

The mermithid species *Isomermis lairdi* (Nematoda, Mermithidae), previously only known in Africa, found in Europe

Denis Gradinarov¹

¹ Department of Zoology and Anthropology, Faculty of Biology, Sofia University “St. Kliment Ohridski”, 8 Dragan Tsankov Blvd., 1164 Sofia, Bulgaria

Corresponding author: Denis Gradinarov (dgradinarov@abv.bg)

Academic editor: H-P Fagerholm | Received 24 March 2014 | Accepted 23 October 2014 | Published 12 November 2014

<http://zoobank.org/36ADDB32-2FE9-423A-8241-D5BC3A7590F1>

Citation: Gradinarov D (2014) The mermithid species *Isomermis lairdi* (Nematoda, Mermithidae), previously only known in Africa, found in Europe. ZooKeys 454: 1–11. doi: 10.3897/zookeys.454.7577

Abstract

The present work contributes to the knowledge on the aquatic mermithids (Nematoda, Mermithidae) occurring in black flies – an insufficiently studied group of parasitic nematodes. *Isomermis lairdi* Mondet, Poinar & Bernadou, 1977, described from larvae of *Simulium damnosum* Theobald, 1903 in Western Africa, is reported to occur in Bulgaria. The species was isolated from larvae of *Simulium ornatum* Meigen, 1818 in a local population of simuliids in a mountain stream near Jeleznitsa Village, Sofia district. Postparasitic juveniles of mermithids were obtained from the hosts and reared to the adult stage. The species was identified by morphological and morphometrical characters of postparasitic juveniles, and of male and female individuals. In the summer of 2012 a relatively high rate of mermithid infection in a local host population was detected (prevalence up to 44.1%). In August of the next year host abundance had considerably declined and other simuliid species, *S. variegatum* Meigen, 1818 and *S. reptans* (Linnaeus, 1758), predominated in the investigated locality. In West Africa, *I. lairdi* is considered to be a potential biological agent for reducing the population density of the *S. damnosum* complex – the main vector of human onchocerciasis. In Europe, species of the *S. ornatum* complex are among the vectors of onchocerciasis of cattle and deer. The mermithids presumably play a certain role in the epidemiology of these diseases. A brief discussion on the taxonomy of the genus *Isomermis* Coman, 1953, and of the feasibility of molecular methods in mermithid taxonomy is provided. The species *I. lairdi* is reported for the first time from Europe.

Keywords

Entomoparasitic nematodes, morphology, taxonomy, parasite ecology, distribution, *Simulium ornatum*, disease vectors, black fly control, Bulgaria

Introduction

Mermithids (Nematoda, Mermithidae) are lethal parasites of arthropods, mainly insects. Species of at least 15 different orders of insects are among the hosts of the family (Nickle 1972). Mermithids occurring in black flies (Diptera, Simuliidae) are an insufficiently studied group with problematic taxonomy (Molloy 1981, St-Onge et al. 2008). Descriptions of many species are not satisfactory and many described species are considered as *species inquirendae* (Curran and Hominick 1981, Poinar and Takaoka 1979). The adult nematodes, essential for a correct morphological identification (Poinar 1979), need in most cases to be obtained by laboratory rearing of emerged postparasitic juveniles. Thus, morphology-based taxonomy requires significant time and effort. Recently, molecular methods have been introduced in the taxonomy of the group (St-Onge et al. 2008, Crainey et al. 2009).

Mermithids may play an important role in the regulation of population densities of simuliid hosts (Rubzov 1974, Molloy 1981, Crainey et al. 2009), but problems in taxonomy and insufficient data on the biology and ecological requirements (St-Onge and Charpentier 2008) complicate the use of mermithids for black fly control. The difficulties in the identification of immature stages of the hosts, as well as unsolved taxonomic problems in the Simuliidae (Molloy 1981, Adler and Crosskey 2013) further discourage research on the host–parasite relationships within this group.

The aim of the present study was to *i*) perform identification of newly isolated mermithids from a local population of Simuliidae in Bulgaria, *ii*) analyze the taxonomic position of these species within the genus and their geographical distributions, and *iii*) provide original data on the rate of mermithid infection in the investigated host population and discuss the host–parasite relationships at population level.

Materials and methods

Larvae and pupae of Simuliidae were collected from (1) the Selska Reka River (mountain stream) just above Jeleznitsa Village, Vitosha Mts. (42°32.04'N; 23°21.79'E, 1050 m a.s.l.), and (2) from a channel which diverts the water from the river and supplies barrage ponds in the village square (42°32.05'N; 23°21.91'E, 1030 m a.s.l.). The sampling was carried out in July–September of 2012 in both localities and in August–September of 2013 in the second locality only. Denotations of nematode individuals used for measurements and species identification are: July (25.07., 1♀), August (03.08., 4♂♂, 1♀, 1♂J, 3♀♀Js; 12.08., 2♂♂, 2♀♀, 1♂J) and September (22.09., 1♂J) of 2012.

