penis is, however, slightly broader in *H. diversipunctatus*, while parameres seem to be a little more slender, compared with corresponding structures in male genitalia of *H. subrotundatus*.

Description. Body: Almost entirely blackish ferruginous, with no distinct color pattern. Body-shape not globular but slightly elongated. Broadest posterior to humeral region and from there posteriorly slightly narrowed until abruptly curved towards apex of elytra. Lateral margin between epipleura and elytra pronounced and clearly discernible from above (Fig. 1a). Length of body 3.1–3.3 mm, width 2.0–2.1 mm.

Head: Blackish ferruginous; near frontal margin head slightly paler, dark ferruginous. Very finely and sparsely punctate. At eyes and in rather shallow, frontal depressions with some fine punctures. Rather shiny, although finely microsculptured. Reticulation clearly discernible except on minor tubercles frontally close to eyes where reticulation is obliterated. Frontal outline of head rounded, medially slightly straightened. Frontal

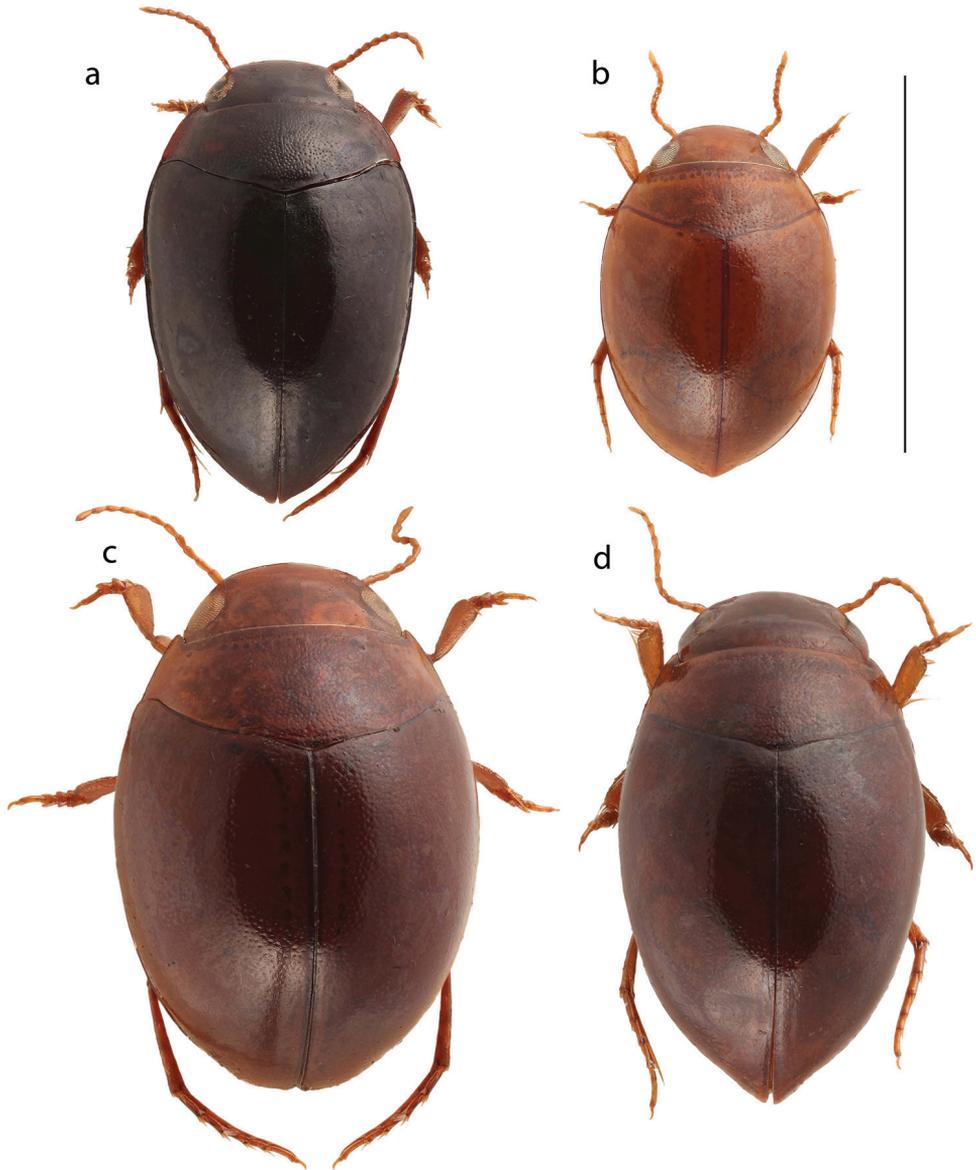


Figure 1. Dorsal habitus of *H. diversipunctatus* sp. n. (a), *H. subrotundatus* (b), *H. globosus* sp. n. (c) and *H. r. rufoniger* (d). Scale bar 3 mm.

margin fades away on minor tubercles close to eyes. Antenna pale ferrugineous, slender and with no modifications.

Pronotum: Blackish ferrugineous, laterally with vague dark ferrugineous areas. Densely and distinctly punctate; laterally punctures become sparse and slightly finer. Rather shiny, although distinctly microsculptured; meshes clearly discernible. Sides of pronotum slightly rounded to almost straight; anteriorly distinctly curved inwards.

Elytra: Finely and sparsely punctate. Rows of punctures indistinct and weakly developed except from discal row, which basally is quite distinct. Rather shiny, although very finely microsculptured; reticulation weak but extensively still discernible. Narrowly, close to epipleura reticulation in part obliterated. Epipleura dark ferrugineous; finely punctate frontally at inner margin.

Ventral aspect: Dark ferrugineous, except abdomen, apically slightly paler, ferrugineous. Almost impunctate, except for metacoxal plates and metathorax, which in part are covered with fine to rather fine punctures. Rather shiny with fragments of microsculpture, except abdomen which is entirely microsculptured. Prosternal process laterally with fine margin; medial surface almost flat and punctured. No stridulatory apparatus on metacoxal plates.

Legs: Pale ferrugineous to ferrugineous. Pro- and mesotarsus slightly enlarged. Claws simple.

Male genitalia as in Fig. 2a–c.

Female: Externally similar to male.

Distribution. Thailand.

Collecting circumstances. Type material collected at light.

Etymology. The species name *diversipunctatus* refers to the large difference in size between general punctures of pronotum in comparison to those of elytra.

***Hydrovatus globosus* sp. n.**

<http://zoobank.org/F8776495-71E1-4BEF-9AA2-365074523F52>

Type locality. Thailand: Khon-Kaen [city and province in the region of Isan, NE Thailand].

Type material 25 exs. (10 males, 15 females). Holotype, male: “Nordost-Thailand Khon Kaen, ad lucem 22.4. 1980 leg. S. Saowakontha” (HNHM). – Paratypes: Same data as holotype (11 exs. HNHM, 3 exs. FMNH, 3 exs. NHRS); same data as holotype but “20.5. 1980” (2 exs. HNHM, 1 ex. FMNH); same data as holotype but “29.4. 1980 Dr. Saati Saowakontha leg.” (1 ex. HNHM); same data as holotype but “2.9. 1980 Dr. Saati Saowakontha leg.” (1 ex. HNHM); same data as holotype but “19.2. 1981 Dr. Saati Saowakontha leg.” (2 exs. HNHM).

Diagnosis. The new species belongs to a complicated group of *Hydrovatus*, out of which *H. rufoniger* (Clark) (Fig. 1d) seems to be closest. The new species is distinguished from this species but also other close species from the Oriental region, by its globular shaped body with a very weak extension of the elytral apex (Fig. 1c). Deviating structures in the shape of the penis apex are also characteristic for *H. globosus* (Fig. 2d–f).

Description. Body: Almost unicolored ferrugineous to dark ferrugineous; no distinct color-pattern exhibited. Body-shape almost globular with apex of elytra moderately extended (Fig. 1c). Length 3.8–4.0 mm, width 2.4–2.6 mm.

Head: Anteriorly between eyes finely margined; outline slightly undulate (frontal edge medially, weakly curved inwards). At each eye with a quite distinct, triangular depression with irregular punctures in it. Close to eye with a row of fine punctures and

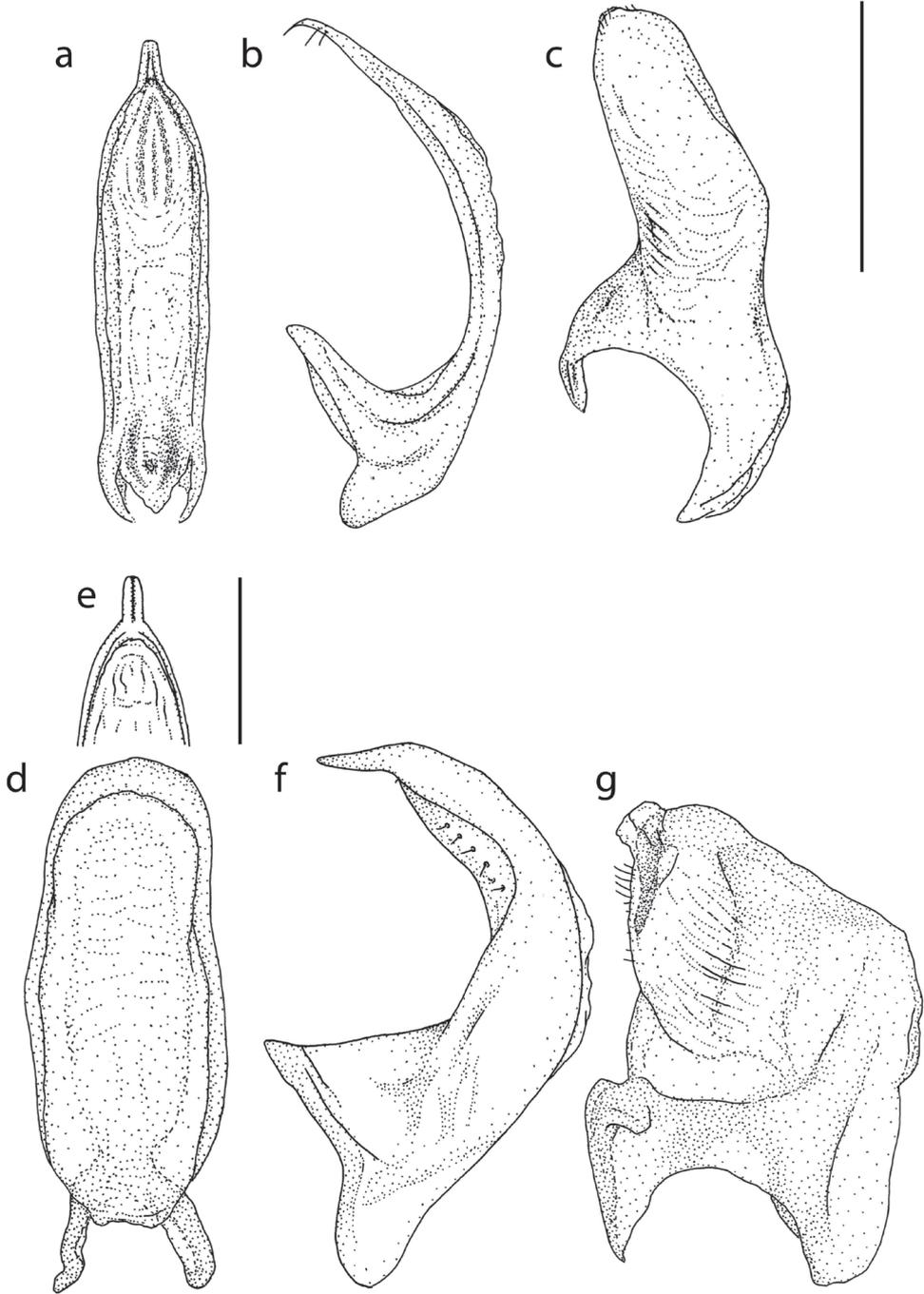


Figure 2. Male genitalia of *H. diversipunctatus* sp. n. (**a–c**) and *H. globosus* sp. n. (**d–g**). **a, d** penis, dorsal aspect **b, f** penis, lateral aspect **c, g** paramere **e** penis, frontal part from above. Scale bar in upper right corner 0.5 mm for **a–d, f–g**. Scale bar next to **(e)** 0.5 mm, applies to only **e**.

from frontal depression a row of punctures continues sparsely (disappears gradually) towards middle of head. Other parts of head surface impunctate with scattered, fine and hardly discernible punctures anteriorly. Head slightly matte to rather shiny; extensively finely reticulated. Antenna filiform, with no distinct modifications.

Pronotum: With dense and fine punctures, which laterally fade away gradually. Surface between punctures shiny, almost without reticulation. Laterally, fine, in part indistinct reticulation discernible.

Elytra: Finely and densely punctate. Laterally, punctures fade away and become indistinct/disappear in part. Discal, dorsolateral and lateral row of punctures rather indistinct and in part hardly discernible. Between punctures, surface rather shiny; reticulation very fine and sporadically discernible; extensively reticulation almost absent.

Ventral aspect: Finely to fairly finely and somewhat sparsely punctate. Abdomen almost impunctate. Shiny, reticulation almost absent; hardly visible, rudimentary meshes of microsculpture discernible on metacoxal plates. Abdomen slightly matte; with very fine, elongated meshes of microsculpture. Stridulation apparatus rather narrow, provided with numerous minute striae. Apex of prosternal process laterally finely margined; medial surface flattened with sparse and vague punctures. Apical ventrite medially with a distinct depression; extreme apex of ventrite with a fine bulb (a minor enlargement).

Legs: Ferruginous. Pro- and mesotarsus slightly enlarged. Protarsal claws asymmetric; internal claw distinctly angled and thickened.

Male genitalia as in Fig. 2d–g.

Female: Elytra posteriorly rather distinctly microsculptured, matte. Protarsal claws not modified. No stridulation apparatus on metacoxal plates.

Distribution. Thailand.

Collecting circumstances. Entire type material collected at light.

Etymology. The species name *globosus* refers to the spherical body-shape of the new species.

Determination keys

For comparisons, see illustrations in Biström (1997).

Key to Old World species of the *pustulatus* species group (sp. gr. 3 sensu Biström 1997):

- 1 Lateral margin between elytron and epipleuron for a long distance not discernible from above (as in Fig. 1a–b) **2**
- Lateral margin between elytron and epipleuron discernible from above (Fig. 1c–b) **3**
- 2 Elytra provided with distinct, pale ferruginous spots; penis (lateral aspect) slender *H. cardoni* Severin, 1890
- Elytra provided with narrow, marginal, pale ferruginous spots; penis (lateral aspect) broad *H. sringeriensis* Manivannan & Madani, 2011

- 3 Smaller species (length of body 2.3–2.9 mm), rufotestaceous and rather compact (Fig. 1b); no clear difference in size of punctures on pronotum and elytra; penis (dorsal aspect) not expanded ***H. subrotundatus* Motschulsky, 1859**
- Larger species (length of body 3.1–3.3 mm), darker ferruginous and more elongate (Fig. 1a); punctures on pronotum distinctly larger than on elytra (punctures hardly visible); penis (dorsal aspect) slightly expanded.....
..... ***H. diversipunctatus* sp. n.**

Key to Oriental species of the *oblongipennis* species group (sp. gr. 11 sensu Biström, 1997). The taxonomic status of *H. castaneus*, *H. rufoniger* and *H. bonvouloiri* is unclear and in need of further study (synonymies cannot be excluded):

- 1 Small species, length of body 2.2–2.7 mm... ***H. seminarius* Motschulsky, 1859**
- Larger species, length of body 3.0–4.2 mm..... **2**
- 2 Metacoxal plates (males) lack stridulation apparatus
..... ***H. rufescens* Motschulsky, 1859**
- Metacoxal plates (males) with stridulation apparatus **3**
- 3 Body shape globular; apical extension of elytra indistinct (Fig. 1c).....
..... ***H. globosus* sp. n.**
- Body shape elongated; apex of elytra distinct, posteriorly clearly extended (Fig. 1d) **4**
- 4 Penis apex (dorsal aspect) narrows smoothly to tip.....
..... ***H. castaneus* Motschulsky, 1855**
- Penis apex (dorsal aspect) narrows abruptly/unevenly to tip..... **5**
- 5 Penis apex broad, narrows abruptly to slender tip; ridges of stridulatory file larger, clearly discernible; male protarsal claws not distinctly thickened
..... ***H. picipennis* Motschulsky, 1859**
- Penis apex more slender and narrows less abruptly to slender tip; ridges of stridulatory file very fine, hardly discernible; male protarsal claws distinctly thickened..... **6**
- 6 Penis apex (lateral aspect) with protruding frontal flaps
..... ***H. naviger* Biström, 1997**
- Penis apex (lateral aspect) lacks frontal flaps..... **7**
- 7 Penis (dorsal aspect) medially broad, narrows evenly forwards to slender tip; elytral punctures fine to rather fine (Fig. 1d)..... ***H. rufoniger* (Clark, 1863)**
- Penis (dorsal aspect) medially broad, narrows more abruptly forwards to slender tip; elytral punctures sometimes coarser..... ***H. bonvouloiri* Sharp, 1882**

Acknowledgement

Dr. Otto Merkl, curator of the Coleoptera collection in the Budapest Museum, is thanked for kind assistance during the stay of the senior author in the museum.

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A new species of *Iotarphia* Cameron (Coleoptera, Staphylinidae, Aleocharinae) from Tasmanian seacoasts, Australia

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Academic editor: A. Brunke | Received 27 September 2016 | Accepted 31 October 2016 | Published 16 November 2016

<http://zoobank.org/AB4DD4D2-AD71-4A91-8206-A8D77914EEBD>

Citation: Lee S-G, Osborn AW, Ahn K-J (2016) A new species of *Iotarphia* Cameron (Coleoptera, Staphylinidae, Aleocharinae) from Tasmanian seacoasts, Australia. ZooKeys 632: 67–74. doi: 10.3897/zookeys.632.10657

Abstract

Iotarphia rufobrunnea Lee & Ahn, **sp. n.** is described from Tasmania. The new species is compared with another species of the genus, *I. australis* Cameron. A description, habitus photograph and illustrations of the diagnostic characters are provided.

Keywords

Coleoptera, Staphylinidae, Aleocharinae, Athetini, *Iotarphia*, new species, Tasmania

Introduction

While working on aleocharine beetles collected by the second author from the eastern and southern seashores in Tasmania, Australia, we found specimens very similar to the athetine genus *Iotarphia* Cameron. After detailed examination of the specimens and comparison with *Iotarphia australis* Cameron (type species of *Iotarphia*), we concluded that these specimens represent a new species of the genus.

The athetine genus *Iotarphia* and its single described species have been recorded only in a “maritime habitat” from New South Wales and from Tasmania, both in Australia (Cameron 1943; Frank and Ahn 2011). Recently, Lee and Ahn (2015) synonymized the genus *Psammopora* Pace under *Iotarphia*. Little is known about their biology (Frank and Ahn 2011). In this paper, we provide a description, habitus photograph and line drawings of diagnostic characters of a new species of the genus *Iotarphia*.

Method

Descriptive terms used here follow Sawada (1972), but we followed Ashe (1984) in some cases, particularly for mouthparts, to reduce confusion.

Results

Genus *Iotarphia* Cameron, 1943

Iotarphia Cameron, 1943: 352. Type species: *Iotarphia australis* Cameron, 1943.
Psammopora Pace, 2003: 154. Type species: *Psammopora delittlei* Pace, 2003.

Diagnosis. Members of *Iotarphia* are characterized by the combination of the following characters: labrum distinctly emarginate in anterior margin, with ϵ -sensillum conspicuously robust and blunt at apex; distal lobe of galea and lacinia developed, with many setae; ligula divided into two lobes; mentum emarginate in anterior margin; infraorbital carina absent; mesoventral process blunt at apex, reaching to half of meso-coxa; metaventral process narrow and pointed at apex; tarsal formula 4-5-5; metatarsi long (Pace 2003; Lee and Ahn 2015).

Iotarphia rufobrunnea Lee & Ahn, sp. n.

<http://zoobank.org/B2EABD60-7E6A-491D-834C-DD1520D42415>

Figs 1–12

Material examined. Types. *Tasmania*. Holotype, male (QVM:2014:12:0119), Coal Point, Bruny Island, collected 25.ix.2014, A.W. Osborn. Paratypes: 4, of which 3 (QVM:2016:12:1052 to 1054) share common collection data with holotype, and 1 (QVM: 2014:12:0125) collected from Lighthouse Bay, Bruny Is., collected 24.ix.2014, A.W.Osborn.

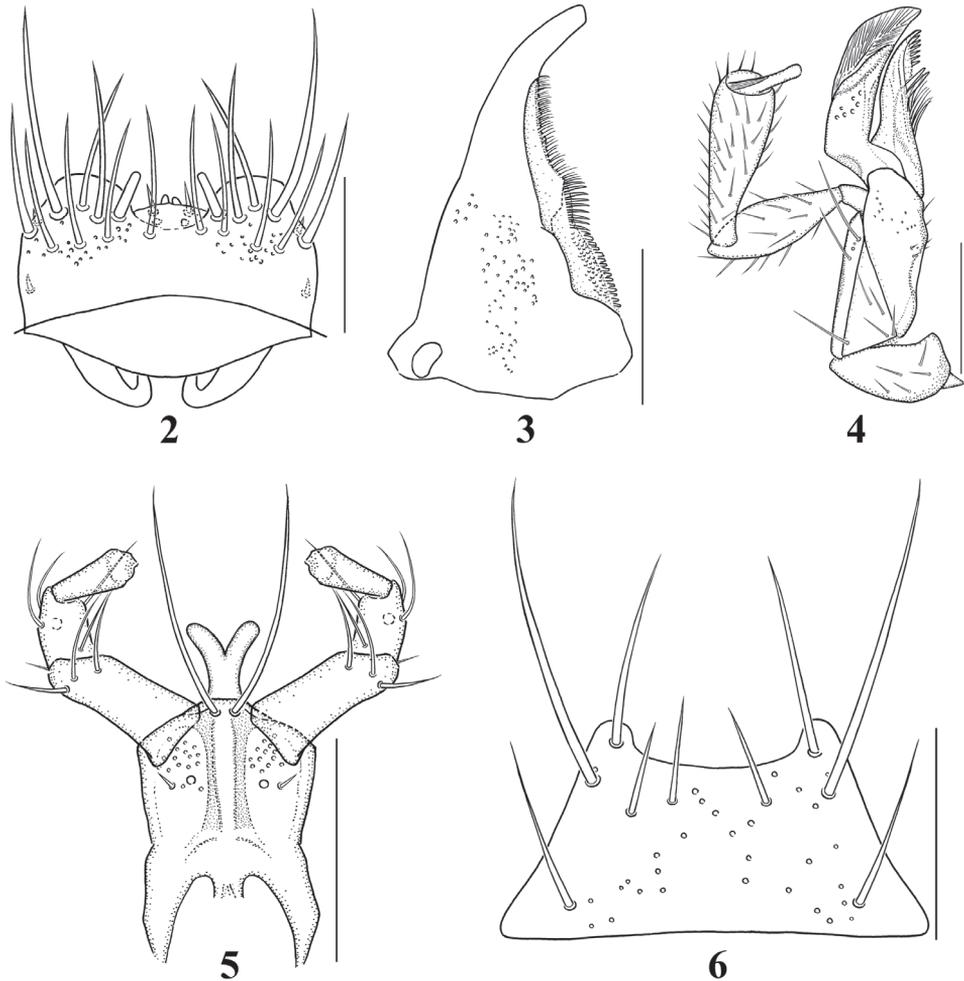
All type specimens have been placed in the Queen Victoria Museum and Art Gallery, Launceston, Tasmania (QVMAG).