Simuliids were collected along with grasses and branches of trees which were dipping in the water. The host larvae were kept in shallow dishes with tap water and were examined periodically for the emergence of postparasitic juveniles of mermithids (Rubzov 1974). Emerged nematodes were placed in Petri dishes with tap water

and maintained in the cold (5–7 °C) (method after Camino 1994). The adults were fixed in 4% formaldehyde, transferred to glycerol (simple evaporation method, after Poinar 1975), and mounted on microscopic slides with paraffin rings. The measurements were performed at magnifications of 10×20 and 10×40 using a light microscope (Olympus BX41). The pictures were taken with a digital camera (Olympus Color View I). The prepared microscope slides with mermithids have been deposited in the collection of the Department of Zoology and Anthropology at Sofia University (slides M-VTM: 1-16).

Mermithid identification was performed according Rubzov (1972, 1974). Original descriptions of closely related (Welch 1962, Rubzov 1968) or later described species (Mondet et al. 1977, Poinar and Takaoka 1979, 1981, 1986, Camino 1987, 1994) were also used. The conclusions concerning diagnostic characters in mermithid taxonomy, as suggested by Curran and Hominick (1981), were considered as well.

The rate of mermithid infection is given for the second locality. Host larvae of middle and late instars (body length of 3 mm or more) were examined individually under the stereomicroscope for the presence of parasitic juveniles of nematodes. In suspicious cases host larvae were dissected. Black flies were determined by larvae and pupae (after Yankovsky 2002, Jedlicka et al. 2004, etc.). Collected pupae were used to facilitate identification and to detect the presence of the species in the locality. To confirm the identification, examined specimens were compared with the reference collections of Dr Stanoy Kovachev, held at the Department of Zoology and Anthropology, Sofia University. Prepared microscopic slides with host parts, used for identification, as well as the host larvae with parasitic juveniles of nematodes, fixed in 4% formaldehyde or 70% alcohol, are deposited in the same institution. Nomenclature of Simuliidae is after Adler and Crosskey (2013).

Results

Larvae of Simuliidae infected with mermithids were established in July, August and September of 2012 and August and September of 2013. Mermithids were found in both localities examined mainly in larvae of *Simulium ornatum* Meigen, 1818 (Fig. 1A, B). In the second locality *S. ornatum* was clearly predominant during the sampling period of 2012 (Table 1). The estimated rate of its infection with mermithids in late July and August varies from 1.8% to 44.1%. Only nine larvae and one pupa of *S. variegatum* Meigen, 1818 were present in quantitative samples, while *S. reptans* (Linnaeus, 1758) was detected by a single pupa, collected on 25 July. In summer and early autumn of 2013 four species of Simuliidae were found in the investigated locality. A considerable decline in the population density of *S. ornatum* was observed in August, when *S. variegatum* and *S. reptans* clearly dominated the samples. The infection rate of *S. ornatum* in all three samples of August and September, despite the small number of host larvae, was still high (60–81.1%).

Table 1. Simuliid species and the rate of their infection with mermithids in the supply channel of the Selska Reka River, Vitosha Mts., July – August of 2012 and August – September of 2013.

Date	Simuliids	Number larvae	Infected larvae	
			N	%
25.07. 2012	<i>S. ornatum</i>	179	79	44,1
	<i>S. variegatum</i>	7	1	14,3
	Total (% infected)	186	80	(43,0)
03.08. 2012	<i>S. ornatum</i>	391	150	38,4
	<i>S. variegatum</i>	2	0	0,0
	Total (% infected)	393	150	(38,2)
12.08. 2012	<i>S. ornatum</i>	239	22	9,2
25.08. 2012	<i>S. ornatum</i>	340	6	1,8
	<i>S. variegatum</i>	182	0	0,0
	<i>S. reptans</i>	50	2	4,0
	<i>S. ornatum</i>	10	6	60,0
	Total (% infected)	242	8	(3,3)
27.08. 2013	<i>S. variegatum</i>	110	1	0,9
	<i>S. reptans</i>	77	3	3,9
	<i>S. ornatum</i>	11	9	81,1
	Total (% infected)	198	13	(6,6)
12.09. 2013	<i>S. reptans</i>	50	2	4,0
	<i>S. ornatum</i>	32	20	62,5
	<i>S. variegatum</i>	16	0	0,0
	<i>Simulium</i> sp.	1	0	0,0
	Total (% infected)	99	22	(22,2)

The emergence of postparasitic juveniles of mermithids was observed only from larvae of *S. ornatum* in the summer and early autumn of 2012. Six males and three females, suitable for measurements, were reared to adult stages. The period of maturation and release from the cuticle remains of postparasitic juveniles under rearing conditions was from 20 to 40 days. The attempts to obtain postparasitic juveniles in the second year were unsuccessful. Based on morphological characteristics of postparasitic juveniles, as well as males and females, all mermithids were identified as belonging to genus *Isomermis* Coman, 1953. These characteristics are the presence of: eight hypodermal chords, six cephalic papillae, terminal position of mouth opening (Fig. 2A), oval amphids located posterior to the head papillae (Fig. 2B), short spine-like tail appendages of postparasitic juveniles in both sexes (Fig. 2C, G), S-shaped vagina (Fig. 2E), and paired moderately curved spicules (Figs 2F, H, 3). The main characters of adult specimens are as follows.