Description. Length 2.8–3.5 mm. Body (Fig. 1) subparallel-sided and reddish brown to reddish black; head and abdomen almost black, antennae and legs reddish



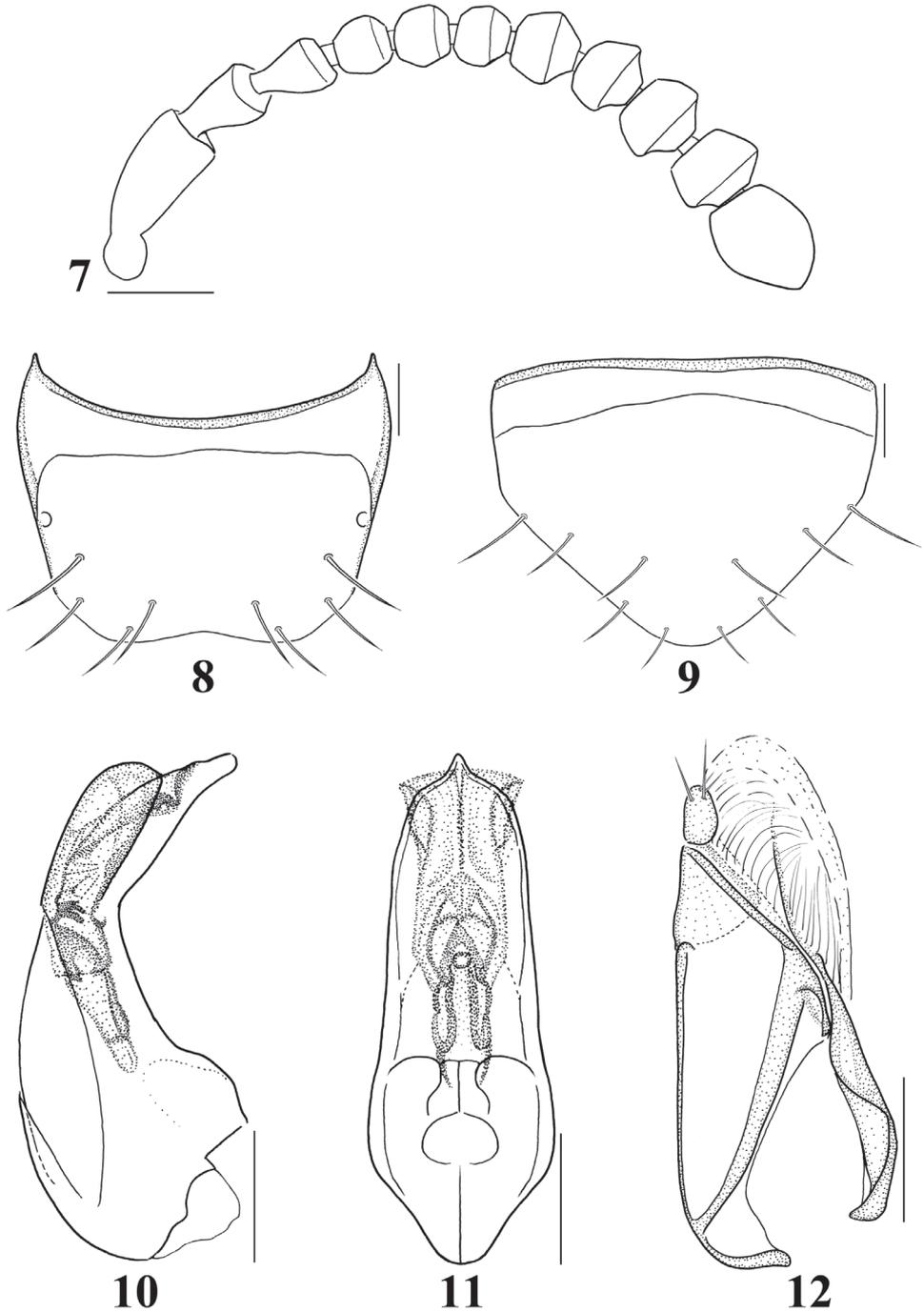
Figure 1. Habitus of *Iotarphia rufobrunnea* sp. n., 3.4 mm.

yellow, elytra reddish brown except for basal darker region; surface slightly glossy, densely pubescent with fine microsculpture. *Head.* Slightly transverse, approximately 1.1–1.2 times as wide as long, widest across eyes, narrower than pronotum; eyes slightly large and prominent, about 1.2 times as long as temples; gular sutures moderately separated, slightly diverged basally. Antennae (Fig. 7) slightly moniliform and about as long as head and pronotum combined; antennomeres 1–3 elongate, 1 longest, 2 distinctly longer than 3, 4–10 slightly to distinctly transverse, 11 longer than wide, slightly shorter preceding two combined. *Mouthparts.* Labrum (Fig. 2) with 8 macrosetae on each side of midline; epipharynx with several sensilla, including 2 lateral sensory rows on each side of midline; α -sensillum setaceous, about as long as ϵ -sensillum; β - and γ -sensilla short. Mandibles (Fig. 3) slightly asymmetrical, subtriangular, decurved and narrow apically, about 1.6 times as long as basal width, with blunt internal tooth; prosthema developed, composed of three portions, many small denticles present in molar region. Galea and lacinia of maxilla (Fig. 4) moderately long and slender; lacinia composed of seven small spines in distal comb region, two isolated spines longer; maxillary palpus distinctly 4-articled, elongate and pubescent; palpomere 1 smallest, 2 about 2.5 times as long as wide, 3 slightly longer than 2, about 3.0–3.2 times as long as wide, 4 digitiform and relatively short, filamentous sensilla reaching to basal half.



Figures 2–6. Mouthparts of *Iotarphia rufobrunnea* sp. n.: **2** labrum, dorsal aspect **3** right mandible, ventral aspect **4** right maxilla, ventral aspect **5** labium, ventral aspect **6** mentum, ventral aspect. Scale bars = 0.1 mm.

Labium (Fig. 5) with ligula relatively broad and parallel-sided, divided into 2 lobes in basal half; medial pseudopore field of prementum very narrow, with several median pseudopores; two medial setae contiguous; two basal pores close together, one laterally behind the other; many lateral pseudopores, 1 setal pore and 1 real pore present on each side of midline; labial palpi 3-articled and elongate, with many setulae; palpomere 1 largest, about 2.0–2.5 times as long as wide, γ -setula slightly close to b-seta, 2 shortest, about 1.5–2.0 times as long as wide, 3 dilated apically and slightly shorter than 1, about 2.0–2.5 times as long as wide. Mentum (Fig. 6) trapezoidal, anterior margin distinctly emarginate. *Thorax*. Pronotum transverse, approximately 1.3 times as wide as long, widest at apical third; pubescence directed anteriorly in midline; hypomera fully



Figures 7–12. Diagnostic characters of *Iotarphia rufobrunnea* sp. n.: **7** antenna **8** male tergite VIII, dorsal aspect **9** male sternite VIII, ventral aspect **10** median lobe, lateral aspect **11** median lobe, ventral aspect **12** paramere, lateral aspect. Scale bars = 0.1 mm.

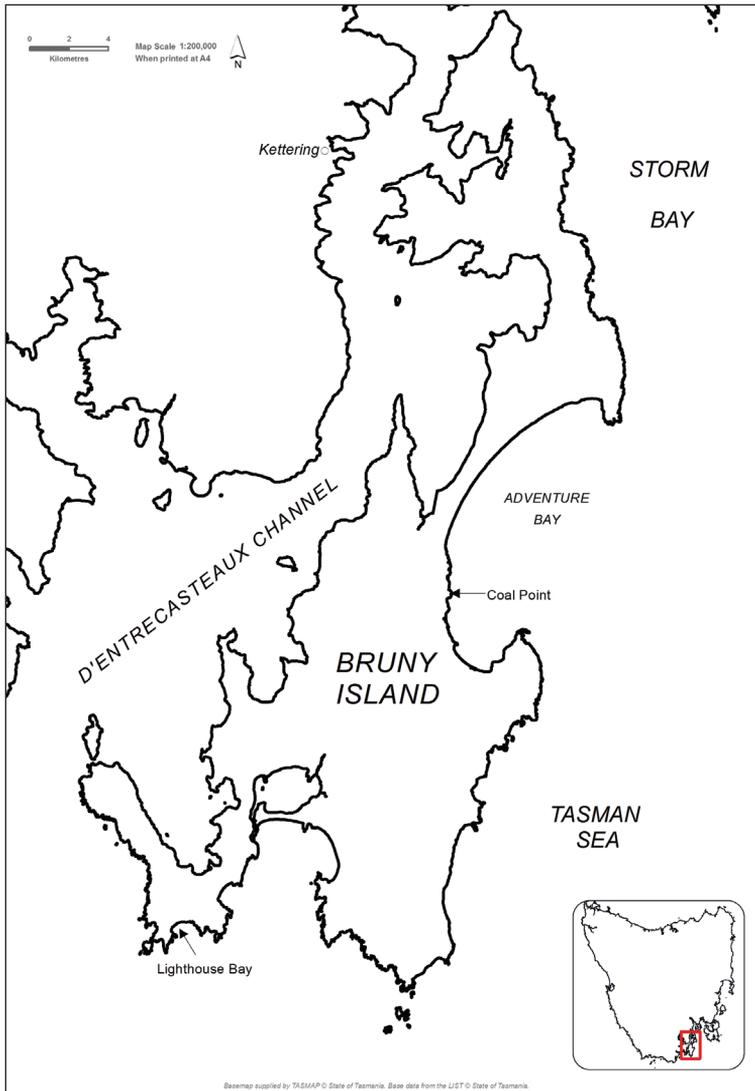


Figure 13. Distribution map.

visible in lateral aspect. Metanotal scutum with 1 long seta and about 3 short setae on each side of midline. Mesoventral process slightly longer than metaventral process, shorter than isthmus and metaventral process combined; isthmus slightly shorter than metaventral process. Metendosternite with distinctly elongate basal stalk and a pair of furcal arms. Elytra slightly longer and wider than pronotum; elytron approximately 1.6 times as long as wide, pubescence directed posteriorly and postero-laterally; postero-lateral margin almost straight; hind wings fully developed, flabellum composed of about 8 setose lobes. *Legs*. Moderately long and slender, with dense pubescence and macrosetae; pro- and mesotibiae with small and blunt spines along outer sur-

Table 1. Differences between *I. australis* Cameron and *I. rufobrunnea* sp. n.

	<i>I. australis</i>	<i>I. rufobrunnea</i> sp. n.
Length	2.2–3.0 mm	2.8–3.5 mm
Elytra color	yellow in most regions	reddish brown
Antennomere 4	about as wide as long	slightly transverse
Mesoventral process	shorter than metaventral process	longer than metaventral process
Meso- and metaventral processes	contiguous	separated

face; length ratio of tarsomeres 36:38:40:78 (protarsus); 40:43:46:48:78 (mesotarsus); 48:55:58:54:80 (metatarsus); one empodial seta present, shorter than claw. *Abdomen*. Subparallel-sided; surface glossy and densely pubescent, with transverse and imbricate microsculpture; male tergite VIII (Fig. 8) with 4 macrosetae on each side of midline, posterior margin slightly emarginate; male sternite VIII (Fig. 9) with about 5 macrosetae, posterior margin convex, long marginal setae present; *Aedeagus*. Median lobe (Figs 10–11) elongate oval, apical process elongate and convergent apically in ventral aspect, and slightly bent in lateral aspect. Apical lobe of paramerites (Fig. 12) narrow apically, with four setae; a-seta longest, b-seta longer than c-seta, d-seta shortest and close to c-seta and positioned at apex.

Etymology. Named from the Latin *rufobrunnea* meaning “reddish brown”, which refers to the elytra color.

Distribution. Bruny Island, at both Lighthouse Bay and Coal Point (refer to map below), Tasmania, Australia (Fig. 13).

Remarks. This species is similar to *I. australis*, but can be distinguished by the characters provided in Table 1 and the shape and structure of the aedeagus. The specimens of the new species were collected on Bruny Island from (i) an entirely sandy substrate just into the supra-littoral zone at Coal Point (geographical coordinates: 43.34211°S and 147.32178°E) and (ii) from a sandy substrate in which some small rocks were present within the littoral zone at Lighthouse Bay (geographical coordinates: 43.48616°S and 147.15022°E).

The description of the new species within the present paper brings the total number of coastal Staphylinidae species in the Tasmanian fauna to five: *Iotarphia australis* (= *Psammopora delittlei* Pace), *Iotarphia rufobrunnea* Lee & Ahn, sp. n., *Teropalpus pictipes* (Lea), *Cafius pacificus* (Erichson), and *Remus sericeus* (Holme).

Acknowledgments

We thank Roger Booth (NHM, London) and David Maynard (QVMAG, Tasmania, Australia) for arranging the loans of type specimens of *Iotarphia australis* and *Psammopora delittlei* (QVM:12:48278). We also are indebted to Judy Rainbird (Collections Officer QVMAG, Tasmania) for all aspects associated with processing the specimens of the new species, and thanks to Kathryn Pugh, QVMAG Honorary Research Associate,

for GIS assistance. In addition we thank Bernard Edwards, Ranger and Scott Thornton, Field Officer, both of the Tasmanian Parks and Wildlife Service Bruny Island Field Centre, for permission to work on the island and to collect the specimens described herein. Finally, we express our sincere appreciation to the Plomley Foundation for awarding the research grant (to AWO) that supported the field work that subsequently led to the collection of the specimens described herein. This work was partially supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (2016R1D1A1B03930178).

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Phylogenetic placement of the Pacific Northwest subterranean endemic diving beetle *Stygoporus oregonensis* Larson & LaBonte (Dytiscidae, Hydroporinae)

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Academic editor: M. Michat | Received 14 July 2016 | Accepted 12 October 2016 | Published 16 November 2016

<http://zoobank.org/2BF08A13-A6AD-448F-A9CC-B2D706745606>

Citation: Kanda K, Gomez AR, Van Driesche R, Miller KB, Maddison DR (2016) Phylogenetic placement of the Pacific Northwest subterranean endemic diving beetle *Stygoporus oregonensis* Larson & LaBonte (Dytiscidae, Hydroporinae). ZooKeys 632: 75–91. doi: 10.3897/zookeys.632.9866

Abstract

Stygoporus oregonensis Larson & LaBonte is a little-known subterranean diving beetle, which, until recently, had not been collected since the type series was taken from a shallow well in western Oregon, USA, in 1984. Here we report the discovery of additional specimens collected from a nearby well in the Willamette Valley. Sequence data from four mitochondrial genes, *wingless*, and histone III place *Stygoporus* Larson & LaBonte in the predominantly Mediterranean subtribe Siettitiina of the Hydroporini. Morphological support for these results is discussed, and details of the collecting circumstances of the new specimens are presented. We argue that the biogeographic patterns of Nearctic Siettitiina highlight the likelihood of additional undiscovered subterranean dytiscids in North America.

Keywords

Stygobiont, aquatic Coleoptera, Hydroporini, aquifer, Siettitiina, Nearctic, Oregon

Introduction

In the spring of 1984 an unusual, pale, blind diving beetle was found in a bathtub in a private residence near the town of Dallas, Oregon, USA. The bathtub received water directly from a shallow well that was drawing from the Willamette Lowland aquifer system in the central Willamette Valley. The residents sent the specimen to an entomology extension specialist, Dr. J. Capizzi at Oregon State University, who recognized the beetle as distinct and suggested to the residents that they collect more specimens (Larson and LaBonte 1994). An additional eight specimens were found, and shortly thereafter, the residents treated the well with chlorine. No additional specimens were collected at the type locality following the well's chlorine treatment (Larson and LaBonte 1994). The species was described and given the name *Stygoporus oregonensis* Larson & LaBonte in honor of its subterranean predilections and the state from which it was thus far known (Larson and LaBonte 1994). In the more than 30 years since the type series was collected, no additional specimens of *S. oregonensis* have been reported prior to the present study.

Stygoporus oregonensis is a small-bodied diving beetle with pale, mostly yellow cuticle, long elytral marginal setae, fused elytra, minute flight wings, and without eyes (Larson and LaBonte 1994; Fig. 1). These morphological features are commonly observed in various, often widely unrelated subterranean lineages and are considered to typify stygobitic Dytiscidae from around the world (Leys and Watts 2008; Leys et al. 2003; Miller et al. 2013; Spangler and Decu 1998; Watts and Humphreys 2009). An additional morphological feature common among stygobitic dytiscids is a discontinuous body outline, contrasted with the more streamlined habitus of many diving beetles.

Inferring the phylogenetic placement of stygobitic species is crucial for shedding light on their origins and developing a framework for studying adaptation and other responses to subterranean environments. Addressing the mechanisms responsible for the unusual though oft-repeated appearance of the stygobitic fauna and their often unexpected distributions is an active field (Juan et al. 2010). Cave faunas are some of the most visually striking examples of convergence, and several recent studies of stygobitic and troglobitic life have used the character-rich information present in molecular sequence data to help place these morphologically similar species into phylogenetic hypotheses (Faille et al. 2010; Gómez et al. 2016; Leys et al. 2003; Miller et al. 2013; Ribera et al. 2010; Toussaint et al. 2015; Wiens et al. 2003).

In the United States, three aquatic beetle families are known to include stygobitic species: Dryopidae (*Stygoparnus comalensis* Barr & Spangler, 1992), Elmidae (*Typhloelmis* Barr, 2015: 3 species), and Dytiscidae (*Ereboporus naturaconservatus* Miller, Gibson & Alarie, 2009, *Haideoporus texanus* Young & Longley, 1976, *Psychopomporus felipi* Jean, Telles & Miller, 2012, *Comaldessus stygius* Spangler & Barr, 1995, and *Stygoporus oregonensis* Larson & LaBonte, 1994). Apart from *S. oregonensis*, all US stygobitic beetles are only known to occur in the Edwards-Trinity aquifer system in central Texas.

Whereas the relationships of *Stygoparnus* Barr and Spangler and *Typhloelmis* to other members of their respective families have yet to be explored with phylogenetic



Figure 1. Dorsal habitus of female *Stygoporus oregonensis*. Scale bar = 1 mm.

methods, the placement of three of the four described Texas stygobitic dytiscids within the very diverse subfamily Hydroporinae was recently inferred using molecular sequences (Miller et al. 2013). Miller et al. (2013) did not include *C. stygius* in their analyses because it possesses several morphological synapomorphies that unambiguously place it within Bidessini. The other Texas stygobites were placed in two clades, the *Graptodytes* group (*E. naturaconservatus* and *P. felipi*) and the *Hydroporus* group (*H. texanus*). Both of these generic groups are traditionally classified within the large, heterogeneous tribe Hydroporini *sensu lato*, which has been shown to be polyphyletic by several authors (Miller et al. 2006; Ribera et al. 2002; Ribera et al. 2008). Recently, Miller and Bergsten (2014) formalized the subgroups of Hydroporini *s. l.* establishing

the subtribe Siettitiina for *Graptodytes* group and Hydroporina for *Hydroporus* group; they also provisionally placed *S. oregonensis* in Hydroporina.

In their paper describing *S. oregonensis*, Larson and LaBonte (1994) hypothesized that *Stygoporus* is related to the Nearctic genus *Sanfilippodytes* Franciscolo (also placed in Hydroporina by Miller and Bergsten (2014)) based on similarly large metatrochanters, apically produced metaventral processes, and *Sanfilippodytes* exhibiting character states that “form a good base from which a truly subterranean beetle could evolve” (Larson and LaBonte 1994). In addition, several *Sanfilippodytes* species are known from a variety of habitats including acidic pools (Post 2010), interstitial spaces along margins of springs and creeks, within sand-clay or gravel substrate of cold springs, limnocene pools, under beach debris or cover along the margins of alpine lakes, under mosses in springs and seeps, and caves (Larson et al. 2000), which may be steps along the way to colonization of subterranean aquifers by the ancestor of *S. oregonensis*. However the relationship between these genera has yet to be tested.

In this paper, we report additional specimens of *S. oregonensis* from a separate well, also in the central Willamette Valley, Oregon. These specimens yielded DNA, from which we amplified six genes used in Miller et al.’s (2013) phylogeny of Hydroporinae. We incorporate our new sequences with data from Miller et al. (2013) to infer the phylogenetic placement of *S. oregonensis* and discuss morphological aspects of *S. oregonensis* in light of these results.

Methods

Discovery of *Stygoporus oregonensis* specimens

Two mostly intact specimens of *Stygoporus oregonensis* and fragments of additional individuals were recovered from accumulated sand and detritus in the filter of a residential well system (USA: Oregon: Marion County, Talbot, south of Talbot Road South). The well sits near an old oxbow of the Willamette River and the wellhead is located roughly 14 m below the surface. This site is roughly 27km SSE of the type locality (Fig. 2). Between 2014 and 2016, the accumulated material in the well filter was checked six times (Suppl. material 3). The first two surveys of the filtrate contained minute and pale beetle fragments assumed to be remnants of *S. oregonensis*. These fragments did not appear to contain any soft tissue; they may have died long before the filtrate was examined.

The mostly intact beetle specimens were both caught during the rainy winter months and contained soft tissue, which appeared to be suitable for DNA extraction and PCR sequencing. The specimens were found with the prothorax and head slightly separated from the rest of the body and the genitalia extruded as if they had expanded slightly. This damage may have occurred during depressurization: the removal of the filter causes a change in pressure from 8–10 psi to atmospheric pressure in approximately 2 seconds.