Males (n=6): body length: 10.81 mm \pm 1.51 (9.10–13.26), width of the head at the level of cephalic papillae: 52 μ m \pm 5 (47–59), width of the body at the level of nerve ring: 93 μ m \pm 11 (82–105), greatest width of the body: 148 μ m \pm 16 (127–163), width of the body at cloaca: 123 μ m \pm 15 (106–141), distance from the head to the nerve ring: 191 μ m \pm 27 (158–231), tail length: 277 μ m \pm 37 (238–332), length of amphidial pouch (n=2): 24 μ m \pm 1 (24–25), width of amphidial pouch (n=2): 17 μ m,

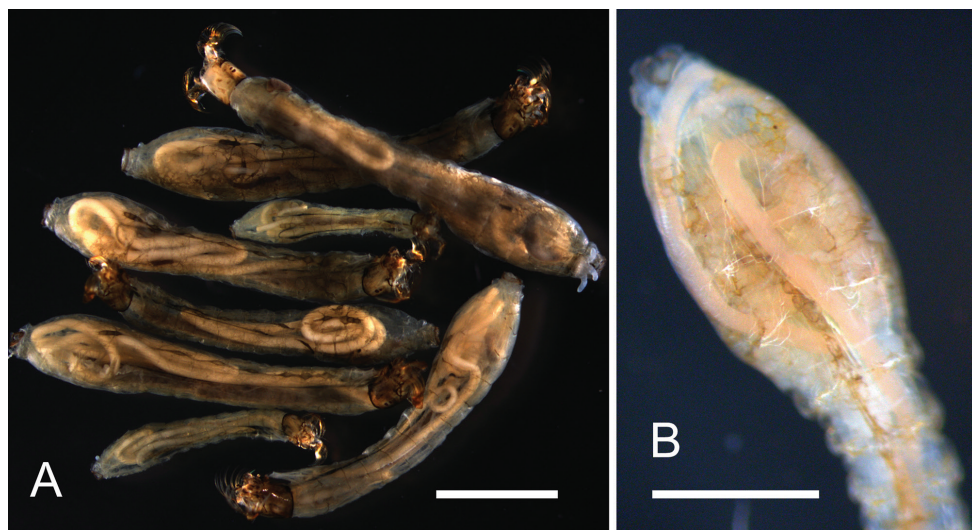


Figure 1. Larvae of *Simulium ornatum* with parasitic juveniles of *Isomermis lairdi*, Selska Reka River. **A** Fixed in 70% alcohol material, 03.08.2012 **B** Live host larva, 12.09.2013. Scale bars: **A**: 2 mm; **B**: 1 mm.

number of the genital papillae: 18–21 in lateral rows and 56–62 in ventral row, arrangement of the papillae as follows: precloacal – 11–14 in lateral rows and 31–38 in ventral row, postcloacal – 7–8 in lateral rows and 23–26 in ventral row, length of spicules (measured along median): $203\ \mu\text{m} \pm 10$ (191–218), length of spicules (measured along chord): $179\ \mu\text{m} \pm 8$ (168–193). Spicules yellowish-colored, clearly separated at the base and close towards the tip, with elongate distal and arcuate proximal part.

Females (n=3): body length: $17.44\ \text{mm} \pm 3.95$ (12.96–20.42), width of the head at the level of cephalic papillae: $71\ \mu\text{m} \pm 5$ (67–77), width of the body at the level of nerve ring: $113\ \mu\text{m} \pm 19$ (94–131), greatest width of body: $251\ \mu\text{m} \pm 39$ (208–285), width of the body at vulva: $233\ \mu\text{m} \pm 42$ (186–267), distance from head to the nerve ring: $191\ \mu\text{m} \pm 26$ (171–220), width of the body at posterior end of the trophosome: $111\ \mu\text{m} \pm 5$ (106–116), length of vagina: $219\ \mu\text{m} \pm 22$ (205–245), width of vagina: $54\ \mu\text{m} \pm 2$ (52–57), length of amphidial pouch (n=1): $20\ \mu\text{m}$, width of amphidial pouch (n=1): $16\ \mu\text{m}$, V%: 52.1 (50.2–54.8). Vagina is slightly curved, with the first bend extended posteriorly.

Color of the trophosome of the living individuals of both sexes varies from pale pink to brownish red, more intense in parasitic and postparasitic juveniles (Fig. 1B).

After a detailed comparison with the original descriptions of the species the mermithids were identified as *Isomermis lairdi* Mondet, Poinar & Bernadou, 1977, originally described from West Africa. The main reasons for the identification were good conformity with most morphometric characters of the species, the compliance of morphology of the caudal region of the males with the figure in the original description, as well as the morphology of caudal appendage of postparasitic juveniles (Mondet et al. 1977). Taxonomic traits of special importance were the general shape and position of

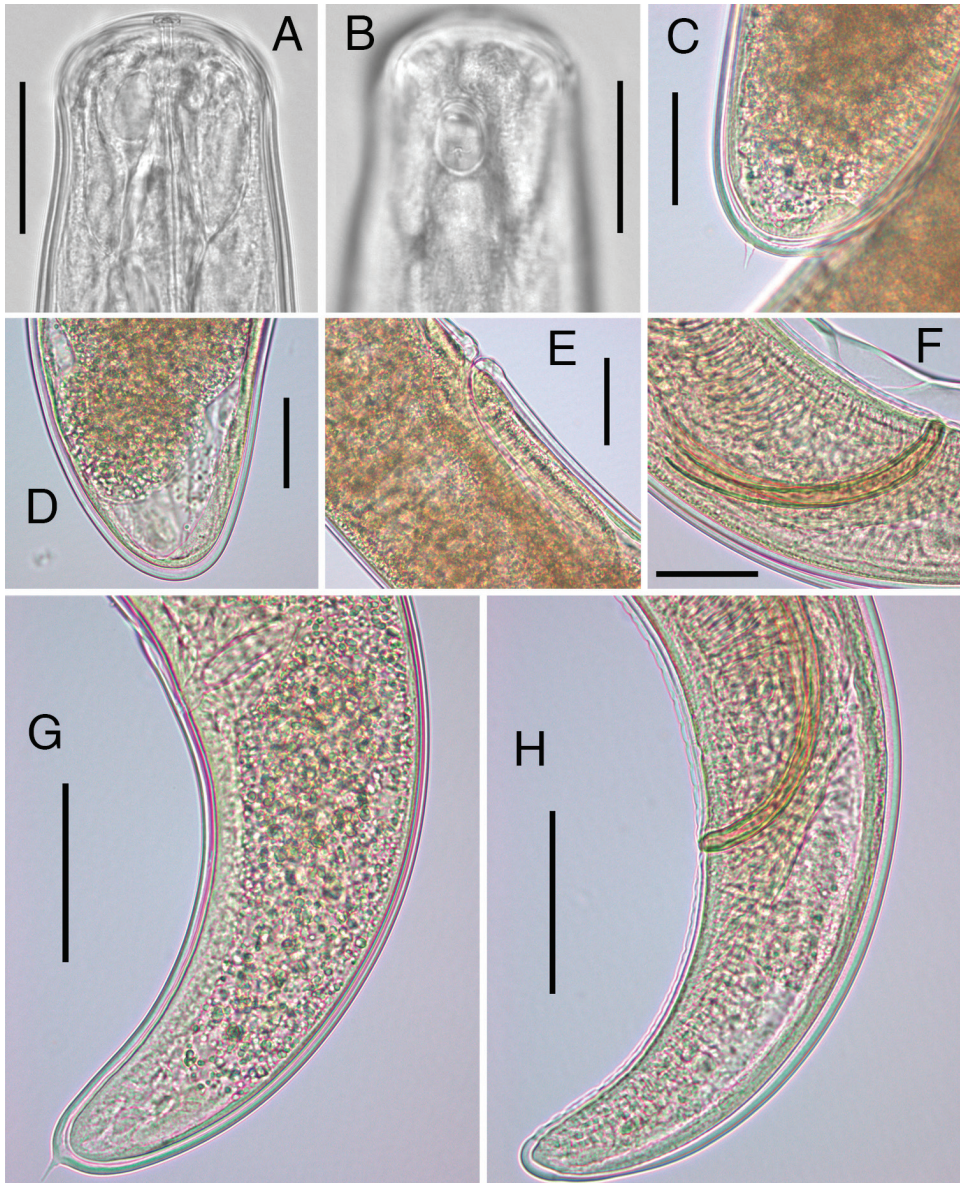


Figure 2. Main morphological characters of *Isomermis lairdi* from Jeleznitsa (**A–H**). **A, B** Mature male, anterior region with terminal mouth opening (**A**) and amphid (**B**), lateral view. **C** Female postparasitic juvenile, posterior end with tail appendage **D** Mature female, posterior end **E** Female, vulvar region with vagina **F** Male, spicules **G** Male postparasitic juvenile, tail region with tail appendage **H** Mature male, tail region. Scale bars: **A, B**: 50 µm; **C–F**: 70 µm; **G, H**: 100 µm.

the spicules, the number and arrangement of genital papillae (especially in the lateral rows), including their cohesion in pairs, and the morphology of the tail tip of the males (Figs 2F, H, 3).