In addition to *S. oregonensis*, we recovered crustaceans (ostracods, copepods, and Bathynellacea), numerous oribatid mites, and a few other insects (Throscidae (Coleoptera),

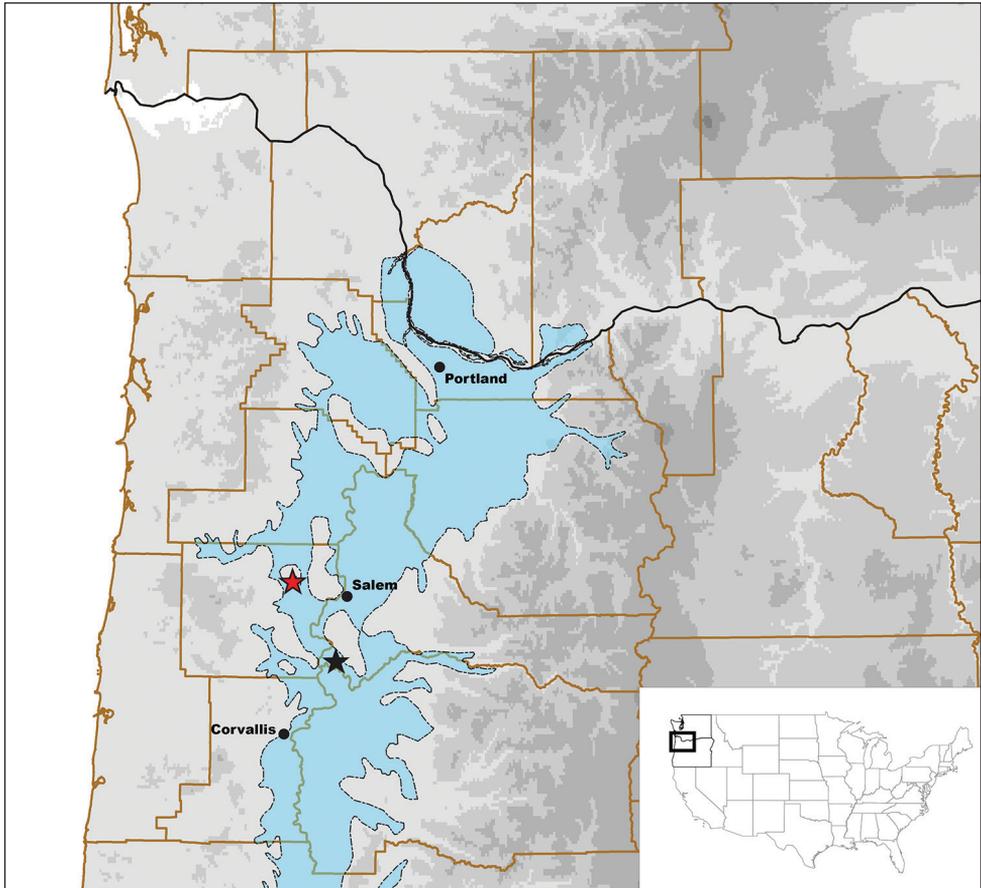


Figure 2. The two known collection localities of *Stygoporus oregonensis*. Oregon/Washington State boundary in black. County boundaries in brown. Blue shaded region outlined with a dotted line corresponds to Willamette Lowland basin-fill aquifers. Type locality indicated by red star with black border. New collection locality indicated by black star.

Chironomidae larvae (Diptera), and unattributed elytral fragments). While the Throscidae appears to be an obvious terrestrial contaminant, we could not determine if the other taxa are associated with the aquifer or not. The pair of pale elytra recovered in one of the samples (OSAC Lot 20160620-03) was markedly smaller and stouter than that of *S. oregonensis* and while it may have come from a surface dwelling species, it raises the possibility of additional undiscovered species inhabiting the aquifer.

DNA extraction and sequencing

We extracted DNA from the two fairly intact specimens of *S. oregonensis* using DNeasy Blood and Tissue kits (Qiagen) following the manufacturer's protocols. Specimens

were disarticulated between the abdomen and thorax prior to extraction; we did not grind any tissue, and thus the exoskeleton was preserved. We successfully amplified and sequenced six of the seven gene fragments used in Miller et al. (2013): 12S rRNA (12S), 16S rRNA (16S), cytochrome c oxidase I (COI), cytochrome c oxidase II (COII), *wingless* (*wg*), and histone III (H3), but were unsuccessful at amplifying elongation factor 1-alpha. PCRs were performed in 25 microliter reactions on either an Eppendorf Mastercycler gradient or Mastercycler ProS using TaKaRa Ex Taq following manufacturer's protocols. We used primer pairs and amplification conditions described in Miller et al. (2013) for 12S, 16S, COI (Pat/Jerry), COII, and H3, and Kanda et al. (2015) for *wg* and the barcoding region of COI (Suppl. material 4). PCR cleanup, quantification, and sequencing were performed at the University of Arizona's Genomic and Technology Core Facility (UAGC) using a 3730 XL Applied Biosystems automatic sequencer.

Sequence processing and phylogenetic analyses

Initial assembly of chromatograms was performed using Phred v. 0.020425.c (Green and Ewing 2002) and Phrap v. 0.990319 (Green 1999) as orchestrated by Mesquite v. 3.04 package Chromaseq v. 1.12 (Maddison and Maddison 2011, Maddison and Maddison 2015) with subsequent manual processing. *S. oregonensis* sequences were combined with single gene matrices from Miller et al. (2013). The taxon sampling used in Miller et al.'s (2013) study encompasses the morphological diversity of Hydroporinae, including numerous representatives of all currently recognized subtribes of Hydroporini (Suppl. material 5) and thus provides an excellent framework for inferring the phylogenetic placement of *S. oregonensis*.

12S and 16S matrices were aligned using MAFFT v. 7.130b (Katoh and Standley 2013) and the L-INS-i method. Alignment of protein-coding genes were performed manually since they either had no indels (COI, COII, and H3) or just a single inferred amino acid indel (*wg*). All nucleotide alignments were also combined into a single concatenated dataset.

Optimal data partition schemes and model of molecular evolution for protein-coding genes were inferred using PartitionFinder v. 1.1.1 (Lanfear et al. 2012) starting from an initial partition scheme based on codon position. Examined models were restricted to those available in RAxML, BIC was used to compare models, and the greedy algorithm was used for searches. Models for 12S and 16S were inferred using BIC implemented in jModelTest 2.0 (Darriba et al. 2012). PartitionFinder analysis was also conducted on the concatenated dataset starting with an initial partition scheme based on gene and codon. Optimal models and partitions for all datasets are presented in Table 1.

We conducted Maximum Likelihood (ML) analyses on single gene and concatenated datasets using RAxML v. 8.0.3 (Stamatakis 2014) implemented through the

Table 1. Properties of phylogenetic datasets analyzed for this study. **NTaxa:** The number of taxa represented in the dataset. **Partitions:** Optimal partitioning scheme chosen by PartitionFinder. **NChar (BP):** Number of characters (bases) in the aligned dataset/partition. **Model:** Optimal model of molecular evolution inferred by either jModelTest (12S, and 16S) or PartitionFinder (protein-coding genes).

Dataset	NTaxa	Partitions	NChar (BP)	Model
12S	49	<i>NA</i>	362	GTR+I+G
16S	50	<i>NA</i>	533	HKY+I+G
COI	44	(1) n1, n2	838	GTR+I+G
		(2) n3	418	GTR+G
COII	43	(1) n1, n2	450	GTR+I+G
		(2) n3	224	GTR+G
H3	50	(1) n1, n2, n3	328	GTR+I+G
<i>wg</i>	20	(1) n1, n2	306	GTR+I+G
		(2) n3	154	GTR+G
Concatenated	51	(1) 12S, 16S	895	GTR+I+G
		(2) n1 and n2 of all genes	1812	GTR+I+G
		(3) n3 of COI and COII	642	GTR+G

Mesquite package Zephyr v. 1.1 (Maddison and Maddison 2015) with optimal partition schemes and models of molecular evolution. When different models were chosen for different partitions, we applied the most complex model to the entire dataset. Since the HKY substitution model that was selected for 16S is not available in RAxML, we instead used GTR. We conducted 500 independent searches for the maximum likelihood tree and 1,000 bootstrap replicates on all datasets.

Morphological methods

Methods for gross morphological examination and use of terms follow Miller (2005, 2016). The two extracted specimens were also used for morphological study of female internal reproductive characters. Female genitalia were dissected following DNA extraction, stained with 10% Chlorazol Black diluted in 75% ethanol, and examined on a slide in deionized water. During the course of study, the female genitalia of the recently acquired specimens were heavily damaged or lost accidentally after morphological features were recorded. Because of the extensive damage or loss, we chose not to image the genitalia. The female genital structures were mounted in Euparal on cardstock and pinned beneath the specimen.

The dorsal habitus image was taken with a Leica Z6 and JVC KY-F75U camera using Microvision's Cartographer to take a stack of pictures at different focal planes. Stacking was performed using the PMax procedure implemented in Zerene Stacker (Zerene Systems). Removal of background and minor color adjustment was performed using Photoshop and Illustrator CS5 (Adobe).

Data availability

All specimens examined in this study and the two DNA extractions are deposited in the Oregon State Arthropod Collection (OSAC), Oregon State University. Associated OSAC lot and voucher codes are given in Suppl. material 3. Final sequences for both specimens are available through GenBank (accession numbers KX882130-KX882141). Matrices used in the analyses are available as supplemental content (Suppl. material 6: MatricesForAnalyses.nex).

Results

Additional morphological characters for *Stygoporus oregonensis*

Morphological characters discussed below are based on the original description of *S. oregonensis* (Larson and LaBonte 1994) and material examined for the present study; the latter allowed us to examine previously unstudied characters of the proventriculus and female genitalia.

The proventriculus of *S. oregonensis* has a simple transverse tooth similar to that of *Hydroporus* Clairville with fields of papillae laterally. The female genitalia are of hydroporine-type (Miller 2001) with elongate ductwork. The external genitalia lack laterotergites, gonocoxosternites are broadly triangular and finely setose ventrally with an anteriorly rounded projection, gonocoxae are unfused, slender basally, broadening apically to a narrowly rounded apex, with numerous minute apical setae. Internally, the bursa is small and lacks a ring-like sclerite, the spermathecal duct is elongate and slender for most of its length, broadening before attaching to the small bulbous spermatheca, and the shorter fertilization duct is similarly slender and inserts ventrally on the vagina posterior to the common oviduct.

Phylogenetic placement of *Stygoporus oregonensis*

The maximum likelihood (ML) tree of the concatenated dataset is shown in Figure 3 and majority rules consensus tree from 1000 bootstrap replicates is shown in Figure 4. ML trees and bootstrap consensus trees for single-gene datasets are provided in Suppl. material 1 and 2. ML bootstrap support percentages (BSP) are summarized across phylogenetic reconstructions in Table 2 for hypotheses regarding the taxonomic placement of *Stygoporus oregonensis*.

Maximum likelihood analysis of the concatenated dataset recovers *S. oregonensis* as sister to the Texas stygobite *E. naturaconservatus* (Figs 3, 4) with high bootstrap support (BSP=99.3). This clade is placed within the hydroporine subtribe Siettitiina, which is recovered with moderate support (BSP=75). Additional recovered genus or tribal-level groups largely correspond to the ML inference of phylogeny by Miller et al. (2013).

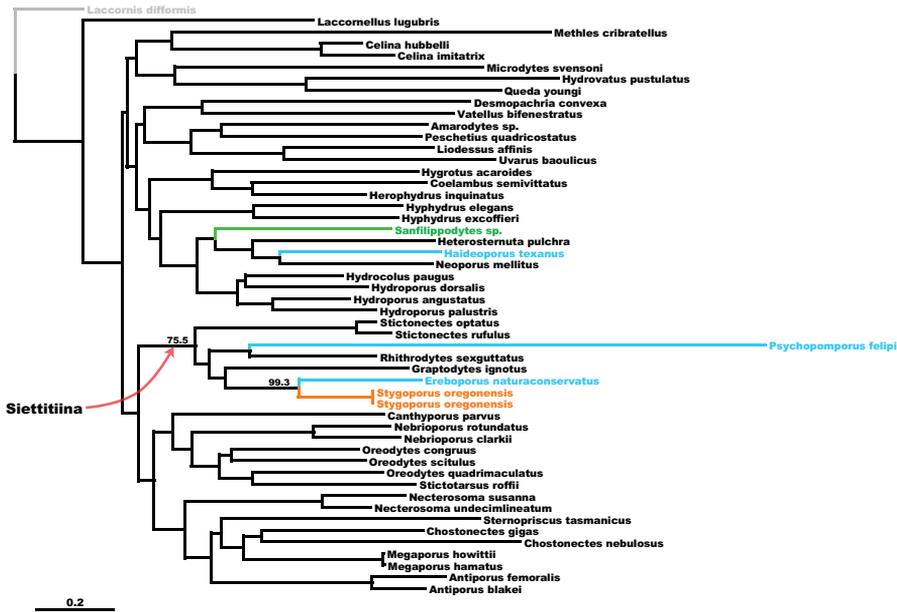


Figure 3. Maximum likelihood tree from concatenated dataset. Scale bar = 0.2 expected substitutions per position as estimated by RAxML. *Stygoporus oregonensis* in orange; other stygobitic dytiscids in blue; the epigean genus *Sanfilippodytes*, hypothesized by Larson and LaBonte (1994) to be the closest relative to *S. oregonensis*, in green. Bootstrap support given at nodes for Siettitiina and *S. oregonensis* + *Ereborporus naturaconservatus*.

Table 2. Bootstrap support for placement of *Stygoporus oregonensis*. Taxonomic hypotheses are in the first column. Bootstrap support given as a percentage for each hypothesis for all analyzed matrices. “Con” refers to the analysis of the concatenated matrix.

Taxonomic hypotheses	Con	12S	16S	COI	COII	H3	wg
<i>Stygoporus oregonensis</i> + <i>Ereborporus naturaconservatus</i>	99.3	79.2	41.1	60.1	70.7	86.0	90.0
<i>S. oregonensis</i> + <i>Sanfilippodytes</i>	0	0	0	0	0.2	3.0	0.5
Siettitiina including <i>S. oregonensis</i>	75.5	4.6	87.7	45.7	0	0	31.0
Siettitiina excluding <i>S. oregonensis</i>	0	0	1.3	1.2	0	0	0
<i>S. oregonensis</i> in Hydroporina	0	0.1	0	0	0	0	0

Ereborporus naturaconservatus and *S. oregonensis* are recovered as sister species in all single gene ML analyses (Suppl. material 1). This relationship is moderately to highly supported across single gene bootstrap analyses except in 16S (Table 2, Suppl. material 2). Although Siettitiina (*Graptodytes* group) is not equally well sampled for all genes, *S. oregonensis* and *E. naturaconservatus* are recovered within a monophyletic Siettitiina in ML analyses of 16S, COI, and wg. Support for Siettitiina (including *Stygoporus*) is high in bootstrap analyses of 16S but low to non-existent in other genes.

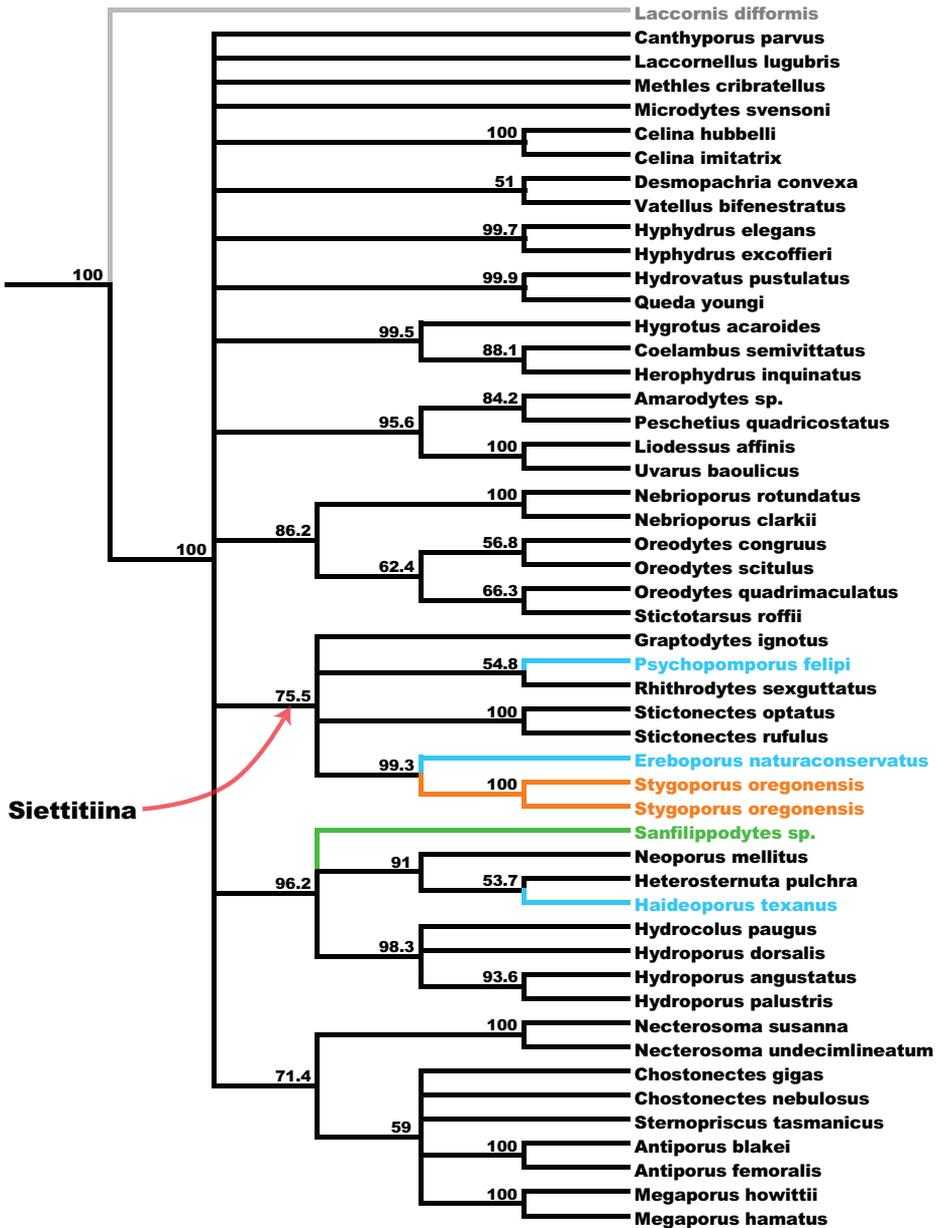


Figure 4. Majority rule consensus of 1,000 bootstrap replicates performed on concatenated dataset. Bootstrap percentages given for clades recovered with more than 50% support. Branches and taxa colored as in Figure 3.

Stygoporus oregonensis is never placed with *Sanfilippodytes* nor in Hydroporina in ML analyses of either the concatenated or single gene ML trees, and this hypothesis has no bootstrap support across analyses.

Discussion

In their original description of *Stygoporus*, Larson and LaBonte (1994) placed it in the Hydroporini based on (1) posterior margin of metacoxal lobes continuous and sinuate, (2) posterior margin of metacoxal lobes unfused to abdominal ventrites II and III, (3) metafemur broadly separated from metacoxal lobe by large metatrochanter, (4) base of metafemur hidden ventrally by metacoxal lobe, and (5) male lateral lobes with a single segment. None of these morphological characters are synapomorphic for a tribal-level clade of Hydroporinae. Historically, Hydroporini included those Hydroporinae without a distinctive set of apomorphies, and clarifying relationships within Hydroporini has been a prominent goal of modern Dytiscidae systematics (Miller and Bergsten 2014). Recently, Miller and Bergsten (2014) reclassified the Hydroporini, giving genus group clades that were well supported with molecular and morphological data available higher-level names: *Deronectina* (*Deronectes* group), *Hydroporina* (*Hydroporus* group), *Sternopriscina* (*Necterosoma* group), and *Siettitiina* (*Graptodytes* group). While they did not have molecular sequence data for *Stygoporus*, they tentatively classified it within the *Hydroporina* (Miller and Bergsten 2014).

Larson and LaBonte (1994) hypothesized that *Stygoporus* is sister to *Sanfilippodytes* based on similar anteriorly produced metaventral processes, large metatrochanters, and habitat data. Contrary to this hypothesis, our molecular data places *S. oregonensis* within *Siettitiina* and not near *Hydroporina* and *Sanfilippodytes*. Though the phylogenetic analyses of Miller et al. (2013) and Miller and Bergsten (2014) strongly support the monophyly of *Siettitiina*, this clade is morphologically poorly defined. One potential synapomorphy is a ring-sclerite on the bursa copulatrix adjacent to the attachment of the spermathecal duct (Miller and Bergsten 2014). This structure is known to occur in *Ereboporus* and other *siettitiines* but is notably missing from *Graptodytes* Seidlitz (Miller et al. 2013), which is also the most diverse genus within the subtribe (Nilsson 2001). As in *Graptodytes*, the bursa copulatrix of *S. oregonensis* lacks a ring-like sclerite. We note that although the female genitalia in our specimen was damaged, it is clear that there is not a region along the bursa that looks more sclerotized or distinct from the remaining structure.

There are additional morphological characters in support of inclusion of *S. oregonensis* within *Siettitiina*, though it remains unclear whether these characters are strong synapomorphies for *Siettitiina* as a whole. In particular, the pronotum of *S. oregonensis* has prominent paralaral longitudinal creases or striae similar to many members of the larger group (e.g. *Graptodytes* Seidlitz, *Siettitia* Abeille de Perrin and *Etruscodytes* Mazza, Cianferoni, and Rocchi). The prosternal process of *S. oregonensis* contacts the anteriorly projecting and narrowly rounded metaventral process, resting dorsad to it and altogether looks remarkably similar to the Italian stygobite *Etruscodytes*. This region of the body has received much attention from biologists interested in stygobitic beetles (Miller et al. 2013; Spangler 1986), and these sclerites are intricately involved in locomotion, particularly wedging (Evans 1977). The similarity in form of these sclerites may be evidence of recent common ancestry, but this may also be the result of

convergence as modifications to the ventral thoracic sclerites and the loss of a streamlined body are commonly observed patterns in distantly related subterranean diving beetles (Miller et al. 2009; Spangler 1986).

Other morphological features in *S. oregonensis* relevant to grouping within Hydroporini are known plesiomorphies. These are, for example, the simple transverse tooth of the proventriculus, the unfused, simple gonocoxae, the basally broad and apically narrowed elytral epipleuron, the male pro- and mesotarsomeres I-III with ventral adhesive setae, and the mesoventral fork separated from the anteromedial metaventral process. Most of these characters are unlike those observed in Deronectina and Sternopriscina, and the morphological evidence separating Hydroporina from Siettitiina is limited. Based on our observations, it appears that *Stygoporus* retains many plesiomorphies and placement based on morphological characters alone is difficult. However, the sequence data support the inclusion of *Stygoporus* within Siettitiina, and they decisively indicate that *Stygoporus* is closely related to *Ereboporus* among sampled species.

The Siettitiina has a predominantly Mediterranean and European distribution and includes many epigeal species as well as other subterranean species (e.g. Ribera and Faille 2010). Intriguingly, the only presently known European stygobitic dytiscids are members of Siettitiina, including some species known only from wells and aquifers (Castro and Delgado 2001; Mazza et al. 2013; Ribera and Faille 2010). Aside from *S. oregonensis* and two described Texas subterranean aquifer endemics, Siettitiina are not represented in the New World, which suggests an ancient origin for these species (Miller et al. 2013). The mechanism and process behind this biogeographic pattern is not known. Conclusions invoking vicariance, dispersal, and extinction can certainly be applied to this pattern, but we prefer the practical hypothesis that at least part of this result is attributable to our ignorance. Instead of being dismayed, however, we are excited by the possibility that there are many unknown stygobitic beetles in aquifers between Oregon and Texas as well as other parts of the world for which little sampling of this habitat has been done.