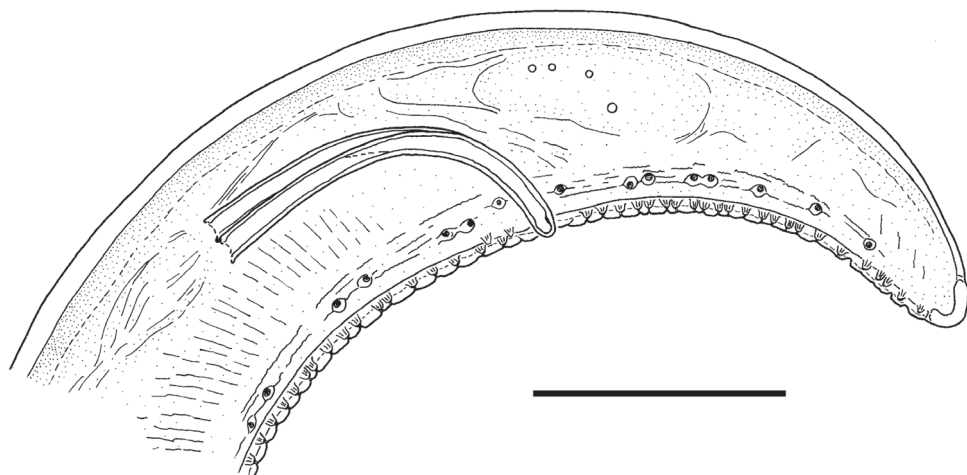


Figure 3. Tail region of male *Isomermis lairdi* from Jeleznitsa with spicules and genital papillae, lateral view. Scale bar: 100 μ m.

No other mermithids, except *I. lairdi*, emerged from larvae of *S. ornatum* or were received from them at the selective dissections. Sporadic infection of *S. reptans* and *S. variegatum* larvae (Table 1), as shown by performed dissections, seems to be caused by other mermithid species, possibly belonging to the genus *Gastromermis* Micoletzky, 1923 (indicated by the presence of a longer tail appendage of parasitic juveniles). The poor condition and the early age of the specimens received at dissection, however, did not allow their exact identification.

Discussion

The genus *Isomermis*, as well as the whole family Mermithidae (Stock and Hunt 2005), is in need of comprehensive revision. Many characters used in species descriptions exhibit significant intraspecific and ontogenetic variability and are not proven to be useful for species separation (Curran and Hominick 1981). Therefore, in many cases the original diagnoses of the species are inconclusive. Camino (1987) accepts as valid approximately 12 species of the genus, without listing them, and describes three new species (Camino 1987, 1994). Species of *Isomermis* have been reported from Europe (Coman 1961, Rubzov 1968, Rubzov and Doby 1970, Katyukha and Lukhovoz 2008), North America (Welch 1962, St-Onge and Charpentier 2008, St-Onge et al. 2008), Central (Poinar and Takaoka 1979, 1981) and South America (Camino 1987, 1994, Ginarte et al. 2003), Africa (Rubzov 1972, Mondet et al. 1977, Maduabum and Iwuala 1990, Crainey et al. 2009) and Asia (Poinar and Takaoka 1986). The host range of the genus includes different species of Simuliidae (Crosskey and Poinar 2002) and rarely Chironomidae (Rubzov 1968, Camino 1987).

Isomermis lairdi resembles most closely three species of the genus. These are *I. rossica* Rubzov, 1968, described from Russia, *I. benevolus* Poinar & Takaoka, 1979 from Guatemala and *I. wisconsinensis* Welch, 1962 from North America. Among the diagnostic characters of *I. lairdi* Mondet et al. (1977) point out the strongly S-shaped vagina. At the same time, in our case bending of the vagina is considerably smaller (Fig. 2E) and corresponds to that of the species *I. wisconsinensis* (Welch 1962) and *I. rossica* (Rubzov 1968). Curran and Hominick (1981) showed, however, that the shape and direction of the vagina are ontogenetically variable. In the description of *I. lairdi* a picture of a mature female with formed eggs was presented, while the individuals we have worked with are young females with retained trophosome, and this does not allow this feature to be used as a diagnostic character in our case.

Isomermis rossica is the only repeatedly reported species of *Isomermis* from Europe. It was found in different regions of Russia, Belarus, (Rubzov 1968), France (Rubzov and Doby 1970) and Ukraine (Katyukha and Lukhovoz 2008). *Isomeris rossica*, however, possesses spicules of a different shape – without an elongate distal part, the whole spicule being uniformly and relatively strongly curved (Rubzov 1968, 1972). The number of genital papillae in the lateral rows, mentioned in species description of *I. rossica*, is considerably larger (30–40). *Isomeris rossica* was found in larvae of *Simulium erythrocephalum* (De Geer, 1776), *S. morsitans* Edwards, 1915, *S. rostratum* (Lundstrom, 1911), *S. vernum* Macquart, 1826, *S. cryophilum* (Rubzov, 1959), *S. lundstromi* (Enderlein, 1921), rarely in other simuliids and chironomids (Rubzov 1968, Crosskey and Poinar 2002). Despite the broad host range of the species, Rubzov (1968, 1974) expressly noted that larvae of *S. ornatum* are „immune“ to mermithid invasion in long-term surveys in localities with high occurrence of *I. rossica*. Thus this host specialization can in our case be used as an additional diagnostic feature.

Isomermis lairdi was described in Cote d'Ivoire from larvae of *S. damnosum* Theobald, 1903 (Mondet et al. 1977) and was subsequently reported to occur in Ghana, Togo, Benin (after Crainey et al. 2009) and Nigeria (Maduabum and Iwuala 1990). The hosts of the species are simuliids belonging to the *S. damnosum* complex (after Crainey et al. 2009), as well as *S. hargreavesi* Gibbins, 1934 (Maduabum and Iwuala 1990). Species from the *S. damnosum* complex do not occur in Europe, as the northern border of the distribution of this complex in West Africa passes through Mali and Niger (Adler and Crosskey 2013). At the same time, the southern border of the distribution of the *S. ornatum* complex passes through Morocco and Algeria. Thus, no strong geographic isolation between both host complexes exists, which is a precondition for the dissemination of the mermithids. It appears that in different geographic regions *I. lairdi* could parasitize different hosts. Yet Rubzov (1974) suggests the presence of other African species of the genus *Isomermis*, also described from larvae of *S. damnosum* – *I. tansaniensis* Rubzov, 1972 in western Europe, despite the absence of the type host. The latest species, however, was described based on juveniles only (Rubzov 1972) and Poinar and Takaoka (1979) considered it as *species inquirendae*.

Simuliids of the *S. damnosum* complex are among the main vectors of human onchocerciasis in Africa (Adler 2004). Thus, *I. lairdi* has been considered as a possible

biological agent for the control of these simuliids (Crainey et al. 2009). The same authors published sequencing data of the 18S rDNA region of *I. lairdi* (Crainey et al. 2009). However, authors used parasitic juveniles, recovered from the hosts and identified to genus level as material for isolation of DNA samples. This step of the method per se raises serious suspicions about affiliation of the DNA sequences obtained to the species *I. lairdi*. The figures of taxonomic characters of parasitic juveniles presented by these authors are inconclusive. On the first figure, the position of the mouth opening could not be clearly determined. In some species of *Gastromermis*, i.a. *G. viridis* Welch, 1962 the ventral displacement of the mouth is less pronounced (Welch 1962). The relatively long caudal appendage of the female parasitic juvenile in the second figure also resembles that of some species of *Gastromermis* (Rubzov 1974). *Isomermiss lairdi* possesses a considerably shorter and spine-like caudal appendage (Fig. 2 and Mondet et al. 1977). It is therefore not surprising that in the resulting phylogenetic tree, constructed with the obtained sequences, *I. lairdi* sensu Crainey et al. formed a monophyletic group with *G. viridis*, rather than with the closely related *I. wisconsinensis* (Crainey et al. 2009). Generally, the obtained sequences are unusable for identification of *I. lairdi* and for other taxonomical purposes within the genus. For an accurate molecular characterization of mermithid species, the identification of the material should be performed on adult specimens. For a taxonomic revision of the genus, interbreeding experiments with closely related species would also be helpful. The latter was recommended by Poinar and Takaoka (1979) in the description of *I. benevolus* with respect to *I. lairdi*, as the authors noted the similarities between the two species despite geographical isolation.

According to previous research on simuliid fauna in Bulgaria, *S. ornatum* and *S. variegatum* are common in the rivers on Vitosha Mts., while *S. reptans* is relatively rare (Kovachev 1990). Mermithid parasitism is a possible cause of the decrease of the population density of *S. ornatum* in the investigated locality in August of 2013. During the survey period, cases of infection of simuliid larvae, including *S. ornatum*, with several microsporidian species, were also observed (D. Gradinarov, D. Pilarska, unpublished data). The impact of microsporidia on the host population, however, does not appear to be significant, because of the relatively low rates of infection detected with similar degrees in the different simuliid species. On the other hand, the cases of epizootics in host populations, caused by mermithid parasitism, are noted and discussed by Rubzov (1974) and Molloy (1981). The high infection rate of single host species can lead to a change in species composition in a local habitat in the subsequent years and the appearance of “substitute species” which may be “immune” to nematode invasion (Rubzov 1974). In our case, such substitute species seem to be *S. variegatum* and *S. reptans*. In the Palearctic Region, including Europe, black flies of the *S. ornatum* complex are known as vectors of *Onchocerca lienalis* (Stiles, 1892) and *O. skrjabini* Ruchljadev, 1964 (syn. *O. tarsicola* Bain & Schulz-Key, 1974), caused onchocerciasis of cattle and deer respectively (Adler 2004). Mermithids, able to decrease the population density of these vectors, and to affect species composition of the simuliid populations, could be considered as an essential epidemiology factor of these diseases.