Acknowledgements

We sincerely thank the private landowners who allowed us access to their land. Portions of this project were supported by the Harold E. and Leona M. Rice Endowment Fund at Oregon State University (to D.R. Maddison) and NSF grants #DEB-0845984 and #DEB-1353426 (to K.B. Miller).

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Supplementary material 1

Figure 1

Authors: Kojun Kanda, R. Antonio Gomez, Richard Van Driesche, Kelly B. Miller, David R. Maddison

Data type: Adobe PDF file

Explanation note: Maximum likelihood trees for single gene datasets. Scale bar indicates the expected substitutions per site as estimated by RAxML.

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Supplementary material 2

Figure 2

Authors: Kojun Kanda, R. Antonio Gomez, Richard Van Driesche, Kelly B. Miller, David R. Maddison

Data type: Adobe PDF file

Explanation note: Majority rule consensus of 1,000 bootstrap replicates performed on single gene datasets. Bootstrap percentage given for clades recovered with more than 50% support.

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Supplementary material 3

Table 1

Authors: Kojun Kanda, R. Antonio Gomez, Richard Van Driesche, Kelly B. Miller, David R. Maddison

Data type: MS Word file

Explanation note: Collection and specimen data for material examined in this study.

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Supplementary material 4

Table 2

Authors: Kojun Kanda, R. Antonio Gomez, Richard Van Driesche, Kelly B. Miller, David R. Maddison

Data type: MS Word file

Explanation note: PCR primers and amplification conditions for sampled gene fragments.

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Supplementary material 5

Table 3

Authors: Kojun Kanda, R. Antonio Gomez, Richard Van Driesche, Kelly B. Miller, David R. Maddison

Data type: MS Word file

Explanation note: Taxa from Miller et al. (2013) sampled in this study with updated tribal and subtribal classification of Miller and Bergsten (2014).

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Supplementary material 6

Data availability

Authors: Kojun Kanda, R. Antonio Gomez, Richard Van Driesche, Kelly B. Miller, David R. Maddison

Data type: NEXUS file

Explanation note: NEXUS formatted single-gene and concatenated nucleotide sequence alignments.

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Description of the first species of *Fiorianteon* Olmi (Hymenoptera, Dryinidae) from the Afrotropical region

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Academic editor: M. Ohl | Received 20 September 2016 | Accepted 3 November 2016 | Published 16 November 2016

<http://zoobank.org/E423B750-5629-47BE-A3C4-D9A356336508>

Citation: Guglielmino A, Olmi M, Marletta A, Speranza S (2016) Description of the first species of *Fiorianteon* Olmi (Hymenoptera, Dryinidae) from the Afrotropical region. ZooKeys 632: 93–98. doi: 10.3897/zookeys.632.10576

Abstract

Fiorianteon sulcatum sp. n. is described from Fianarantsoa Province (Madagascar). It is the first species of *Fiorianteon* found in the Afrotropical region. The genus *Fiorianteon* can be distinguished from the closely related genus *Conganteon* by the distal part of the stigmal vein, which is as long as, or shorter than the proximal part of the stigmal vein (longer than the proximal part of the vein in *Conganteon*).

Keywords

Taxonomy, *Fiorianteon sulcatum*, Madagascar, Conganteoninae, Chrysoidea

Introduction

Dryinidae (Hymenoptera Chrysoidea) are parasitoids of Hemiptera, Auchenorrhyncha (Guglielmino et al. 2008, 2013). The biology of this small group of wasps is still poorly known (Carcupino et al. 1998; Guglielmino 2000; Guglielmino and Bückle 2003, 2010; Guglielmino et al. 2006, 2015; Guglielmino and Virla 1998).

The genus *Fiorianteon* Olmi, 1984 (Conganteoninae) is only present in the Oriental and Eastern Palaearctic zoogeographical regions (Olmi and Xu 2015). Four species have been described from the above regions (Xu et al. 2013; Olmi and Xu 2015). The hosts are unknown.

The genus was originally revised at world level by Olmi (1984) and more recently by Xu et al. (2013) and Olmi and Xu (2015) for the Oriental and the Eastern Palaearctic regions respectively.

In 2015, we examined additional specimens of Dryinidae from Madagascar, which included the new species of *Fiorianteon* described in this paper.

Material and methods

The descriptions follow the terminology used by Olmi (1984), Olmi and Guglielmino (2010) and Olmi and Virla (2014). The reported measurements are relative, except for the total length (head to abdominal tip, without antennae), which is expressed in millimeters. In the descriptions, POL is the distance between the inner edges of the two lateral ocelli; OL is the distance between the inner edges of a lateral ocellus and the median ocellus; OOL is the distance from the outer edge of a lateral ocellus to the eye; OPL is the distance from the posterior edge of a lateral ocellus to the occipital carina; and TL is the distance from the posterior edge of an eye to the occipital carina. The material studied in this paper is deposited in the collections of the California Academy of Sciences, San Francisco, USA (CAS).

The multifocal pictures were taken by a stereomicroscope Leica M205A and Leica DFC450 video camera, captured using Leica Application Suite v. 4.2.0.

Results

Genus *Fiorianteon* Olmi, 1984

Fiorianteon Olmi, 1984: 108. Type species: *Fiorianteon junonium* Olmi, 1984, by original designation.

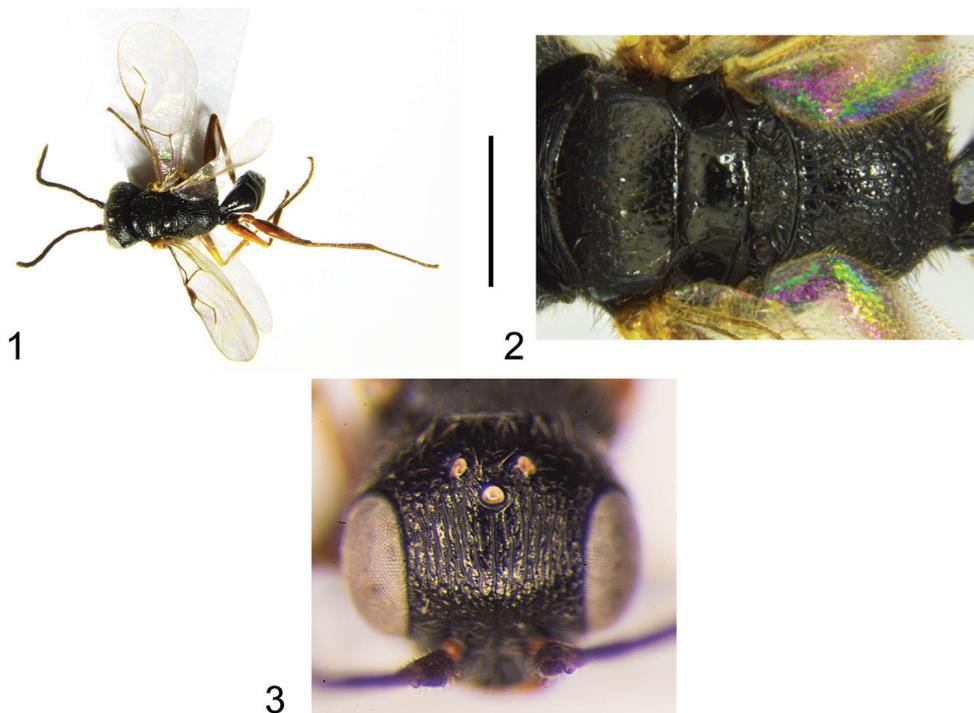
Diagnosis. Female: fully winged; occipital carina complete; mandible quadridentate, with one intermediate rudimentary tooth; antenna without rhinaria; palpal formula 6/3; pronotal tubercles present; forewing with two cells enclosed by pigmented veins (costal and median); forewing with stigmal vein and pterostigma present; distal part of stigmal vein as long as, or shorter than proximal part of stigmal vein; protarsus chelate; chela with rudimentary claw; tibial spurs 1/1/2. **Male:** fully winged; occipital carina complete; mandible quadridentate, with one intermediate rudimentary tooth; palpal formula 6/3; forewing with two cells enclosed by pigmented veins (costal and median); fore wing with stigmal vein and pterostigma present; distal part of stigmal vein as long as, or shorter than proximal part of stigmal vein; tibial spurs 1/1/2.

***Fiorianteon sulcatum* Guglielmino, Olmi, Marletta & Speranza, sp. n.**

<http://zoobank.org/6D43414A-BCB9-4C75-BF6C-39D6498599B5>

Diagnosis. head completely sculptured by longitudinal subparallel keels, on face (Fig. 3), vertex and temple; paramere (Fig. 4) with distal part of inner margin provisioned with many sensorial processes.

Description. Male. Fully winged (Fig. 1). Body length 2.8 mm. Head black, except mandible testaceous; antenna brown; mesosoma and metasoma black; legs brown, except most part of coxae black. Antenna filiform; antennal segments in following proportions: 11:5:13:14:13:12:10:9:8:10. Head shiny, completely sculptured by longitudinal subparallel keels, on face (Fig. 3), vertex and temple; frontal line complete; occipital carina complete; POL = 5; OL = 3; OOL = 7; OPL = 7; TL = 10; greatest breadth of lateral ocelli about as long as OL. Scutum (Fig. 2) shiny, with anterior half slightly rugose; posterior half, punctate, unsculptured among punctures. Notauli incomplete, reaching approximately 0.5× length of scutum. Scutellum punctate, unsculptured among punctures. Metanotum dull, rugose. Propodeum reticulate rugose, without transverse or longitudinal keels. Forewing hyaline, without dark transverse bands; distal part of stigmal vein about as long as proximal part (Fig. 1), about as long as antennal segment 3. Paramere (Fig. 4) with distal part of inner margin provided of many sensorial processes. Tibial spurs 1/1/2. **Female.** Unknown.



Figures 1–3. Male holotype of *Fiorianteon sulcatum* sp. n.: habitus (1) and mesosoma (2) in dorsal view; head in frontal view (3). Scale bar = 2.53 mm (1), 0.37 mm (2); 0.45 mm (3).

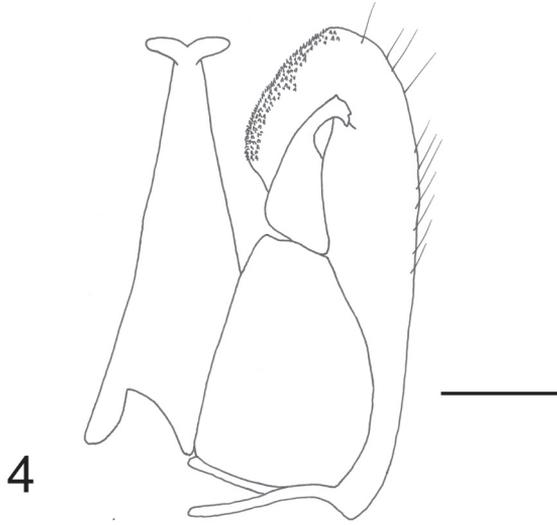


Figure 4. Male holotype of *Fiorianteon sulcatum* sp. n.: male genitalia (left half removed). Scale bar = 0.10 mm.

Material examined. Holotype: male, MADAGASCAR: Fianarantsoa Province, Andringitra National Park, Plateau d’Andohariana, 35.9 km 205° Ambalavao, 22°09.08’S 46°53.57’E, 2000 m, 15.IV.2006, Malaise trap, BL Fisher et al. leg., BLF13755 (CAS).

Hosts. Unknown.

Distribution. Madagascar.

Remarks. The two main characters distinguishing the new species are detailed in the above diagnosis. These characters are not present in any of the known species of Conganteoninae (Olm and Xu 2015; Xu et al. 2013).

Etymology. The species is named *sulcatum* because the head is sculptured by many longitudinal subparallel keels.

Discussion

Azevedo et al. (2010) listed 123 species, 15 genera and 7 subfamilies of Dryinidae from the Malagasy region. The recorded genera and subfamilies were as follows: Anteoniinae: *Anteon* Jurine, 1807 (28 species), *Deinodryinus* Perkins, 1907 (13 species), *Lonchodryinus* Kieffer, 1905 (three species); Aphelopinae: *Aphelopus* Dalman, 1823 (three species); Apodryininae: *Apogonatopus* Olmi, 2007 (two species), *Gondwanadryinus* Olmi, 2007 (one species), *Madecadryinus* Olmi, 2007 (six species); Bocchinae: *Bocchus* Ashmead, 1893 (eight species); Conganteoninae: *Conganteon* Benoit, 1951 (two species); Dryininae: *Dryinus* Latreille, 1804 (16 species), *Thaumatodryinus* Perkins, 1905 (six species); Gonatopodinae: *Echthrodolphax* Perkins, 1903 (two species), *Gonatopus*

Ljungh, 1810 (30 species), *Haplogonatopus* Perkins, 1905 (one species) and *Neodryinus* Perkins, 1905 (two species). With the description of the above new species the number of species in the Malagasy region is elevated to 124 and the genera to 16.

Acknowledgements

Many thanks to Bob Zuparko (California Academy of Sciences, San Francisco) for the loan of the specimen studied in the present paper. We are grateful to Dr. Simon van Noort (Iziko South African Museum, Cape Town, South Africa) for checking the English language of this paper. The authors are grateful to Massimo Vollaro (Department of Agriculture and Forestry Sciences (DAFNE), University of Tuscia) for his picture of the face (Fig. 3).

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Checklist of the continental fishes of the state of Chiapas, Mexico, and their distribution

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Academic editor: *Kyle Piller* | Received 2 July 2016 | Accepted 19 October 2016 | Published 16 November 2016

<http://zoobank.org/45D6156F-CA64-4DBF-B779-F6A97410C7F4>

Citation: Velázquez-Velázquez E, López-Vila JH, Gómez-González AE, Romero-Berny EI, Lievano-Trujillo JL, Matamoros WA (2016) Checklist of the continental fishes of the state of Chiapas, Mexico, and their distribution. ZooKeys 632: 99–120. doi: 10.3897/zookeys.632.9747

Abstract

An updated checklist of the distribution of fishes that inhabit the continental waters of the Mexican state of Chiapas is presented. The state was compartmentalized into 12 hydrological regions for the purpose of understanding the distribution of fish fauna across a state with large physiographic variance. The ichthyofauna of Chiapas is represented by 311 species distributed in two classes, 26 orders, 73 families, and 182 genera, including 12 exotic species. The families with the highest number of species were Cichlidae, Poeciliidae, Sciaenidae, Carangidae, Ariidae, Gobiidae, and Haemulidae. This study attempts to close gaps in knowledge of the distribution of ichthyofauna in the diverse hydrological regions of Chiapas, Mexico.

Keywords

Distribution, endemism, fish diversity, ichthyology, southern Mexico

Introduction

The hydrological wealth of Chiapas is manifested through its 72 perennial rivers and abundant streams, lakes, and ponds. The presence of large hydroelectric dams has significantly increased the surface area of the state's bodies of water (Velasco-Colín 1976). Chiapas has a coastline of 270 km and more than 70,000 hectares of estuaries and coastal lagoons (Contreras-Espinosa 2010), which favors the presence of rich fish diversity (Velasco-Colín 1976, Lozano-Vilano and Contreras-Balderas 1987, Rodiles-Hernández et al. 2005). Much of the state is located in the Usumacinta ichthyographic province/area of endemism (Miller et al. 2005, Matamoros et al. 2015), which means that its continental waters host a high number of endemic species, making Chiapas a freshwater biodiversity hotspot (Hudson et al. 2005, Matamoros et al. 2015).

Several attempts have been made to record continental water fish diversity in Chiapas through numerous works such as checklists, annotated checklists, books and scattered records in the literature (e.g. Velasco-Colín 1976, Lozano-Vilano and Contreras-Balderas 1987, Lazcano-Barrero and Vogt 1992, Tapia-García et al. 1998, Rodiles-Hernández et al. 1999, Rodiles-Hernández 2005, Rodiles-Hernández et al. 2005, 2013, Lozano-Vilano et al. 2007, González-Díaz et al. 2008, Espinosa-Pérez et al. 2011, Velázquez-Velázquez et al. 2013, Gómez-González et al. 2012, 2015). The first comprehensive publication on continental fishes of Chiapas was made by Velasco-Colín (1976), who reported 74 species distributed across 28 families. He also included brief information about the ecology, biology and distribution of several species and, in some cases, added relevant fishing information.

Subsequently Lozano-Vilano and Contreras-Balderas (1987) published an annotated checklist in which they registered 135 species belonging to 38 families in the state's continental waters. In addition to an increase in the number of data records, for the first time the distribution of fishes was associated with seven of the state's physiographic regions. Eighteen years later Rodiles-Hernández (2005) and Rodiles-Hernández et al. (2005) recorded 205 species in 44 families and 207 species in 45 families respectively. In the first study, distributions were reported at the level of the two main Chiapas river basins, the Grijalva-Usumacinta and the Coast of Chiapas, whereas, in the second study, the distributional geographic units were the Atlantic and the Pacific slope. Velázquez-Velázquez et al. (2013) was the last published attempt to summarize continental fishes of Chiapas. They reported 262 species across 57 families, and once again the geographic distribution units were the Grijalva and the Usumacinta River basins and the coast of Chiapas.

Two interesting trends emerge about the continental fishes of Chiapas. First, the number of recorded species has continued to increase over time likely due to an increase in sampling localities, implementation of new sampling techniques, new records and species descriptions. The second trend is related to the geographic units in which the state has been divided. For instance, Lozano-Vilano and Contreras-Balderas (1987) divided the state into seven physiographic regions, based on terrestrial relief. Most studies used broad delineations limited to the three major hydrologic regions (coast of Chiapas

and the Grijalva and Usumacinta River basins) masking detailed information on finer distributional patterns like localized endemism and drainage interconnections.

Therefore, the aim of this study is to provide an updated checklist of the continental fishes of Chiapas, including distribution data, based on extensive literature research and complemented with material deposited in the ichthyological collection of the Museum of Zoology at the University of Arts and Sciences of Chiapas (MZ-P-UNICACH). For the first time, we use finer scale geographic divisions for the state, implemented at the sub-basin level, following the National Institute of Statistics and Geography (INEGI 2010).

Materials and methods

The bulk of records came from the material of 204 species deposited in the ichthyological collection of the MZ-P-UNICACH Museum of Zoology (MZ-P-UNICACH, SEMARNAT: CHIS-PEC-210-03-09). In addition, we performed an extensive literature review for records of continental fishes of Chiapas. The checklists previously published by Lozano-Vilano and Contreras-Balderas (1987), Rodiles-Hernández (2005), Rodiles-Hernández et al. (2005), Espinosa-Pérez et al. (2011), and Velázquez-Velázquez et al. (2013) were taken as the basis for this work and were supplemented with publications by Lazcano-Barrero and Vogt (1992), Tapia-García et al. (1998), Rodiles-Hernández et al. (1999), Lozano-Vilano et al. (2007) and Gómez-González et al. (2012, 2015) who developed lists for particular regions of the state. We also included Castro-Aguirre et al. (1999) and Miller et al. (2005).

Species were systematically arranged by order and family following Nelson (2006). Genera and species were arranged alphabetically; scientific names and authorities were corroborated following Eschmeyer et al. (2016). Tolerance to salinity was based on Myers (1938).

The 12 geographical units for Chiapas (Figure 1) were utilized to determine the distribution of each species across the state. These 12 units were based on existing hydrological sub-basins of the state (INEGI 2010). The main rivers, ponds, lakes and coastal lagoons of each sub-basin are listed in Table 1.

Results

The continental fishes of the state of Chiapas are represented by two classes, 26 orders, 73 families, 182 genera and 311 species (Table 2), including 12 exotic species (*Ctenopharyngodon idella*, *Cyprinus carpio*, *Micropterus salmoides*, *Oncorhynchus mykiss*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Parachromis managuensis*, *Pterygoplichthys disjunctivus*, *Pterygoplichthys multiradiatus*, *Pterygoplichthys pardalis*, and *Tilapia zilli*). Only five species were endemic: the catfish *Lacantunia enigmatica*, the cichlids *Rocio ocoatl* and *Thorichthys socolofi*, the killifish *Tlaloc hildebrandi* and the molly *Poecilia*

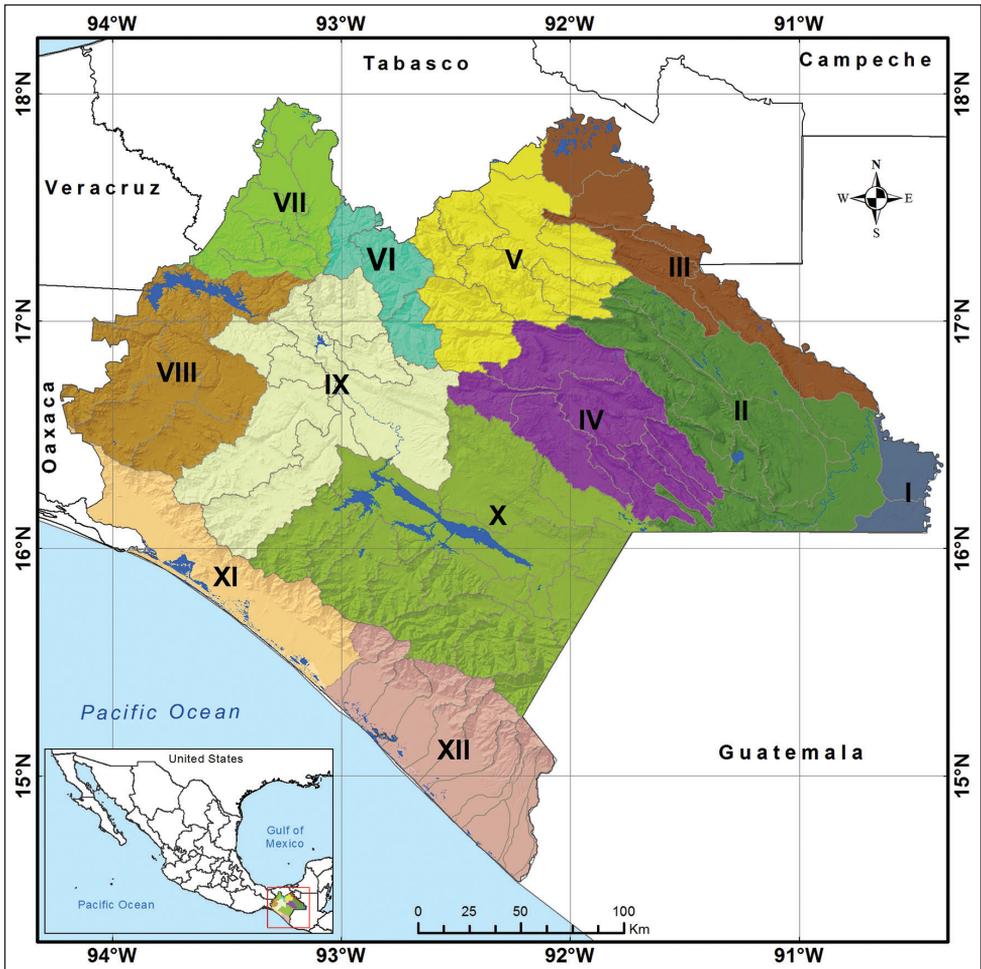


Figure 1. Geographical units for the study of the distribution of the fish fauna of the state of Chiapas: **I** (Usumacinta-Chixoy) **II** (Usumacinta-Lacantún) **III** (Usumacinta-Catazajá) **IV** (Usumacinta-Jataté) **V** (Grijalva-Tulijá) **VI** (Grijalva-Teapa) **VII** (Grijalva-Peñitas) **VIII** (Grijalva-Malpaso), **IX** (Grijalva-Chicoasén) **X** (Grijalva-La Angostura) **XI** (Costa-Itzmo) **XII** (Costa-Soconusco).

thermalis. Based on species richness the most important families were: Cichlidae (35), Poeciliidae (29), Sciaenidae (18), Carangidae (17), Ariidae (16), Gobiidae (12), and Haemulidae (11). Almost all of these families, except the first two, contains peripheral species. These eight families represented 44.37% (138) of the state's total species richness. Thirteen species are included in risk categories under Mexican law (NOM-059-SEMARNAT-2010; SEMARNAT, 2010): *Poecilia sulphuraria* and *Tlaloc hildebrandi* are listed as endangered; *Priapella compressa*, *Thorichthys socolofi*, *Vieja hartwegi* and *Xiphophorus clemenciae* are listed as threatened; finally *Chiapaheros grammodes*, *Gambusia eurystoma*, *Hippocampus ingens*, *Potamarius nelsoni*, *Priapella intermedia*, *Rhamdia guatemalensis* and *Chuco intermedium* are listed as species under special protection. Based on general salinity

Table 1. Geographic units utilized to study the distribution of the fish fauna of Chiapas and sub-basins that form them.

Hidrological region	Basin	Sub-basin	Geographic unit	
COSTA DE CHIAPAS	R. SUCHIATE AND OTHERS	R. Suchiate	Costa-Soconusco	
		R. Cozoloapan		
		R. Cahuacán		
		Puerto Madero		
		R. Coatán		
		R. Huehuetán		
	R. HUIXTLA AND OTHERS	R. Huixtla		
		R. Despoblado		
		L. del Viejo y Tembladeras		
		R. Cacaluta		
		R. Sesecapa		
		R. Novillero		
	R. PIJJIAPAN AND OTHERS	R. Margaritas y Coapa	Costa-Istmo	
		R. Pijjiapan		
		R. San Diego		
El Porvenir				
R. Jesús				
L. de la Joya				
MAR MUERTO	R. Zanatenco			
	Mar Muerto			
	R. La Punta			
	R. Las Arenas			
	R. Tapanatepec			
GRIJALVA - USUMACINTA	R. USUMACINTA	R. Usumacinta		Usumacinta-Catazajá
		R. Chacamax		
		R. Chacaljáh		
	R. CHIXOY	R. Chixoy	Usumacinta-Chixoy	
		R. Negro		
	R. GRIJALVA - VILLAHERMOSA	R. GRIJALVA - VILLAHERMOSA	R. Viejo Mezcalapa	Grijalva-Peñitas
			R. Mezcalapa	
			R. Tzimbac	
			R. Zayula	
			R. Platanar	
			R. Paredón	
			R. Pichucalco	
R. Tacotalpa				
R. Samaria				
R. de la Sierra			Grijalva-Teapa	
R. Almendro				
R. Plátanos				
R. Chacté				
R. Puxcatán	Grijalva.Tulijá			
R. Macuspana				

Hidrological region	Basin	Sub-basin	Geographic unit				
GRIJALVA - USUMACINTA		R. Shumulá					
		R. Yashijá					
		R. Tulijá					
		R. Bascá					
		R. Chilapa					
	R. GRIJALVA - TUXTLA GUTIÉRREZ	P. Nezahualcóyotl	R. La Venta	Grijalva-Malpasó			
			R. Encajonado				
			R. Cintalapa				
			R. de Zoyatenco				
			R. Alto Grijalva				
			R. Hondo	Grijalva-Chicoasén			
			R. Chicoasén				
			R. Suchiapa				
			Tuxtla Gutiérrez				
			El Chapopote				
	R. GRIJALVA - LA CONCORDIA	P. La Angostura	R. Selegua	Grijalva-La Angostura			
			R. Lagartero				
			R. Aguacatenco				
			R. San Pedro				
			R. La Concordia				
			R. Grande o Salinas				
			R. Aguazurco				
			R. San Miguel				
			R. Yahuayita				
			R. Zacualpa				
			R. Tapizaca				
			R. Comitán				
			R. LACANTÚN		R. Lacantún	R. Ixcán	Usumacinta- Lacantún
						R. Chajul	
	R. Lacanjá						
R. San Pedro							
L. Miramar							
	R. Perlas	Usumacinta-Jataté					
	R. Jataté						
	R. Azul						
	R. Tzaconejá						
	R. Margaritas						
	R. Santo Domingo						
	R. Seco						
	R. Caliente						
	R. Euseba						

No	Taxon	Ecological classification	Grijalva-La Angostura	Grijalva-Chicoasén	Grijalva-Malpaso	Grijalva-Pénitas	Grijalva-Teapa	Grijalva-Tulijá	Usumacinta-Jataté	Usumacinta-Lacantún	Usumacinta-Chixoy	Usumacinta-Catazajá	Costa-Istmo	Costa-Soconusco
Order Albuliformes														
XII Family Albulidae														
22	<i>Albula esuncula</i> (Garman, 1899)	P											x	
Order Anguiliformes														
XIII Family Ophichthidae														
23	<i>Myrichthys xysturus</i> (Jordan & Gilbert, 1882)	P											x	
24	<i>Ophichthus zophochir</i> Jordan & Gilbert, 1882	P											x	x
Order Clupeiformes														
XIV Family Pristigasteridae														
25	<i>Pliosteostoma lutipinnis</i> (Jordan & Gilbert, 1882)	P											x	
26	<i>Odontognathus panamensis</i> (Steindachner, 1876)	P											x	
27	<i>Opisthopterus dovii</i> (Günther, 1868)	P												x
XV Family Engraulidae														
28	<i>Anchoa argentivittata</i> (Regan, 1904)	P											x	
29	<i>Anchoa curta</i> (Jordan & Gilbert, 1882)	P											x	x
30	<i>Anchoa ischana</i> (Jordan & Gilbert, 1882)	P											x	x
31	<i>Anchoa lucida</i> (Jordan & Gilbert, 1882)	P											x	x
32	<i>Anchoa mitchilli</i> (Valenciennes, 1848)	P									x			
33	<i>Anchoa mundeola</i> (Gilbert & Pierson, 1898)	P											x	x
34	<i>Anchoa walkeri</i> Baldwin & Chang, 1970	P											x	
35	<i>Anchoa starksii</i> (Gilbert & Pierson, 1898)	P											x	x
36	<i>Anchovia macrolepidota</i> (Kner, 1863)	P											x	x
XVI Family Clupeidae														
37	<i>Dorosoma anale</i> Meek, 1904	P (V)	x	x	x	x	x	x		x	x	x		
38	<i>Dorosoma petenense</i> (Günther, 1867)	P (V)	x	x	x	x	x	x		x	x	x		
39	<i>Harengula thrissina</i> (Jordan & Gilbert, 1882)	P											x	
40	<i>Lile gracilis</i> Castro-Aguirre & Vivero, 1990	P											x	x
41	<i>Lile nigrofasciata</i> Castro-Aguirre, Ruiz-Campos & Balart, 2005	P											x	x
42	<i>Opisthonema libertate</i> (Günther, 1867)	P											x	x
43	<i>Opisthonema medivastre</i> Berry & Barret, 1964	P											x	
Order Gonorynchiformes														
XVII Family Chanidae														
44	<i>Chanos chanos</i> (Forsskål, 1775)	P											x	x
Order Cypriniformes														
XVIII Family Cyprinidae														
45	<i>Ctenopharyngodon idella</i> (Valenciennes, 1844) ^{Ex}	Ex				x	x	x		x	x	x		
46	<i>Cyprinus carpio</i> (Linnaeus, 1758) ^{Ex}	Ex	x	x				x				x		
XIX Family Catostomidae														
47	<i>Ictiobus meridionalis</i> (Günther, 1868)	PF			x	x	x	x		x	x	x		
Order Characiformes														
XX Family Characidae														
48	<i>Astyanax aeneus</i> (Günther, 1860)	PF	x	x	x	x	x	x	x	x	x	x	x	x
49	<i>Bramocharax</i> sp.	PF						x		x	x	x		

No	Taxon	Ecological classification	Grijalva-La Angostura	Grijalva-Chicoasén	Grijalva-Malpaso	Grijalva-Pénitas	Grijalva-Teapa	Grijalva-Tulijá	Usumacinta-Jataté	Usumacinta-Lacantún	Usumacinta-Chixoy	Usumacinta-Catazajá	Costa-Itzmo	Costa-Soconusco
LXIV Family Acanthuridae														
289	<i>Acanthurus xanthopterus</i> Valenciennes, 1835	P											x	
LXV Family Sphyrnidae														
290	<i>Sphyrna ensis</i>	P											x	
LXVI Family Trichiuridae														
291	<i>Trichiurus nitens</i> Garman, 1899	P												x
LXVII Family Scombridae														
292	<i>Scomberomorus sierra</i> Jordan & Starks, 1895	P											x	x
Order Pleuronectiformes														
LXVIII Family Paralichthyidae														
293	<i>Citharichthys gilberti</i> Jenkins & Evermann, 1889	P											x	x
294	<i>Cyclopsetta panamensis</i> (Steindachner, 1876)	P											x	
295	<i>Etropus crossotus</i> Jordan & Gilbert, 1882	P											x	
296	<i>Syacium latrifrons</i> (Jordan & Gilbert, 1882)	P											x	
297	<i>Syacium ovale</i> (Günther, 1864)	P											x	
LXIX Family Achiridae														
298	<i>Achirus mazatlanus</i> (Steindachner, 1869)	P											x	x
299	<i>Achirus scutum</i> (Günther, 1862)	P											x	x
300	<i>Achirus zebrinus</i> Clark, 1936	P											x	
301	<i>Trinectes fimbriatus</i> (Günther, 1862)	P												x
302	<i>Trinectes fonsecensis</i> (Günther, 1862)	P											x	x
LXX Family Cynoglossidae														
303	<i>Symphurus chabanaudi</i> Mahadeva & Munroe, 1990	P												x
304	<i>Symphurus elongatus</i> (Günther, 1868)	P											x	
305	<i>Symphurus melanurus</i> Clark, 1936	P											x	
Order Tetraodontiformes														
LXXI Family Balistidae														
306	<i>Pseudobalistes naufragium</i> (Jordan & Starks, 1895)	P											x	x
LXXII Family Tetraodontidae														
307	<i>Arothron meleagris</i> (Bloch & Schneider, 1801)	P												x
308	<i>Sphoeroides annulatus</i> (Jenyns, 1842)	P											x	x
309	<i>Sphoeroides rosenblatti</i> Bussing, 1996	P											x	x
LXXIII Family Diodontidae														
310	<i>Diodon holocanthus</i> Linnaeus, 1758	P												x
311	<i>Diodon hystrix</i> Linnaeus, 1758	P											x	x
Total species by geographical units			23	31	45	55	36	46	11	63	54	72	174	153

tolerance, and excluding exotic species, 16 are primary freshwater fishes, 65 secondary freshwater fishes, and the rest of the species are peripheral (Table 2).

Of the 12 geographical units (Fig. 1), the region with the highest number of species was Costa-Itzmo with 174 species, followed by Costa-Soconusco with 153 species and

the third was Usumacinta-Catazajá with 72 species. The region with the lowest recorded species was Usumacinta-Jataté with only 11 species. Numbers of species from other geographical units are presented in Table 2. Spatially, *Astyanax aeneus* and *Rhamdia guatemalensis* appeared in all regions within Chiapas. Other species with widespread distributions were *Poecilia sphenops* and the exotic cichlid *Oreochromis niloticus* (10 and 11 regions respectively). *Atherinella alvarezii*, *Brycon guatemalensis*, *Dorosoma anale*, *Dorosoma petenense*, and *Ictalurus meridionalis* were distributed in nine regions, while *Aplodinotus grunniens*, *Gambusia sexradiata*, *Ophisternon aenigmaticum*, *Parachromis managuensis*, *Poecilia mexicana*, *Pseudoxiphophorus bimaculatus*, and *Thorichthys helleri* were recorded in eight regions.

Eight marine species were newly recorded as species found in continental waters of Chiapas: *Acanthurus xanthopterus*, *Atherinella panamensis*, *Fistularia commersonii*, *Halichoeres dispilus*, *Nicholsina denticulata*, *Orthopristis chalceus*, *Stegastes flavilatus*, and *Sphyaena ensis*.

Discussion

Knowledge of the species richness of continental fishes in Chiapas has increased significantly over recent years compared to previous assessments (e.g. Rodiles-Hernández et al. 2005, Velázquez-Velázquez et al. 2013). The increasing number of known species is the result of collections in new localities, improvement in sampling effort, and larger systematic and taxonomic reviews. For instance, an extensive literature search provided many reports of marine species, principally elasmobranchs, in continental waters of Chiapas by Castro-Aguirre et al. (1999). The large increment in the checklist is due to the inclusion of many elasmobranchs fishes that were included previously in the work of Castro-Aguirre et al. (1999), but that for some reason these records were ignored in more recent accounts of fishes in the continental waters of Chiapas. Castro-Aguirre et al. (1999) reported 41 species of marine fishes including an important number of sharks and sting-rays in the state continental water.

Two species previously reported were removed from the list of species in Chiapas in this study: the American eel (*Anguilla rostrata*) and the Mexican tetra (*Astyanax mexicanus*). The American eel was mentioned in the pioneering work of Velasco-Colín (1976), and since then listed in subsequent publications (Lozano-Vilano and Contreras-Balderas 1987, Rodiles-Hernández 2005, Rodiles-Hernández et al. 2005, Espinosa-Pérez et al. 2011, Velázquez-Velázquez et al. 2013). However, these works do not offer precise geographical locations for these species and there are no vouchered specimens from Chiapas in national or international collections. Records of the Mexican tetra in Chiapas probably contain misidentifications as mentioned by Lozano-Vilano and Contreras-Balderas (1987) and Ornelas-García et al. (2008), thus supporting the absence of this species in Southern Mexico. We have included Important and recent taxonomic changes made in the family Cichlidae by McMahan et al. (2015) and Říčan et al. (2016), the family Poeciliidae by Palacios et al. (2016) and the family Profundulidae by Morcillo et al. (2016).

More than 1000 species of fishes have been reported in the continental waters of Mexico, including freshwater and estuarine fishes (Espinosa-Pérez 2014). The continental fish fauna of the state of Chiapas represents approximately 29% of the continental fish fauna of the entire country of Mexico. This highlights the great diversity of fishes inhabiting continental environments of Chiapas as a result of the region's hydrological wealth. Our results are comparable with those from other southern Mexican states such as Quintana Roo (Schmitter-Soto 1998), Oaxaca (Martínez-Ramírez et al. 2004) and Tabasco (Espinosa-Pérez and Daza-Zepeda 2005).

The native obligate freshwater (primary and secondary) species of Chiapas accounted for only 26% (81) of the state's total species richness. The communities are dominated by peripheral species, many of them permanent (vicarious) residents of the Grijalva-Usumacinta basin (e.g. *Aplodinotus grunniens*, *Eugerres mexicanus*, *Hyporhamphus mexicanus*, *Strongylura hubbsi*), but the majority are distributed in brackish environments of the Costa-Itzmo and Costa-Soconusco sub-basins. Some of these communities also permeate nearby rivers. In terms of slopes, the Pacific slope houses 68% of the state fish fauna while the Gulf slope houses 33%, and in terms of regional diversity the Usumacinta region is considered one of the most diverse areas of endemism for freshwater fishes in Central America; however, from a biogeographical perspective the entire Central American region has a depauperate freshwater fish fauna compared with the vast diversity of ostariophysan fishes found in North and South America (Miller 1966, Myers 1966, Bussing 1985, Chakrabarty and Albert 2011, Matamoros et al. 2015). This could explain the presence of a great number of peripheral species recorded in the continental environments of Chiapas. This pattern is comparable with other countries of Central America such as Guatemala (Kihn-Pineda et al., 2006), Honduras (Matamoros et al. 2009) and El Salvador (McMahan et al. 2013).

Mexican law protects thirteen freshwater species; however, *Rhamdia guatemalensis* is quite abundant in Chiapas and possesses a wide distribution through other geographic areas of Mexico and Central America (Miller et al. 2005, Hernández et al. 2015). Its inclusion should be reconsidered in the NOM-059-SEMARNAT-2010. Conversely, we suggest that Mexican laws should consider including *Lacantunia enigmatica*, *Rhamdia laluchensis* and *Vieja breidobri* as protected species on the grounds of their restricted distribution.

Since the pioneering work of Lozano-Vilano and Contreras-Balderas (1987), this is the first time the state of Chiapas has been regionalized in a more detailed scale than the three great basins (Grijalva, Usumacinta and Costa). Lozano-Vilano and Contreras-Balderas (1987) proposed seven physiographic regions; however, their proposal was based on physiographic characteristics of landscape relief rather than hydrology. In this study we present a zonation based on the level of hydrological regions (sub-basins), which provides a more robust delineation of the geographical areas for fish species and facilitates a closer examination of the distribution of endemic species. This approach demonstrates that gaps in knowledge of the distribution of species is still quite large and indicates that some portions of the territory remain moderately sampled or unex-

plored. For instance, the Usumacinta-Jataté sub-basin, with only 11 species recorded, remains largely unexplored. The detailed regionalization of Chiapas highlights the necessity of increasing sampling efforts in certain zones.

Although hydrological regions Grijalva, Usumacinta and Costa of Chiapas have been used in previous studies to discover endemism in the state (Rodiles-Hernández, 2005, Rodiles-Hernández et al. 2005, Velázquez-Velázquez et al. 2013), the zonation of our study allows identification of smaller geographic units, permitting us to be more specific in studies of endemism. Thus, the distribution of endemic species in Chiapas includes: *Lacantunia enigmatica* in Usumacinta-Lacantún, *Rocio ocotal* in Usumacinta-Lacantún, *Thorichthys socolofi* in Grijalva-Tulijá and Usumacinta-Lacantún, *Tlaloc hildebrandi* in Grijalva-Teapa and Usumacinta-Jataté, and *Poecilia thermalis* in Grijalva-Teapa. Of the 12 units, Usumacinta-Lacantún stands out as it houses three endemic species: *Lacantunia enigmatica*, *Rocio ocotal*, and *Thorichthys socolofi*.

Forty years of scientific research on the continental fish fauna of Chiapas has gone a long way since the work of Velasco-Colín (1976). However, this does not seem nearly enough time to completely finish to record the real extend of the state species richness with its distribution. In this work we present distributional data at 12 geographic units. However, although this is the finest distributional scale for the state, a major goal should be to complete distributional data for the 92 existing sub-drainages in the state. Many of these water bodies have never been sampled either for lack of financial resources or because they are located in remote areas of the state.

Acknowledgements

This work has been possible due to several research grants to MZ-P-UNICACH from Consejo Nacional de Ciencia y Tecnología (CONACYT), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Comisión Nacional de Áreas Naturales Protegidas (CONANP). Recent ichthyological explorations in Chiapas have been possible by grants provided by the Comisión Federal de Electricidad (CFE). We are very grateful to all members of the UNICACH Museum of Zoology for their field and lab contributions. We are in particular debt to UNICACH for their unconditional support of our research initiatives. Thanks to Allison M. Matamoros and Caleb D. McMahan for proofreading the manuscript.

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Two new *Liolaemus* lizards from the Andean highlands of Southern Chile (Squamata, Iguania, Liolaemidae)

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Academic editor: A. Bauer | Received 12 June 2016 | Accepted 16 October 2016 | Published 16 November 2016

<http://zoobank.org/0910B0A2-3CA9-4C37-B6AD-1DEB92ADDFD>

Citation: Troncoso-Palacios J, Diaz HA, Puas GI, Riveros-Riffo E, Elorza AA (2016) Two new *Liolaemus* lizards from the Andean highlands of Southern Chile (Squamata, Iguania, Liolaemidae). ZooKeys 632: 121–146. doi: 10.3897/zookeys.632.9528

Abstract

Liolaemus is a diverse genus of lizards, subdivided into two subgenera: *Liolaemus (sensu stricto)* and *Eulaemus*, distributed mainly in Chile and Argentina. The *L. elongatus-kriegi* complex is the most diverse group within *Liolaemus (sensu stricto)*, especially the species closely related to *L. elongatus*, which form a clade currently comprising nine species. Several Chilean species of this group have been recently described, mainly from volcanoes and poorly explored mountains. Here molecular and morphological evidence are provided for a new species of the *L. elongatus* clade, which is characterized by its small size and lack of dorsal pattern, unusual features for the species of this group of lizards. Additionally, the lack of precloacal pores in males of *Liolaemus (sensu stricto)* is a trait found in few species, which do not constitute a monophyletic group. A second new southern Chilean species is also described, without precloacal pores and supported by molecular phylogenetics to be related to *Liolaemus villaricensis*. Both new species were found in the same locality, near a lake located in a pre-Andean zone with *Araucaria* and *Nothofagus* forest.

The two species are dedicated to prominent Lonkos (tribal chiefs) of the Mapuche and Pehuenche people: Janequeo and Leftraru. Additionally, the phylogenetic results suggest that *L. lonquimayensis* is a synonym of *L. elongatus*.

Keywords

Cytochrome b, *Liolaemus elongatus*, *L. villaricensis*, mtDNA, new species, precloacal pores

Introduction

Liolaemus is one of the most diverse genera of lizards, including 252 species (Uetz and Hošek 2015) that are grouped into two subgenera: *Liolaemus (sensu stricto)* and *Eulaemus* (e.g. Laurent 1985, Schulte et al. 2000), distributed mainly in Chile and Argentina (Abdala and Quinteros 2014). Recently, the exploration of volcanoes and rarely visited highlands in central and southern Chile has led to the discovery and description of several new species of lizards (Escobar-Huerta et al. 2015, Esquerré et al. 2013, 2014, Troncoso-Palacios et al. 2015, 2016), most of them belonging to the *L. elongatus-kriegi* complex of the *Liolaemus* subgenus. This complex consists of four clades: the *punmahuida*, *petrophilus*, *kriegi* and *elongatus* groups (Avila et al. 2004, 2012, Morando et al. 2003). The *L. elongatus* clade was characterized by Avila et al. (2015) as a group of lizards of medium to large size, having long-tails, with reduced sexual dichromatism, viviparous, insectivorous, and almost exclusively saxicolous. Currently, this clade comprises nine species distributed in central and southern Chile and Argentina: *L. antumalguen* Avila, Morando, Perez and Sites, 2010; *L. burmeisteri* Avila, Pérez, Medina, Sites and Morando, 2012; *L. carlosgarini* Esquerré, Núñez and Scolaro, 2013; *L. choique*; *L. elongatus* Koslowsky, 1896; *L. shitan*; *L. smaug* Abdala, Quinteros, Scrocchi and Stazzonelli, 2010; *L. crandalli* Avila, Medina, Fulvio-Pérez, Sites and Morando, 2015; and *L. lonquimayensis* Escobar-Huerta, Santibáñez-Toro and Ortiz, 2015. Although several new species have been described in recent years, it has been suggested that the diversity within the *L. elongatus-kriegi* complex is underestimated and the number of species could be doubled (Morando et al. 2003).