References

- Adler PH (2004) Black flies, the Simuliidae. In: Marquardt WC (Ed.) Biology of Disease Vectors. Elsevier, San Diego, 127–140.
- Adler PH, Crosskey RW (2013) World Blackflies (Diptera: Simuliidae): A Comprehensive Revision of the Taxonomic and Geographical Inventory, 120 pp. <http://entweb.clemson.edu/biomia/pdfs/blackflyinventory.pdf> [accessed 25 December 2013]
- Camino NB (1987) Dos especies nuevas del género *Isomermis* Coman, 1953 (Nematoda: Mermithidae), parásitos de larvas acuáticas de Dípteros en Argentina. *Revista Iberica de Parasitologia* 47: 153–158.
- Camino NB (1994) *Isomermis sierrensis* sp. n. (Nematoda: Mermithidae) a parasite of *Simulium wolffhuegeli* Roubaud (Diptera: Simuliidae) in Argentina. *Nematologia Mediterranea* 22: 141–143.
- Coman D (1961) Mermithidae – Fauna Republicii Populare Romine. Academia Republicii Populare Romine, Volumul II, Fascicula 3, 61 pp.
- Crainey JL, Wilson MD, Post RJ (2009) An 18S ribosomal DNA barcode for the study of *Isomermis lairdi*, a parasite of the blackfly *Simulium damnosum* s.l. *Medical and Veterinary Entomology* 23: 238–244. doi: 10.1111/j.1365-2915.2009.00814.x
- Crosskey RW, Poinar GO (2002) A synoptic list of the named mermithid parasites described from simuliid hosts. *British Simuliid Group Bulletin* 19: 13–26.
- Curran J, Hominick WM (1981) Description of *Gastromermis metae* sp. n. (Nematoda: Mermithidae) With an Assessment of Some Diagnostic Characters and Species in *Gastromermis*. *Nematologica* 27: 258–273. doi: 10.1163/187529281X00494
- Ginarte CA, Andrade CF, Campos-Gaona J (2003) Larvas de simulídeos (Diptera: Simuliidae) do Centro Oeste, Sudeste e Sul do Brasil, parasitadas por Microsporídeos (Protozoa) e Mermítídeos (Nematoda). *Iheringia. Série Zoologia* 93: 325–334. doi: 10.1590/S0073-47212003000300011
- Jedlicka L, Kúdela M, Stloukalová V (2004) Key to the identification of blackfly pupae (Diptera: Simuliidae) of Central Europe. *Biologia* 59: 157–178.
- Katyukha SN, Lukhovoz LK (2008) The activity potential agents of biological checking maggots of black-flies in the drainages of West Polyssya of Ukraine. *Scientific Messenger of Lviv National University of Veterinary Medicine and Biotechnologies named after S. Z. Gzhytskyj* 10: 99–102. [in Ukrainian]
- Kovachev SG (1990) Black-flies (Insecta, Diptera, Simuliidae) from Vitoša. *Fauna of South-western Bulgaria, Part 3*. Publishing House of the Bulgarian Academy of Sciences, Sofia, 150–153. [in Bulgarian]
- Maduabum MA, Iwuala MOE (1990) Studies of mermithid and microsporidian infestation of *Simulium* (black fly) larvae in River Assob, Plateau State, Nigeria. *Tropical Ecology* 31: 16–21.
- Molloy DP (1981) Mermithid Parasitism of Black Flies (Diptera: Simuliidae). *Journal of Nematology* 13: 250–256.
- Mondet B, Poinar GO Jr, Bernadou J (1977) Etude du parasitisme des simulies (Diptera: Simuliidae) par des Mermithidae (Nematoda) en Afrique de l'ouest. IV : Description de

- Isomermis lairdi*, n. sp., parasite de *Simulium damnosum*. Canadian Journal of Zoology 55: 2011–2017. doi: 10.1139/z77-261
- Nickle WR (1972) A contribution to our knowledge of the Mermithidae (Nematoda). Journal of Nematology 4: 113–146.
- Poinar GO Jr (1975) Entomogenous Nematodes: A Manual and Host List of Insect-Nematode Associations. Brill, Leiden, 317 pp.
- Poinar GO Jr (1979) Nematode for Biological Control of Insects. CRC Press, Boca Raton, 277 pp.
- Poinar GO Jr, Takaoka H (1979) *Isomermis benevolus* sp. n. (Mermithidae, Nematoda), a parasite of *Simulium metallicum* (Diptera: Simuliidae) in Guatemala. Medical Entomology and Zoology 30: 305–307.
- Poinar GO Jr, Takaoka H (1981) Three new mermithids (Nematoda) from Guatemalan blackflies (Diptera: Simuliidae). Systematic Parasitology 3: 13–19. doi: 10.1007/BF00012234
- Poinar GO Jr, Takaoka H (1986) *Isomermis bipapillatus* n. sp. and *Gastromermis mesostoma* n. sp. (Mermithidae: Nematoda), parasites of *Simulium japonicum* (Simuliidae: Diptera) in Japan. Systematic Parasitology 8: 51–55. doi: 10.1007/BF00010309
- Rubzov IA (1968) A new species of *Isomermis* (Nematoda, Mermithidae) - parasite of blackflies and its variability. Zoologicheskii Zhurnal 47: 510–524. [in Russian]
- Rubzov IA (1972) Aquatic Mermithidae. Vol I. Nauka, Leningrad, 254 pp. [in Russian]
- Rubzov IA (1974) Aquatic Mermithidae. Vol II. Nauka, Leningrad, 222 pp. [in Russian]
- Rubzov IA, Doby JM (1970) Mermithides parasites de simules (diptères) en provenance du nord et de l'ouest de la France. Bulletin de la Société Zoologique de France 95: 803–836.
- Stock SP, Hunt DJ (2005) Morphology and systematics of nematodes used in biocontrol. In: Grewal PS, Ehlers RU, Shapiro-Ilan DI (Eds) Nematodes as biocontrol agents. CABI Publishing, New York, 3–43. doi: 10.1079/9780851990170.0003
- St-Onge M, Charpentier G (2008) Mermithids (Nematoda: Mermithidae) parasitizing different blackfly (Diptera: Simuliidae) populations in Quebec: environmental parameters related to their presence or absence in the studied brooks. Journal of the American Mosquito Control Association 24: 438–443. doi: 10.2987/5712.1
- St-Onge M, LaRue B, Charpentier G (2008) A molecular revision of the taxonomic status of mermithid parasites of black flies from Quebec (Canada). Journal of Invertebrate Pathology 98: 299–306. doi: 10.1016/j.jip.2008.04.001
- Welch HE (1962) New species of *Gastromermis*, *Isomermis* and *Mesomermis* from blackfly larvae. Annals of the Entomological Society of America 55: 535–542.
- Yankovsky AB (2002) Keys to the blackflies (Diptera: Simuliidae) of Russia and adjacent territories (former USSR). Saint Petersburg, Publishing House of the Russian Academy of Sciences, 570 pp. [in Russian]