The males of most *Liolaemus* species have precloacal pores (Esquerré et al. 2013) and these are extensively used as taxonomic characters and for sex determination (Lobo 2005; Valdecantos et al. 2014). In fact, Esquerré et al. (2013) listed only five species of *Liolaemus (sensu stricto)* which lack precloacal pores, to which can now be added two newly described species: *L. chavin* Aguilar, Wood, Cusi, Guzmán, Huari, Lundberg, Mortensen, Ramírez, Robles, Suárez, Ticona, Vargas, Venegas & Sites, 2013, and *L. trengenzai* Pincheira-Donoso & Scolaro, 2007.

In a field campaign to southern Chile in January 2014, two sympatric species of *Liolaemus* were found which cannot be assigned to any known species. Here molecular and morphological evidence for a new species of the *L. elongatus* clade are provided. Molecular and morphological evidence are also given for another new species of *Liolaemus (sensu stricto)*, which is the first species closely related to *L. villaricensis* Müller & Hellmich, 1932, based on molecular phylogeny.

Materials and methods

Morphological data and analyses. Morphological characters were examined according to Etheridge (1995), Lobo (2005) and Avila et al. (2010, 2012). Body measurements were made with a digital vernier caliper (0.02 mm precision). Measurements are provided as mean \pm standard deviation ($x \pm SD$). Scales were observed with different magnifying lenses. The scale characterization and measurements were recorded on the right side of the specimen, unless otherwise indicated. Dorsal scales were counted between the occiput and the level of the anterior border of the hind limbs. Ventral scales were counted from mental scale to the anterior margin of the cloacal opening. Stomach and intestinal contents were analyzed under a binocular stereoscope for one specimen of each new species. Specimens were collected in four field campaigns: January 2014, February 2015, January 2016 and September 2016. Both species are characterized by their low abundance and, to our knowledge, by highly restricted distributions. Despite four field campaigns, we only were able to collect seven specimens for each new species. All specimens were sexed through internal examination of testes or oocytes/embryos. We examined specimens of all Chilean species currently considered within the *Liolaemus elongatus* clade, including nine adult specimens of *L. carlosgarini*, six adult specimens of *L. cf. elongatus* and eleven adult specimens of *L. scorialis*; plus six adult specimens of *L. villaricensis* Müller and Hellmich, 1932. Additional data for eight adult specimens of *L. carlosgarini* were taken from Esquerré et al. (2013) and additional data for two adult specimens of *L. villaricensis* were taken from literature (Hellmich 1934). The specimens examined are listed in Suppl. material 1: Appendix I. Acronyms used in this work are: MZUC (Colección del Museo de Zoología de la Universidad de Concepción), MRC (Museo de Historia Natural de Concepción) and SSUC (Colección Patricio Sánchez Reyes, Pontificia Universidad Católica de Chile). Data for all species endemic to Argentina were taken from literature as follow. *Liolaemus choique*; *L. shitan*; and *L. smaug* was taken from Abdala et al. (2010). Data for *L. antumalguen* were taken from Avila et al. (2010), data for *L. burmeisteri* was taken from Avila et al. (2012) and data for *L. crandalli* were taken from Avila et al. (2015). Data for *L. coeruleus* Cei and Ortiz, 1983; and *L. neuquensis* Müller and Hellmich, 1939; were taken from Scolaro et al. (2007). Data for *L. punmahuida* Avila, Pérez and Morando, 2003; were taken from Avila et al. (2003). Data for *L. tregenzai* were taken from Pincheira-Donoso and Scolaro (2007). For the diagnosis, we performed a statistical analysis with data taken from all adult specimens directly examined (Suppl. material 1: Appendix I) plus data taken from published data set of *L. antumalguen*, *L. carlosgarini* and *L. lonquimayensis*. For the statistical analysis, we applied a Kolmogorov-Smirnov test to verify data normality, a subsequent t-test or Mann-Whitney U test was used if data passed or failed the normality test, respectively, to compare each variable. The statistical results are provided only when the differences were significant. Additionally, we performed a principal component analysis (PCA) to visualize and discriminate species in the morphological space, using the following variables: head length, head width, head height, snout-vent length (SVL), axilla-groin distance (AGD), arm length, foot length, midbody scales (SAMB), dorsal scales, ventral

scales, supralabial scales, infralabial scales and fourth toe lamellae. This was performed with FactoMineR and R6 packages in RStudio and missing data were previously imputed with missMDA (RStudio Team 2015). Eigenvalues and the correlation of each variable with each of the first three PCs are provided in Appendices III and IV. For species that we did not examine and for which no published data sets exist, we performed a diagnosis based in the scale count ranges and SVL range, following the diagnoses previously published for the descriptions of *Liolaemus* included in this work (Abdala et al. 2010, Avila et al. 2010, 2012, 2015, Escobar-Huerta et al. 2015, Esquerré et al. 2013). Color pattern features were used as qualitative features of diagnosis between the two new species and all related species.

Genomic DNA purification, PCR amplification, and Sequencing. Samples from liver and thigh muscle were obtained from ethanol-fixed lizards and subjected to a rehydration process according to Coura (2005). Samples were washed twice in distilled water for 5 min at 55 °C to remove the fixative and then rehydrated with 1x Tris/EDTA for 5 min at 55 °C and then with 1M Tris pH 7.5, at 55 °C overnight, followed immediately by digestion with proteinase K (20 mg/ml) at 55 °C overnight. Genomic DNA isolation (mitochondrial and nuclear) was done with the Wizard® Genomic DNA Purification kit (Cat # A1120, Promega, USA) following manufacturer's instructions. The mitochondrial gene *Cyt-b* was amplified from total DNA through two phase conventional PCR with the primers GLUDGL (5'-TGA CTT GAA RAA CCA YCG TTG-3') and CB3 (5'-GGC AAA TAG GAA RTA TCA TTC-3'), reported in Torres- Pérez et al. (2009), to generate a 665 bp amplicon. PCR reactions were performed with the SapphireAmp® Fast PCR Master Mix (Cat # RR350A, Takara Clontech, USA) using 100 ng of total genomic DNA as a template and following the instruction manual. Two-phase PCR cycling was as follows: Phase 1, initial 98 °C denaturation for 3 min, then 5 cycles of 98 °C denaturation for 30 s, 47 °C annealing for 45 s and 72 °C extension for 45 s. The Phase 2, next 40 cycles of 98 °C denaturation for 30 s, 58 °C annealing for 45 s and 72 °C extension for 45 s. A final 72 °C extension step for 5 min was added to finish the PCR. The 665 bp PCR amplicon was checked by DNA electrophoresis on a 1% agarose gel in 1x Tris-Acetate-EDTA (TAE) buffer. The amplicons were purified with the E.Z.N.A.® Cycle-Pure Kit (Cat # D6492-02, Omega Biotek, USA) and sent for capillary sequencing to Macrogen, Korea.

Phylogenetic reconstruction. The GenBank accession numbers of the *Cyt-b* mitochondrial loci sequences generated in this study and the sequences obtained from GenBank are indicated in Suppl. material 1: Appendix II. Additionally, Gustavo Escobar-Huerta sent us the *Cyt-b* sequences of the type series of *Liolaemus lonquimayensis* (MZUC 40365–68). Cesar Aguilar and Jack Walter Sites Jr. sent us the *Cyt-b* sequence of one of the two specimens of *Liolaemus* sp.2 included in the phylogeny (SSUC Re 716). One hundred sixteen nucleotide sequences used in the analysis were aligned using MUSCLE (Edgar 2004). JModelTest v2.1.7 (Darriba et al. 2012, Guignon and Gascuel 2003) was used to select an appropriate substitution model (HKY + G + I), based on both the BIC and AIC indices. Bayesian inference (BI) analyses were performed with

MrBayes v3.1.5 (Ronquist and Huelsenbeck 2003). Two independent analyses, each consisting of two groups of four chains that ran independently, were run for 10.0×10^6 generations and at sample frequency of 1000 using default priors. *Phymaturus vociferator* Pincheira-Donoso, 2004, was selected as the outgroup. Twenty-five percent of samples were discarded as burn-in when calculating the convergence diagnostic, assessed by examining values of average standard deviation of the Potential Scale Reduction Factor (PSRF = 1.000 for all parameters) (Gelman and Rubin 1992) and the minimum and average Estimated Sample Size (ESS > 4000 for all parameters). The nodes were considered as strongly supported when $pp \geq 0.95$ (Huelsenbeck and Ronquist 2001). Additionally, a maximum likelihood phylogenetic analysis (ML) was performed with 1000 bootstrap replicates and calculated the average uncorrected pairwise difference (p-distance) using MEGA v6.06 (Tamura et al. 2013). Nodes with a bootstrap value $\geq 95\%$ were considered as strongly supported (Felsenstein and Kishino 1993).

Results

In our BI phylogeny (Fig. 1), the first species described in this work is found to be a member of the *Liolaemus elongatus* clade, which is strongly supported ($pp = 0.99$) and includes *L. antumalguen*, *L. burmeisteri*, *L. choique*, *L. elongatus*, *L. lonquimayensis*, *L. shitan*, *L. smaug*, the species described here, an unidentified *Liolaemus* from Chillán and two candidate species (*L. sp. 6* and *L. sp. 7*) previously suggested by Morando et al. (2003). In the ML phylogeny (Fig. 2) the *L. elongatus* clade was recovered with moderate support (bootstrap = 88%) but with the same composition. In both analyses the first species described here is found as sister taxon of the clade *L. elongatus* + *L. lonquimayensis* + *L. shitan* ($pp = 0.99$ and bootstrap = 74%, respectively). The topology found in the ML phylogeny (Fig. 2) is very similar to the topology found in the BI phylogeny, but curiously *L. petrophilus* was found outside of the remainder of the *L. petrophilus* clade, which has low support (bootstrap = 48%). In both, ML and BI phylogenies, *L. shitan* and *L. lonquimayensis* appear to be conspecific with *L. elongatus*; and also *L. sp. 7* and *L. antumalguen* appear to be conspecifics. The addition of other species of the *elongatus* clade to the phylogeny might resolve these issues (see Discussion). Average uncorrected pairwise distance between the first new species and the clade *L. elongatus* + *L. lonquimayensis* + *L. shitan* is 3.4%, consistent with a 3% divergence previously proposed for identification of candidate species in *Liolaemus* (Breitman et al. 2012).

The second species described here is found to be the sister species of *Liolaemus villaricensis* in both analysis (BI $pp = 1.00$, ML bootstrap = 99%, Figs 1 and 2), being the first species identified as closely related to this taxon based on molecular phylogeny. Average uncorrected pairwise distance between the species is 7.3%, more than double that value proposed for identification of candidate species (Breitman et al. 2012).

In regards to the PCA analysis, only the first three principal components (PCs) account each more than 10% of the variation (Suppl. material 1: Appendix III). PC1 is mainly positively correlated with variation in morphological measures (SVL, head

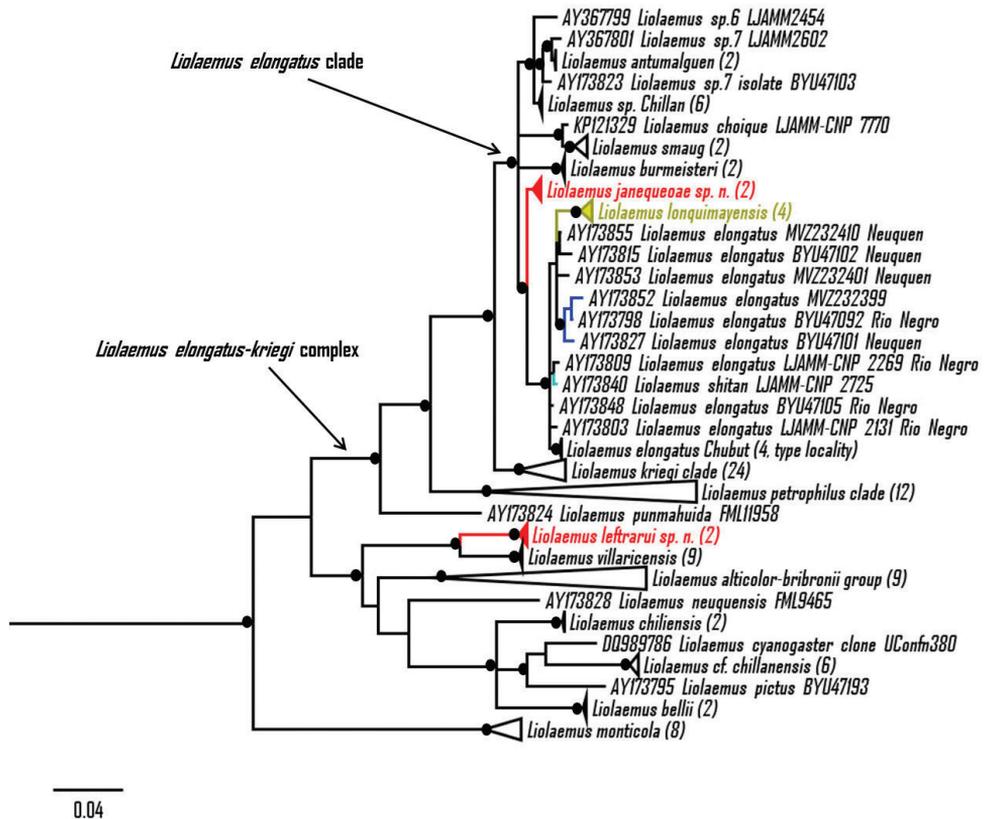


Figure 1. Bayesian inference of phylogeny (BI) tree based on *Cyt-b*, showing phylogenetic relationships of *Liolaemus janequeoae* sp. n. and *L. lefrarui* sp. n. (in red) (HKY+G+I). *Liolaemus shitan* is in light green, *L. lonquimayensis* is in yellow and *L. elongatus* samples used by Escobar-Huerta et al. (2015) are in blue. Posterior probability ≥ 0.95 are indicated with a black dot. Numbers in parentheses indicate the amount of collapsed sequences. Scale shows the number of changes per site.

length, head width, axilla-groin distance and foot length, Suppl. material 1: Appendix IV, Fig. 3). PC2 is mainly positively correlated with the number of supralabials, fourth toe lamellae, infralabials and negatively correlated to the dorsal scales (Appendix IV, Fig. 3). PC3 is positively correlated mainly with the ventral, midbody and dorsal scale counts. The first species described here does not overlap in morphological space with *L. elongatus* (Fig. 3), found as its most closely related species in both BI and ML phylogenies (Figs 1 and 2). The second species described here marginally overlaps with *L. villaricensis* in morphological space when ellipses (95% confidence interval around the centroid for each species) are generated with the first two PCs (Fig. 3). However, the second new species overlaps almost completely in morphological space with *L. villaricensis*, *L. cf. chillanensis* and *L. scorialis* when ellipses are generated with the second and third PCs (Fig. 3). Nevertheless, the second species described here is not closely related to *L. cf. chillanensis* (Figs 1 and 2) or *L. scorialis*, a member of the *L. elongatus-kriegi* clade (D. Esquerré,

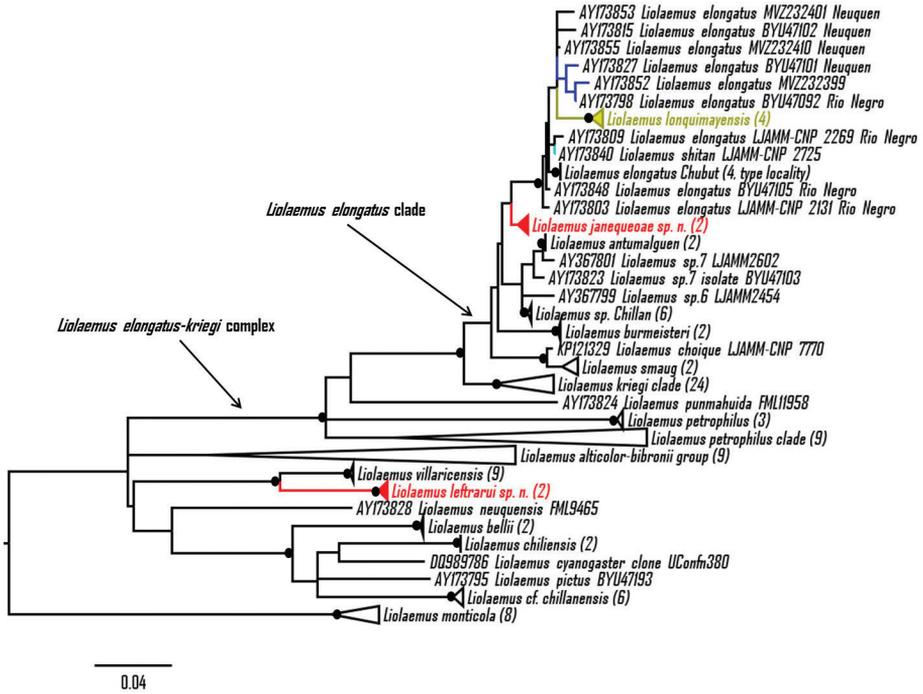


Figure 2. Maximum likelihood phylogeny (ML) tree based on *Cyt-b*, showing phylogenetic relationships of *Liolaemus janequeoae* sp. n. and *L. leftrarui* sp. n. (in red) (HKY+G+I). *Liolaemus shitan* is in light green, *L. longuimayensis* is in yellow and *L. elongatus* samples used by Escobar-Huerta et al. (2015) are in blue. Bootstrap value $\geq 95\%$ are indicated with a black dot. Numbers in parentheses indicate the amount of collapsed sequences. Scale shows the number of changes per site.

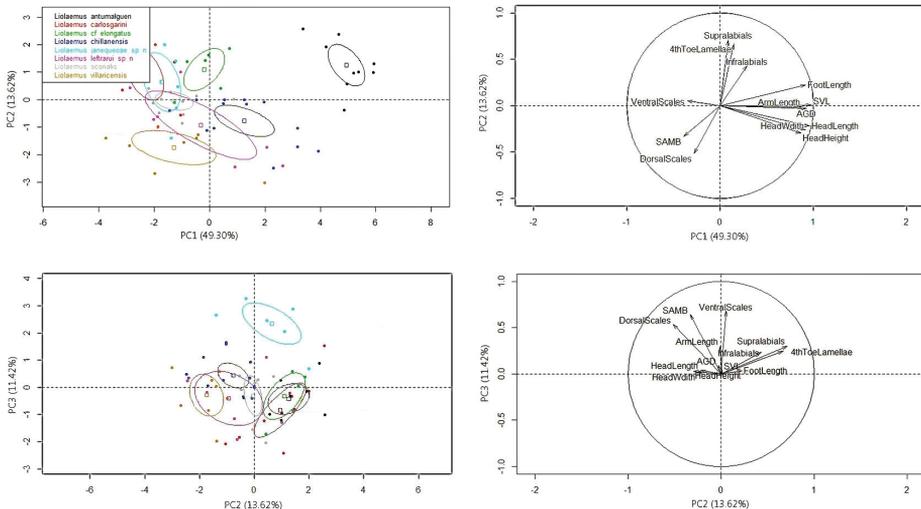


Figure 3. Principal Component Analysis (PCA) results. On the left, ellipses representing the 95% confidence interval around the centroid for each species. Axis correspond to the percentage of the total variance that each PC explains. On the right, contribution of each variable to the construction of the axes.

pers. comm.). Additionally, the morphological and coloration differences between the second species described here and *L. villaricensis* (its sister species), and the uncorrected pairwise difference between them justify the description of this as a new species.

***Liolaemus janequeoae* sp. n.**

<http://zoobank.org/35D080AB-AD1F-4ED5-99E5-CEF925C539FD>

Figure 4

Proposed standard English name: Janequeo's Lizard

Proposed standard Spanish name: Lagarto de Janequeo

Holotype. SSUC Re 712 (Fig. 4). Male collected at Laguna Verde (38°12'S - 71°44'W, 1397 masl), approximately 13.5 km NW of the summit of the Tolhuaca Volcano, Araucanía Region, Chile. Collected by J. Troncoso-Palacios and Edwin Riveros-Riffo. January 15, 2016.

Paratypes. SSUC Re 713–14. Two females (Fig. 4). Same data as the holotype. SSUC Re 715. Female. Collected at the locality of the holotype by Edwin Riveros-Riffo. February 18, 2015. SSUC Re 649–51, three females. Collected at the locality of the holotype by J. Troncoso-Palacios, F. Urrea and H. Díaz. January 5, 2014 (Fig. 4).

Diagnosis. *Liolaemus janequeoae* belongs to the *L. elongatus* clade. This species is characterized by 1) small size (maximum snout vent length = 69.6 mm), 2) lack of dorsal pattern, 3) high number of midbody scales (82–98), 4) precloacal pores present in males, and 5) absence of dark rings on the tail. We provide a differential diagnosis with regards to all species currently considered to be members of this clade, plus *L. scorialis* Troncoso-Palacios Díaz, Esquerré & Urrea, 2015, the assignment of which is under study, but probably is related to the *L. elongatus* clade (Troncoso-Palacios et al. 2015). Table 1 summarizes some of the diagnostic traits. Based on seven specimens.

Liolaemus janequeoae is closely related to *L. elongatus*. However, *L. janequeoae* is smaller (maximum SVL = 69.6 mm, n = 7 adults, vs. max. SVL = 94.7 mm) and has more midbody scales (82–98 vs. 68–87) than *L. elongatus* from Argentina (Table 1). Dorsal color pattern in *L. elongatus* is highly variable from vertebral and lateral dark bands to complete melanism, whereas *L. janequeoae* never has black spots (only small black dots in one female). Interestingly, SVL of *L. cf. elongatus* from Llaima, Chile (SVL = 68.4 ± 2.9 mm), is not significantly different compared with the SVL of *L. janequeoae* (SVL = 65.3 ± 3.4 mm); but head height is lower in *L. janequeoae* than in *L. cf. elongatus* (6.8 ± 0.5 mm vs 8.3 ± 0.7 mm) (t = -4.6, DF = 11, P < 0.01); the head is wider in *L. cf. elongatus* than in *L. janequeoae* (12.7 ± 0.9 mm vs 11.0 ± 0.4 mm) (Mann–Whitney U = 0.001, P < 0.01); *L. janequeoae* has more midbody scales than *L. cf. elongatus* (82–98 vs. 76–88) (t = 3.0, DF = 11, P < 0.05), more dorsal scales (77–89 vs. 67–73) (t = 7.7, DF = 11, P < 0.01) and more ventral scales (124–132 vs. 119–129) (t = 2.5, DF = 11, P < 0.05). Additionally, PCA results show that *L. janequeoae* and *L. cf. elongatus* from Llaima occupy a different region of morphological space, without overlap (Fig. 3).

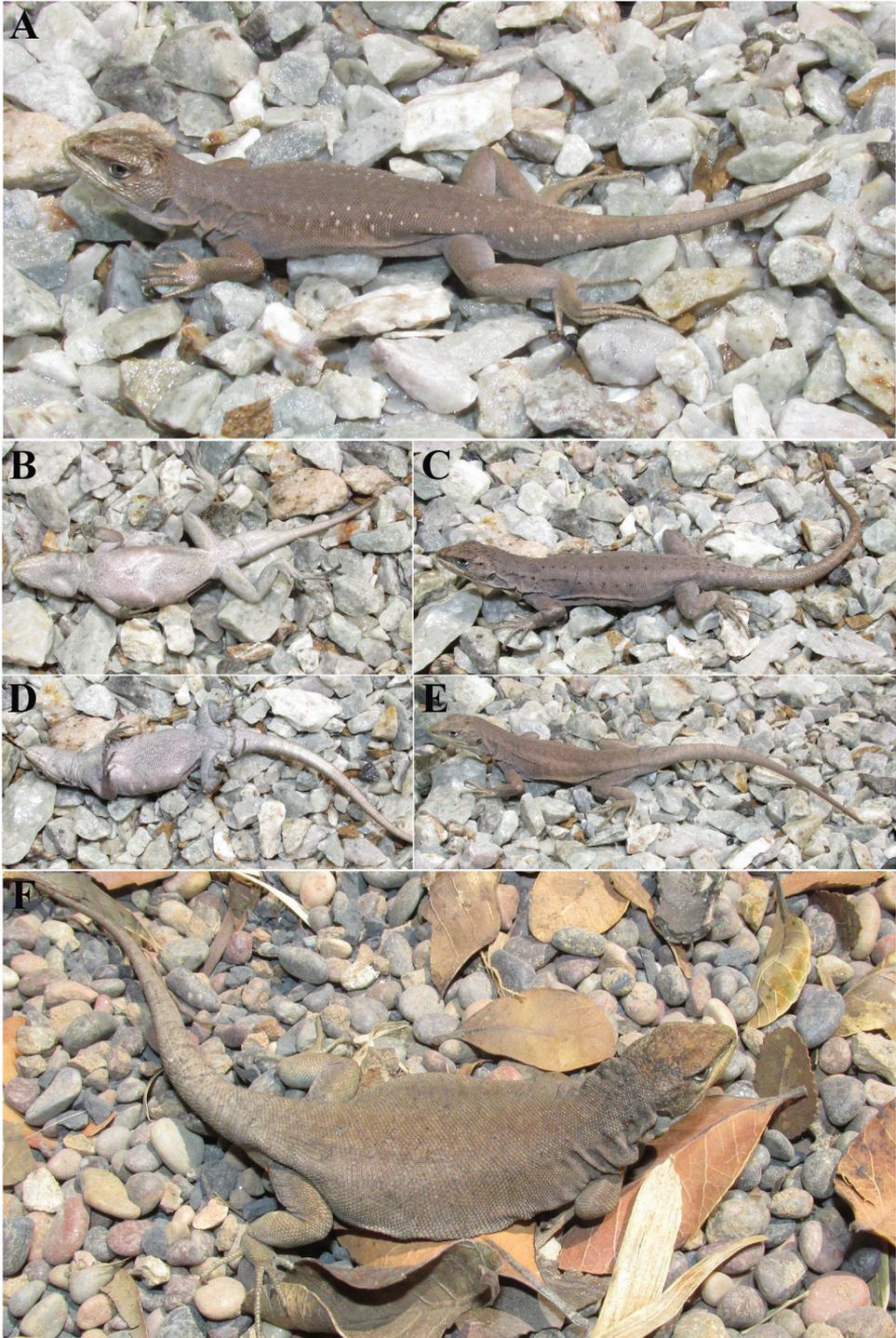


Figure 4. *Liolaemus janequeoae* sp. n. **A** and **B** Holotype, male **C** and **D** Paratype, female with dorsal black dots **E** and **F** Paratypes, typical females.

Table 1. Scale count and morphological characteristics for *Liolaemus janequeae* sp. n. and the geographically proximate species of the *L. elongatus* clade plus *L. lefrarui* sp. n. Juvenile specimens examined are excluded. Source of data for non-examined species are: *L. antumalguen* (Avila et al. 2010), *L. burmeisteri* (Avila et al. 2012) and *L. longuimayensis* (Escobar-Huerta et al. 2015). M = males; F = females.

	<i>L. antumalguen</i>	<i>L. burmeisteri</i>	<i>L. carlosgarini</i> (M = 4, F = 5)	<i>L. cf. elongatus</i> (M = 3, F = 3)	<i>L. janequeae</i> sp. n. (M = 1, F = 6)	<i>L. lefrarui</i> sp. n. (M = 3, F = 4)	<i>L. longuimayensis</i>	<i>L. scorialis</i> (M = 8, F = 3)
Max SVL (mm)	107.8	85.2	68.8	73.3	69.6	81.8	69.7	69.9
Midbody scales range	72–82	70–81	80–95	76–88	82–98	80–88	?	76–90
Ventral scales	105–118	99–110	112–124	119–129	124–132	110–123	?	115–131
Dorsal scales	70–78	76–85	68–82	67–73	77–89	77–87	?	72–81
Dorsal pattern	Variable, from patternless to two dorsolateral series of black ocelli sometimes fused longitudinally	Light brown speckled with white spots, flanked by band of dark brown between axilla and groin, with few white spots	Marked or inconspicuous dark occipital band and dark lateral bands	Marked dark occipital band and dark lateral bands	Absent/White dots/Black dots	Dispersed bluish dots with light green in the flanks	Marked dark occipital band and dark lateral bands	Marked dark occipital band and dark lateral bands
Ventral melanism	Present	Absent	Absent	Absent to partial	Absent	Absent	Absent	Absent
Head color	Variable, from completely black to light-tan or ochre	Ochre	Light brown	Dark brown	Light brown	Brown	Brown	Brown/Light brown
Body color	Light gray to ochre	Light brown/khaki	Yellowish brown or light brown	Almost black	Light brown	Brown	Brown	Brown/Gray
Tail rings	Absent	Weak	Marked/Weak	Marked/Weak/Absent	Absent	Absent/Weak	Marked	Marked
Preloacal pores in males	3–4	0–5	0–3	1–5	3	0	0	3–4

Liolaemus janequeoae is smaller (SVL = 65.3 ± 3.4 mm) than *L. antumalguen* (SVL = 95.0 ± 6.2 mm) ($t = -11.3$, DF = 14, $P < 0.01$); has a shorter axilla-groin distance (27.8 ± 2.9 mm vs 43.0 ± 4.4 mm) (Mann–Whitney U, $P < 0.01$); a shorter arm length (24.7 ± 2.3 mm vs 28.4 ± 0.7 mm) ($t = -4.5$, DF = 14, $P < 0.01$); a lower head height (6.8 ± 0.5 mm vs 10.0 ± 0.6 mm) ($t = -11.2$, DF = 14, $P < 0.01$); a narrower head (11.0 ± 0.4 mm vs 16.6 ± 0.8 mm) ($t = -17.2$, DF = 14, $P < 0.01$); and has shorter foot length (19.4 ± 1.4 mm vs 28.5 ± 1.2 mm) (Mann–Whitney U, $P < 0.01$); whereas *L. janequeoae* has more midbody scales than *L. antumalguen* ($t = 6.2$, DF = 14, $P < 0.01$, Table 1), more dorsal scales ($t = 7.6$, DF = 14, $P < 0.01$, Table 1) and more ventral scales ($t = 8.2$, DF = 14, $P < 0.01$, Table 1). Moreover, *L. antumalguen* has a very variable dorsal pattern of black spots to almost complete melanism, whereas *L. janequeoae* never has black spots (only small black dots in one female). Additionally, PCA results show that both species occupy a different region of morphological space, without overlap (Fig. 3).

Liolaemus carlosgarini, *L. scorialis* and *L. lonquimayensis* have dark lateral and vertebral bands, features that distinguishes these from *L. janequeoae*. Additionally, *L. janequeoae* is larger than *L. carlosgarini* (SVL = 65.3 ± 3.4 mm vs SVL = 60.2 ± 5.1 mm) ($t = 2.4$, DF = 22, $P < 0.05$); *L. janequeoae* has a larger axilla-groin length than *L. carlosgarini* (27.8 ± 2.9 mm vs 24.8 ± 2.9 mm) ($t = 2.3$, DF = 22, $P < 0.05$); *L. janequeoae* has longer arms than *L. carlosgarini* (24.7 ± 2.3 mm vs 21.8 ± 1.8 mm) ($t = 3.4$, DF = 22, $P < 0.01$); *L. janequeoae* has more dorsal scales than *L. carlosgarini* ($t = 4.5$, DF = 14, $P < 0.01$, Table 1) and more ventral scales ($t = 6.8$, DF = 14, $P < 0.01$, Table 1); whereas *L. lonquimayensis* has larger axilla-groin length (34.9 ± 1.7 mm) than *L. janequeoae* (Mann–Whitney U, $P < 0.05$); *L. lonquimayensis* has a greater head height than *L. janequeoae* (8.3 ± 0.1 mm vs 6.8 ± 0.5 mm) ($t = -4.8$, DF = 8, $P < 0.01$); whereas *L. scorialis* has the head wider than *L. janequeoae* (11.9 ± 0.6 mm vs 11.0 ± 0.4 mm) ($t = -3.1$, DF = 16, $P < 0.01$); *L. janequeoae* has more midbody scales than *L. scorialis* ($t = 3.6$, DF = 16, $P < 0.01$, Table 1) and more dorsal scales ($t = 4.8$, DF = 17, $P < 0.01$, Table 1). Additionally, PCA results show that *L. janequeoae* does not overlap in the morphological space with *L. carlosgarini* and *L. scorialis* when ellipses are generated with the second and third PCs (Fig. 3).

Liolaemus janequeoae is smaller (max. SVL = 69.6 mm) than *L. shitan* (max. SVL = 98.3 mm) and has more midbody scales (82–98 vs. 72–85). Dorsal color pattern in *L. shitan* is black, whereas only one female of our sample of *L. janequeoae* has small dorsal black dots.

Liolaemus janequeoae is smaller (max. SVL = 69.6 mm) than *L. choique* (max. SVL = 90.7 mm). Moreover, *L. choique* has a very variable dorsal pattern of black spots to almost complete melanism, whereas *L. janequeoae* never has black spots (only small black dots in one female).

Liolaemus janequeoae is smaller than *L. crandalli* (max. SVL = 69.6 mm vs max. SVL = 93.4 mm). Moreover, *L. crandalli* has dark lateral and vertebral bands with ringed tail, whereas all of these features are completely absent in *L. janequeoae*. According to Avila et al. (2015), *L. crandalli* is the sister taxon of the pair *L. smaug* + *L.*

choique, whereas in our phylogeny *L. janequeoae* is not closely related to *L. smaug* or *L. choique*.

Liolaemus janequeoae is smaller than *L. burmeisteri* (max. SVL = 69.6 mm vs max. SVL = 85.2 mm) and has more midbody (82–98 vs. 70–81) and ventral scales (124–132 vs. 99–110). Moreover, *L. burmeisteri* has dark lateral bands.

Liolaemus janequeoae has more midbody scales than *L. smaug* (82–98 vs 73–80). Moreover, *L. smaug* has dark lateral and vertebral band. In our phylogeny *L. janequeoae* and *L. smaug* are not sister taxa.

Description of holotype. Adult male. SVL: 59.1 mm. Tail length: 42.0 mm (autotomized). Axilla-groin length: 21.8 mm. Head length: 13.1 mm. Head width (distance between the two ear openings): 10.5 mm. Head height (at the level of ear openings): 6.1 mm. Forelimb length: 21.1 mm. Hindlimb length: 36.0 mm. Foot length: 18.6 mm. Hand length: 9.8 mm. Rostral scale wider (2.36 mm) than high (0.8 mm). Subocular length: 4.2 mm. Fifth supralabial length: 1.6 mm. Neck width: 9.4 mm. Interorbital distance: 4.5 mm. Internasal distance: 1.5 mm. Body width: 13.7 mm. Meatus width: 1.4 mm. Meatus height: 2.1 mm.

Two postrostrals. Four internasals. Hexagonal interparietal scale, with a central, small, and whitish “parietal eye” in the center. Interparietal smaller than the parietals, surrounded by other nine scales; ten scales between interparietal scale and rostral; seventeen scales between occiput and rostral (Hellmich Index); orbital semicircles are interrupted by one supraocular scales in both sides, but the rest is formed by ten scales on each side; 6–7 supraoculars (left-right); six superciliary scales. Frontal area is divided into three scales (one posterior, one middle and one anterior). Two scales between the nasal and the canthal. Preocular separated from the lorilabials by a single loreal scale. Nasal separated from rostral by one scale, surrounded by seven scales. One row of lorilabials between the supralabials and the subocular; seven supralabials, the fifth is curved upward without contacting the subocular; six infralabial scales. Mental scale is pentagonal, in contact with four scales; four pairs of postmental shields, the second is separated by two scales. Temporal scales are subimbricated and smooth or slightly keeled. Eleven temporal scales between the level of superciliary scales and the commissure of the mouth. Two projecting scales on the anterior edge of the ear, which do not cover the auditory meatus. Auricular scale is wide and restricted to the upper third of the meatus; 44 gulars between the auditory meatuses. Antehumeral fold and “Y” shaped lateral neck fold. Developed dorsolateral fold. Midbody scales: 94. Dorsal scales are rhomboidal, slightly keeled, without mucrons, subimbricate and with interstitial granules. Dorsal scales are similar in size than ventral ones. Dorsal scales: 89. Ventral scales are rhomboidal, smooth, imbricate, and without interstitial granules. Ventral scales: 124. Three preloacal pores. Hemipenial bulges are evident. The suprafemoral scales are lanceolate, imbricate, and slightly keeled. Infracemoral scales are lanceolate to rounded, smooth, and imbricate. Scales of the dorsal surface of the forearm are lanceolate to rounded, imbricate, and slightly keeled or smooth. Scales of the ventral surface of the forearm are rounded, smooth, and subimbricate. The dorsal scales of the first third of the tail are rhomboidal to lanceolate, subimbricate or juxtaposed, keeled and with inter-

stitial granules. The ventral scales of the tail vary from rhomboidal to triangular, and are imbricate and smooth. Lamellae of the fingers: I: 10, II: 14, III: 22, IV: 24 and V: 15. Lamellae of the toes: I: 11, II: 16, III: 22, IV: 32 and V: 19.

Coloration in life. Light brown head, with dark brown spots in the parietal area and in the posterior nasal area. The snout is olive. Temporal area is light brown. Subocular area and cheeks are slightly lighter than temporal area. The subocular is immaculate. Background color of the dorsum, limbs, and tail is light brown. The vertebral zone of the dorsum is slightly darker than rest, but without forming an occipital stripe. The only dorsal design is a series of white dots, formed by 1–3 white scales, running from the posterior half of the trunk to the first third of the tail. The tail is immaculate. Ventrally, the throat, belly, limbs and the tail are whitish pearly. Thighs and cloaca have a little yellowish coloration. Precloacal pores are orange.

Variation. Despite four field campaigns, no additional males were found. Variation in measures refer to the six female paratypes: SVL: 66.2–69.6 mm. Axilla-groin distance: 27.4–30.2 mm. Head length: 13.5–15.1 mm. Head width: 10.7–11.4 mm. Head height: 6.4–7.6 mm. Foot length: 18.0–21.5 mm. Leg length: 36.5–44.7 mm. Hand length: 9.4–11.7 mm. Arm length: 21.1–26.7 mm. Tail length: 84–110 (n = 3; autotomized in the rest). Relation tail length/SVL = 1.2–1.7. Although more data on males are required, there is no sexual size dimorphism in the *Liolaemus elongatus* clade species (Avila et al. 2012).

Scale number variation in *Liolaemus janequeoae* (all specimens) is as follows. Midbody scales: 82–98 (91.6 ± 5.5). Dorsal scales: 77–89 (85.0 ± 4.2). Ventral scales 124–132 (128.6 ± 3.5). Fourth finger lamellae: 22–24 (23.5 ± 0.8). Fourth toe lamellae: 28–32 (29.5 ± 1.4). Supralabial scales: 6–8 (7.4 ± 0.8). Infralabial scales: 5–6 (5.3 ± 0.5). Interparietal scale is pentagonal or hexagonal, bordered by 5–9 scales (6.6 ± 1.7). The interparietal is smaller than the parietals. The nasal is in contact with the rostral in 28.6% of specimens.

Females have a very similar color pattern to the male holotype but without dorsal white dots or yellowish coloration on the thighs and cloaca. One female has four series of black dots (formed by 1–3 black scales) on the dorsum: two on the paravertebral fields (running from the head to the first third of the tail) and two on the dorsolateral area (running from the head to the middle of the trunk).

Etymology. This species is named after Janequeo, a prominent Lonko (tribal chief) of Mapuche-Pehuenche origins. She fought against colonial Spaniards in the Arauco war, carried out mainly in the Araucanía Region where *Liolaemus janequeoae* was discovered. It is believed that she became involved in the war after her partner (Lonko Hueputan) was captured and tortured to death. She played a leading role in the Battle of Fort Puchunqui, then retreating to Villarrica, where she disappeared.

Distribution and natural history. Only known from the type locality at Laguna Verde (38°12'S - 71°44'W), approximately 13.5 km NW of the summit of the Tolhuaca volcano, Araucanía Region, Chile (Fig. 5).

At Laguna Verde, *Liolaemus janequeoae* was found between 1336–1397 masl. It inhabits the deciduous highland Andean forest (Gajardo 1994), consisting of *Arau-*

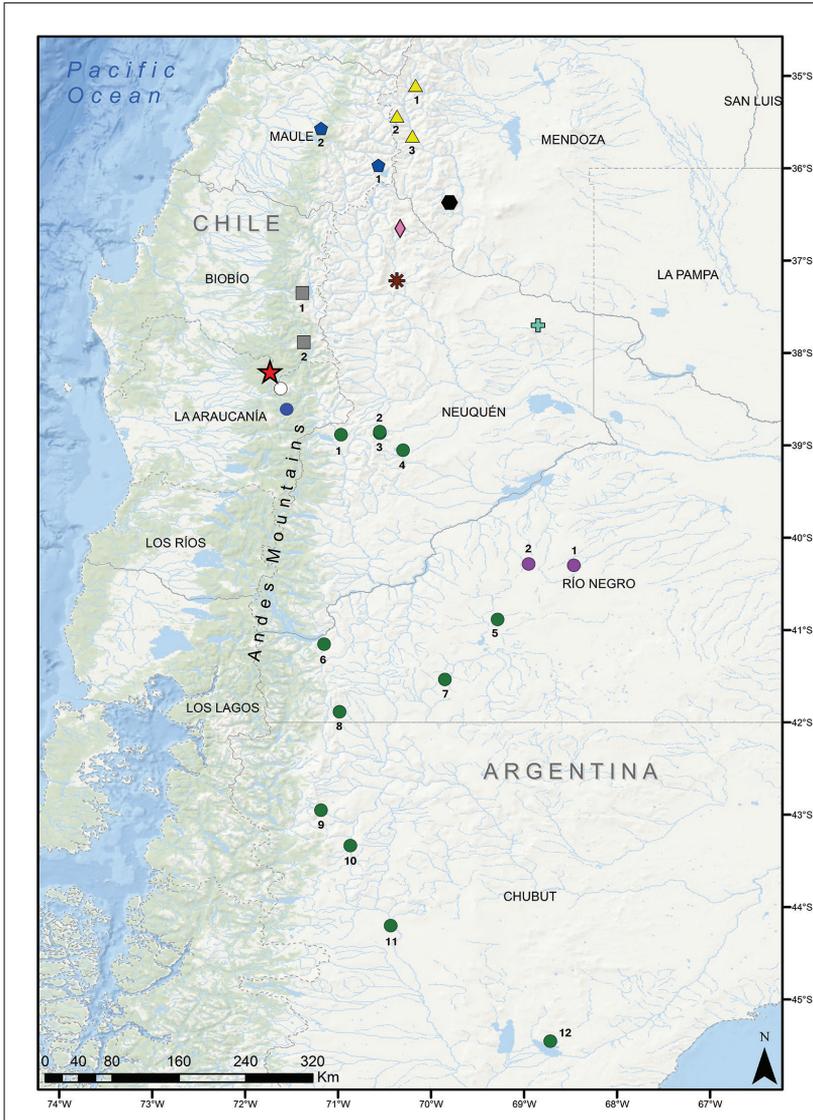


Figure 5. Distribution map for *Liolaemus janequoeae* sp. n. with geographically proximate species of the *L. elongatus* clade. In the case of *L. elongatus* a sample for each locality was included in the phylogeny. Red star: *L. janequoeae* sp. n., Laguna Verde. Yellow triangles: *L. smaug* (1= near Las Leñas, 2= between Las Loicas and Peteroa Volcano, 3= near Las Loicas). Blue pentagon: *L. carlosgarini* (1= Maule Lagoon, 2= Lircay). Black hexagon: *L. choique* (Paso el Choique). Pink diamond: *L. antumalguen* (Domuyo Volcano). Brown asterisk: *L. burmeisteri* (Caepel Malal). Green cross: *L. crandalli* (Auca Mahuida Volcano). Gray squares: *L. scorialis* (1= Laja Lagoon, 2= La Mula Lagoon). White circle: *L. lonquimayensis* (Lonquimay Volcano). Pink circles: *L. shitan* (1= Estancia Piedras Blancas, type locality and 2= near Antonio del Cuy). Blue circle: *L. cf. elongatus* (Llaima Volcano). Green circles: *L. elongatus* (1= Pampa de Lonco Luan, 2= Primeros Pinos, 3= Portal La Atravesada, 4= Laguna Blanca, 5= near Ingeniero Jacobacci, 6= San Carlos de Bariloche, 7= Ojo de Agua, 8= El Maiten, 9= Esquel, 10= Tecka, 11= Gobernador Costa and 12= Los Manantiales).

caria araucana and *Nothofagus dombeyi* (1397 masl). The shrubs are represented by *Chusquea culeou*, *Desfontainia spinosa*, *Drimys andina* and *Pseudopanax laetevirens*. At lower altitudes (1336 masl), the vegetation was dominated by *A. araucana* and *N. pumilio*, with the presence of *Azara alpina*, *C. culeou*, *Colletia hystrix*, *Lomatia hirsuta*, *Maytenus disticha*, *Myrceugenia chrysocarpa* and *Pernettya myrtilloides*. At lower altitudes where there are no *Araucaria araucana*, *L. janequeoae* was not found. It is a diurnal lizard of apparently low abundance. It was seen on rocks and climbing in trees.

Liolaemus janequeoae was found in syntopy with *L. septentrionalis* Pincheira-Donoso and Núñez, 2005; *L. tenuis* (Duméril and Bibron, 1837); *Pristidactylus torquatus* (Philippi, 1861) and the second new species described below. In this zone, it was also recorded the presence of *Tachymenis chilensis* (Schlegel, 1837).

The intestinal content of one specimen (paratype) was examined and remnants of insects and several nematodes were found. At the date of capture (January 5) two females had two and three embryos each. All other females have only several small oocytes.

Liolaemus leftrarui sp. n.

<http://zoobank.org/71CE0862-31F7-4ADD-B977-F00479198873>

Figure 6

Proposed standard English name: Leftraru's Lizard

Proposed standard Spanish name: Lagarto de Leftraru

Holotype. SSUC Re 646 (Fig. 6a, b). Male collected at Laguna Verde (38°12'S - 71°44'W, 1405 masl), approximately 13.5 km NW of the summit of the Tolhuaca volcano, Araucanía Region, Chile. Collected by J. Troncoso-Palacios, F. Urra and H. Díaz. January 5, 2014.

Paratypes. SSUC Re 647–48, 716 (Fig. 6). Three females. Same data as the holotype. SSUC Re 732–734. Two males and one female. Near Lagunillas, Araucanía Region, Chile (38°12'S - 71°46'W, 1483 masl), approximately 4 km NW from the type locality. Collected by J. Troncoso-Palacios & E. Villarroel. September, 2016.

Diagnosis. *Liolaemus leftrarui* is closely related to *L. villaricensis*. This species is characterized by 1) lack of preloacal pores in either sex, 2) large size *Liolaemus* (max. SVL = 81.8 mm), 3) high amount of midbody scales (80–88), 4) light blue dots on the dorsum, and 5) absence of ventral melanism. We provide a diagnosis in regards to *L. villaricensis*, plus four unrelated species that occur geographically near to *L. leftrarui* and that also feature the absence of preloacal pores. Based on seven specimens.

Liolaemus leftrarui has more dorsal scales than *L. villaricensis* (77–87 vs. 80–89) ($t = -2.5$, $DF = 11$, $P < 0.05$). Moreover, *L. villaricensis* has a marked lateral black band and a fragmented vertebral stripe, whereas in *L. leftrarui* these two color features are inconspicuous or less marked than in *L. villaricensis*. *Liolaemus villaricensis* has no light blue dots, which are in all specimens of *L. leftrarui*. Finally, although they are sister species, the average uncorrected pairwise distance between the two taxa is 7.3%, more than double that value proposed for identification of candidate species in *Liolaemus*.



Figure 6. *Liolaemus lefrarui* sp. n. **A** and **B** Holotype, male **C** Dorsal and **D** ventral view of Paratype, female **E** and **F** Paratypes, females.

Additionally, PCA results show that both species only marginally overlap in morphological space when ellipses are generated with the two first PCs (Fig. 3).

Liolaemus lefrarui is larger (max. SVL = 81.8 mm) than *L. coeruleus* (males SVL = 58.7 ± 3.2 mm; females SVL = 58.2 ± 2.8 mm) and *L. neuquensis* (males SVL = 57.4 ± 3.5 mm; females SVL = 58.2 ± 1.9 mm). Moreover, *L. coeruleus* males feature black ventral color and some *L. neuquensis* males also feature a black ventral color, a feature absent in *L. lefrarui*. Females of *L. coeruleus* and *L. neuquensis* have a brown dorsal color, but females of *L. lefrarui* have a bluish brown dorsal color. Finally, in our phylogeny *L. neuquensis* is not closely related to *L. lefrarui* and although we have no molecular data for *L. coeruleus*, this last species and *L. neuquensis* are probably conspecific (Avila et al. 2003).

Liolaemus lefrarui has more midbody scales (80–88 vs. 67–81) than *L. punmahuida*. Dorsal color in *L. punmahuida* is ochre and this species is patternless, whereas *L. lefrarui* has brown dorsal color with dispersed light blue dots. *Liolaemus punmahuida* has reddish color around the cloaca, feature absent in *L. lefrarui*. The species are not closely related according to our phylogeny.

Liolaemus lefrarui differs from *L. tregenzai* in that this last species features black color on the throat, chest and abdomen of males and gray color on the throat, chest and abdomen of females, features totally absent in *L. lefrarui*. The species are not closely related according to our phylogeny.

Description of holotype. Adult male. SVL: 81.7 mm. Tail length: 102.9 mm (not autotomized). Axilla-groin length: 35.4 mm. Head length: 20.1 mm. Head width (distance between the two ear openings): 16.9 mm. Head height (at the level of ear openings): 10.8 mm. Forelimb length: 26.5 mm. Hindlimb length: 46.0 mm. Foot length: 21.8 mm. Hand length: 13.6 mm. Rostral scale wider (4.3 mm) than high (1.6 mm). Subocular length: 5.7 mm. Fourth supralabial length: 3.4 mm. Neck width: 16.2 mm. Interorbital distance: 7.2 mm. Internasal distance: 3.0 mm. Body width: 27.2 mm. Meatus width: 1.0 mm. Meatus height: 3.3 mm.

Two postrostrals. Four internasals. Pentagonal interparietal scale, with a central, small, and whitish “parietal eye” in the center. Interparietal scale is similar in size to parietal one, surrounded by other six scales; seven scales between interparietal scale and rostral; twelve scales between occiput and rostral; orbital semicircle is incomplete in the right side and complete in the left side (formed by 12 scales); 5–4 supraoculars (left-right); five superciliary scales. Frontal area is divided into three scales (two posterior and one anterior). Remarkably, only one scale between the nasal and the canthal. Preocular separated from the lorilabials by a single loreal scale. Nasal in contact with the rostral, surrounded by seven scales. One row of lorilabials between the supralabials and the subocular; six supralabials, the fourth is curved upward without contacting the subocular; five infralabial scales. Mental scale is pentagonal, in contact with four scales; five pairs of postmental shields, the second is separated by two scales. Temporal scales are subimbricate and smooth, very few are slightly keeled. Eight temporal scales between the level of superciliary scales and the level of the commissure of the mouth. Two enlarged projecting scales on the anterior edge of the ear, which do not cover

the auditory meatus. Auricular scale is wide and restricted to the upper third of the meatus; 42 gulars between the auditory meatuses. Antehumeral fold and “Y” shaped lateral neck fold. Present inconspicuous ventrolateral fold. Midbody scales 86. Dorsal scales are rounded to lanceolate, slightly keeled, without mucrons, imbricate and with some interstitial granules. Dorsal scales are smaller than ventral ones. Dorsal scales 81. Ventral scales are rhomboidal to rounded, smooth, imbricate, and without interstitial granules. Ventral scales 118. There are no preloacal pores. Hemipenial bulges are evident. The suprafemoral scales are lanceolate, imbricate, and smooth or slightly keeled. Infracemoral scales are rounded, smooth, and imbricate. Scales of the dorsal surface of the forearm are rounded, imbricate, and slightly keeled or smooth. Scales of the ventral surface of the forearm are rounded, smooth, juxtaposed or subimbricate with interstitial granules. The dorsal scales of the tail are rhomboidal, imbricate, keeled and some with mucrons. The ventral scales of the tail vary from rhomboidal to triangular, and are imbricate and smooth. Lamellae of the fingers: I: 12, II: 14, III: 20, IV: 22 and V: 15. Lamellae of the toes: I: 11, II: 16, III: 21, IV: 27 and V: 18.

Coloration in life. Brown head, with dispersed dark brown spots. Occipital area of the head is dark brown; temporal area is brown with three dark brown stripes and some dispersed light blue scales. Ocular area, snout and cheeks are light green. Subocular scale is light blue with two dark brown vertical lines, one in the middle and other in the anterior edge. Background color of the dorsum is brown. Inconspicuous dorsolateral light brown stripe (two scales of wide) running from the occiput level to the level of the axilla. Dark brown spots dispersed on the dorsum, without forming an occipital band, but forming three lines on the neck; one of which (middle) forms an inconspicuous vertebral stripe on the dorsum. Several light blue dots dispersed on the dorsum (each corresponds to one scale). Inconspicuous dark brown lateral band with dispersed light blue scales. Below lateral band, flanks are yellowish. Limbs are brown with light green and few dispersed light blue scales. Tail is brown with dispersed light green scales and dark brown vertebral line. Ventrally, the throat is dark green, darker towards the tip of the snout. Belly and the tail are light green. Rear portion of belly, cloaca, chest and thighs have a yellowish coloration. Palms are dark brown and soles are light brown.

Variation. Variation in three males (including the holotype): SVL: 76.1–81.8 mm. Axilla-groin distance: 33.2–35.7 mm. Head length: 17.9–20.1 mm. Head width: 14.6–16.9 mm. Head height: 9.3–10.8 mm. Foot length: 20.2–21.8 mm. Leg length: 42.7–46.0 mm. Hand length: 12.0–13.6 mm. Arm length: 26.0–27.3 mm. Tail autotomized in all male paratypes. Variation in four female paratypes is as follows: SVL: 60.5–68.2 mm. Axilla-groin distance: 26.4–30.1 mm. Head length: 13.2–15.0 mm. Head width: 9.7–12.0 mm. Head height: 6.3–7.0 mm. Foot length: 17.4–17.9 mm. Leg length: 32.5–38.2 mm. Hand length: 10.1–11.1 mm. Arm length: 20.5–21.2 mm. Tail autotomized in all females.

Scale number variation in *Liolaemus lefrarui* (all specimens) is as follows. Midbody scales: 80–88 (84.3 ± 3.5). Dorsal scales: 77–87 (81.3 ± 3.6). Ventral scales 108–123 (115.3 ± 5.8). Fourth finger lamellae: 20–23 (21.9 ± 1.1). Fourth toe lamellae: 27–30

(28.1 ± 1.3). Supralabial scales: 6–7 (6.4 ± 0.5). Infralabial scales: 4–5 (4.7 ± 0.5). Holotype has only one scale between the nasal and the canthal, but paratypes have two, as usual in the genus *Liolaemus*. No preloacal pores in the males and no vestigial preloacal pores in the females, which is rare in *Liolaemus*. Interparietal scale is quadrangular, pentagonal, hexagonal or heptagonal, bordered by 5–7 scales (5.7 ± 0.8). The interparietal is similar size or smaller than the parietals. The canthal is in contact with the rostral in all specimens.

Paratype males have similar coloration pattern to the holotype with variation only in shade. Females have similar coloration pattern to the holotype, but with some differences such as: the dark brown color on the occipital area is less marked or absent; the dark brown lateral band (inconspicuous in the holotype) is marked in some females; the dark brown vertebral stripe of the tail is inconspicuous or absent in females; the ventral color is light green or light blue; the throat is reticulated in one female; the yellowish color on the rear portion of belly and the cloaca is less marked or absent in females.

Etymology. This species is named after Leftrarú, the most prominent Lonko (tribal chief) of the Mapuche people, who fought against colonial Spaniards in the Arauco war, carried out mainly in the Araucanía Region where we discovered *Liolaemus leftrarui*. He was captured when he was eleven by Pedro de Valdivia (Governor of the Kingdom of Chile) and became his personal servant. He learned the military strategy of the Spanish and then escaped. Later, he ambushed and killed Valdivia, and won the most remarkable victories over the Spaniards. Finally, he was surrounded and died in battle.

Distribution and natural history. Known from two localities: 1) the type locality at Laguna Verde (38°12'S - 71°44'W), approximately 13.5 km NW of the summit of the Tolhuaca volcano, Araucanía Region, Chile (Fig. 7). At Laguna Verde, *Liolaemus leftrarui* was found between 1336–1397 masl. Vegetation is the same described for the habitat of *L. janequeoae*. At lower altitudes where there are no *Araucaria araucana*, *L. leftrarui* was not found. 2) Near Lagunillas (38°12'S - 71°46'W, 1483 masl), approximately 4 km NW from Laguna Verde, in the *Araucaria araucana* forest. It is probable that the distribution of *L. leftrarui* could extend to Lagunillas (1700 masl) but in September (date of collection) this area is covered with snow and no specimens were found. Remarkably, *L. janequeoae* was not found near Lagunillas. *Liolaemus leftrarui* is a diurnal lizard of apparently low abundance at both localities. It was seen on rocks and trees (in Laguna Verde), clambering to approximately 5 m aboveground in trees when threatened. Near Lagunillas it was seen only in fallen trees.

Liolaemus leftrarui was found in syntopy with *L. septentrionalis*, *L. tenuis*, *L. janequeoae* and *Pristidactylus torquatus* at the type locality. Near Lagunillas it was found in syntopy with *L. septentrionalis* and *L. tenuis*. In this zone the presence of *Tachymenis chilensis* was also recorded.

The intestinal contents of one specimen from the type locality was examined and revealed the remnants of insects. No plant remains were found. One specimen from near Lagunillas had several nematodes in the intestines. The females collected in January had several small oocytes but the female collected in September carried one embryo.

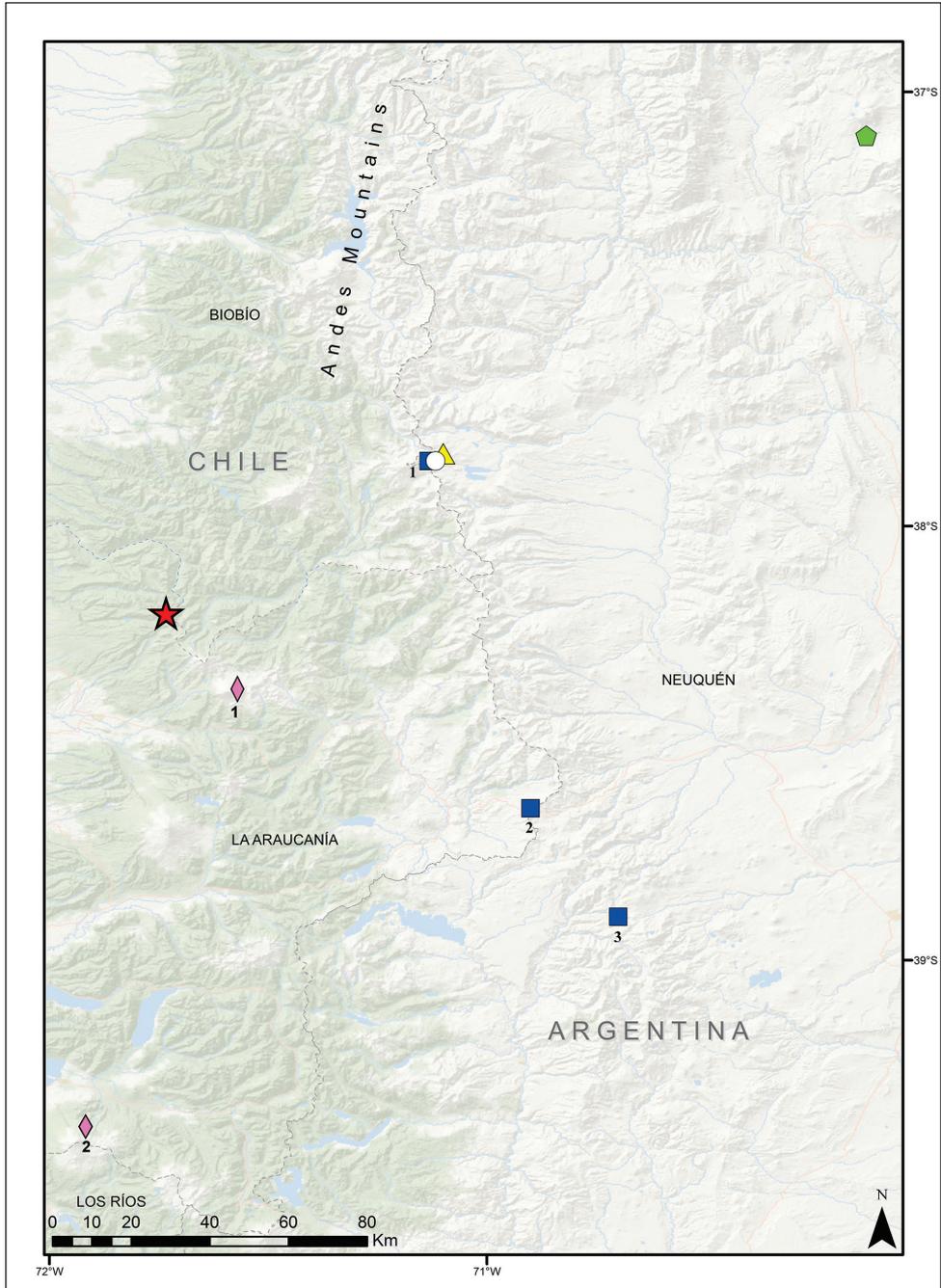


Figure 7. Distribution map for *Liolaemus lefrarui* sp. n. with closely related *L. villaricensis* and geographically proximate species that feature a lack of preloacal pores. Red star: *L. lefrarui* sp. n. (Laguna Verde and Lagunillas). Pink diamond: *L. villaricensis* (1= Lonquimay Volcano, 2 = Villarrica Volcano). Blue squares: *L. coeruleus* (1= Copahue, 2= Pino Hachado, 3= Primeros Pinos). White circle: *L. tregenzai* (Copahue). Yellow triangle: *L. neuquensis* (Copahue). Green pentagon: *L. punmahuida* (Tromen Volcano).

Discussion

The diversity of the Chilean members of the *Liolaemus elongatus-kriegi* complex has been largely underestimated. Recent expeditions to seldom explored highlands and the revision of the taxonomic status of some populations has led to the description of several new species (Escobar-Huerta et al. 2015, Esquerré et al. 2013, 2014, Núñez 2007, Troncoso-Palacios et al. 2015). In fact, it has been thought that Chilean species of the *L. elongatus-kriegi* complex have a small distribution in central Chile (Morando et al. 2003), but currently it is known that this group of lizards is widely distributed in central and southern Chile, and it is also probable that some populations under study could be described as new species in the future (Troncoso-Palacios unpublished data).

The new species, *Liolaemus janequeoae*, was found to be member of the *L. elongatus* clade and the sister species of the clade formed of *L. elongatus* + *L. lonquimayensis* + *L. shitan*, but these findings are preliminary, since there are no *Cyt-b* sequences in GenBank for some species currently assigned to the *L. elongatus* clade (*L. carlosgarini*, *L. crandalli* and *L. scorialis*). A future study with additional species could yield a different topology. Moreover, a limitation in our study is the use of a single mtDNA marker, one limitation also shared by almost all recent descriptions of *Liolaemus* (*sensu stricto*). For example, hybridization and introgression have been found in closely related species of *Liolaemus* (Olave et al. 2011) and a future study of the species described here using nuclear markers would be greatly desirable. Besides, the clade formed by *L. elongatus* + *L. lonquimayensis* + *L. shitan* requires a deeper analysis. A sample of *L. shitan* does not form a monophyletic haplotype with respect to *L. elongatus*. A work published previously to the description of this species showed that this “dark phenotype” from San Antonio del Cuy (25 de Mayo, Argentina) is not genetically distinctive enough to consider it as candidate species (Morando et al. 2003: 178) and it has been suggested as possible synonym of *L. elongatus* by Avila et al. (2015). However, since there are currently no DNA data for *L. shitan* from the type locality (Estancia Piedras Blancas, 25 de Mayo), we tentatively accept this species as valid. In regard to *L. lonquimayensis*, we believe that the relationship between this taxon and *L. elongatus* is not solved. The distinction between them is based in two features: absence of preloacal pores in the males of *L. lonquimayensis* and the fact that the four type specimens of *L. lonquimayensis* form a clade separated from *L. elongatus* samples (Escobar-Huerta et al. 2015). However, Escobar-Huerta et al. (2015) used three sequences of *L. elongatus* in their phylogeny (BYU 47101, MVZ 232399 and BYU 47092). We used thirteen sequences of *L. elongatus* and one sequence of *L. shitan* and obtained a different result, *L. lonquimayensis* does not form a distinctive clade from *L. elongatus* (Figs 1 and 2). In this work, we include in the PCA analysis specimens of *L. cf. elongatus* from Llaima Volcano, located between the type locality of *L. lonquimayensis* and the northern limit of *L. elongatus* (Morando et al. 2003). Based on coloration and morphology, these specimens can be assigned to *L. elongatus*, although there are no molecular data to confirm this.

The second new species that is described here, *Liolaemus lefrarui*, is notable for the absence of preloacal pores and its light blue dorsal dots, because preloacal pores in males a typical feature in *Liolaemus* (Esquerré et al. 2013). The absence of preloacal pores also

occurs in *L. villaricensis* (Torres-Pérez et al. 2009), the most closely related species to *L. leftrarui*. However, molecular evidence indicates that the species of the subgenus *Liolaemus* with complete absence of precloacal pores in males are paraphyletic and not monophyletic, as has been previously proposed (Cei and Videla 2003). For example, in our phylogeny *L. leftrarui*, *L. neuquensis*, *L. punmahuida* and *L. tregenzai* do not constitute a monophyletic group and none of them is the sister species of the others (although precloacal pores are lacking in all these species). Pincheira-Donoso and Núñez (2005) recorded *L. villaricensis* from Lonquimay volcano, but no specimens were deposited in an institutional collection. Here we add a second record of this species from this locality (SSUC Re 729–31).

Certainly, there is still much to be discovered about the diversity of the species of *Liolaemus* in southern and central Chile, especially in the *Liolaemus elongatus-kriegi* complex and the species related to *L. villaricensis*, for which several taxonomic issues still remain unsolved.

Acknowledgements

We thank Damien Esquerré for his help with the PCA analysis and providing a draft for the R script to perform the analysis and for his invaluable comments to the text. We thank the editor and the two anonymous reviewers who helped us to improve the manuscript. We thank P. Zavala (Pontificia Universidad de Católica de Chile) for allowing us to review and deposit material in the collection under his care. We are grateful to the following colleagues and institutions for allowing us to review specimens: M. Lamborot (LCUC), J. Artigas (MZUC) and H. Núñez (MNHNCL). Gustavo Escobar-Huerta for send us DNA data of *L. lonquimayensis*. Cesar Aguilar and Jack Walter Sites Jr. send us DNA data of one of the two specimens of *L. leftrarui* included in the phylogeny; which was generated as part of a work to be published elsewhere (Aguilar et al. in prep.). We thank especially Richard Etheridge (San Diego State University) for all his comments and improving the English. F. Lobo, L.J. Avila, F. Tillack, C. Garín, and A. Laspiur for sending literature. J. Troncoso-Palacios thanks M. Penna and A. Labra for their support. Thanks to F. Urra and E. Villarroel for their assistance in the field. Edwin Riveros-Riffo thanks M. Riveros and F. Ibieta for calling to his attention the presence of *L. janequeoae* during ascent to Laguna Verde. Thanks to the Servicio Agrícola y Ganadero (SAG) for the collecting permit (N°4468). Funding Cochilco-FONDECYT 1100995 (AE), Millennium Institute in Immunology and Immunotherapy, P09-016-F (AE), Nucleo UNAB DI-741-15/N (AE).

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Supplementary material I

Appendices

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Data type: Microsoft Word (docx)

Explanation note:

Appendix I: Museum codes of the specimens examined.

Appendix II: GenBank accession numbers of the specimens used for phylogenetic analysis.

Appendix III: Eigenvalues, the percentage of the total variance and the cumulative percentage of variance in each of the 13 PCs found by the PCA.

Appendix IV: Correlation of each variable with each of the first three PCs.

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