A review of myrmecophilous mites of the family Microdispidae (Acari, Heterostigmata) of Western Siberia

Alexander A. Khaustov¹

¹ Tyumen State University, Tyumen, Russia

Corresponding author: Alexander A. Khaustov (alkhaustov@mail.ru)

Academic editor: Vladimir Pesic | Received 8 October 2014 | Accepted 27 October 2014 | Published 12 November 2014

<http://zoobank.org/58A02874-6BFB-4A80-8F07-F1113C7AF44E>

Citation: Khaustov AA (2014) A review of myrmecophilous mites of the family Microdispidae (Acari, Heterostigmata) of Western Siberia. ZooKeys 454: 13–28. doi: 10.3897/zookeys.454.8709

Abstract

Five species of myrmecophilous microdispid mites (Acari: Microdispidae) are recorded from Western Siberia, Russia. *Unguidispus lasii* Kurosa, 1979, *U. japonicus* Kurosa, 1979, *Caesarodispus minutus* (Sevastianov, 1981), and *C. samsinaki* (Mahunka, 1967), **comb. n.** are reported from Russia for the first time. *Unguidispus polycetenus* (Sevastianov, 1969) and *Caesarodispus samsinaki* are redescribed. The keys to species of the genera *Unguidispus* Mahunka, 1970 and *Caesarodispus* Mahunka, 1977 are provided.

Keywords

Acari, Heterostigmata, systematics, phoresy, ants, Western Siberia

Introduction

The family Microdispidae Cross, 1965 (Acari: Pygmephoroidae) includes 18 genera and about 115 described species (Hajiqanbar and Hosseiniaveh 2014). All representatives from the genera *Unguidispus* Mahunka, 1970, *Caesarodispus* Mahunka, 1977, *Myrmecodispus* Cross, 1965, *Reductodispus* Mahunka, 1977, *Perperipes* Cross, 1965, and *Glyphidomastax* Cross, 1965 are associated with various ants (Hymenoptera: Formicidae) (Hajiqanbar and Hosseiniaveh 2014). Most of microdispid mites are

fungivorous, but the species from the genera *Perperipes* and *Glyphidomastax*, associated with army ants, probably feed on their larvae and/or eggs (Kaliszewski et al. 1995). During the study of myrmecophilous mites of Western Siberia we found five species of the family Microdispidae belonging to the genera *Unguidispus* Mahunka, 1970 and *Caesarodispus* Mahunka, 1977. The main goal of this paper is to redescribe the poorly known species *Unguidispus polycetenus* (Sevastianov, 1969) and *Caesarodispus samsinaki* (Mahunka, 1967), comb. n. and provide new records of myrmecophilous microdispid mites from Western Siberia, as well as the keys to world species of the genera *Unguidispus* and *Caesarodispus*.

Materials and methods

Mites were collected from ants or ant nests and mounted in Hoyer's medium. The terminology of idiosoma and legs follows Lindquist (1986); the nomenclature of subcapitular setae and the designation of cheliceral setae follow Grandjean (1944, 1947), respectively. The system of Pygmephoroidae follows Khaustov (2004, 2008). All measurements are given in micrometers (μm). For leg chaetotaxy the number of solenidia is given in parentheses. The studied material is deposited in the mite collection of the Tyumen State University Museum of Zoology, Tyumen, Russia. SEM photographs were made with the aid of JEOL–JSM-6510LV SEM microscope.

Systematics

Family Microdispidae Cross, 1965

Genus *Unguidispus* Mahunka, 1970

Type species. *Unguidispus stammeri* Mahunka, 1970, by original designation.

Diagnosis. Female. Gnathosoma dorsally with 2 pairs of setae. Pharyngeal pumps 1 and 3 vestigial, pharyngeal pump 2 large, transversely striated. Prodorsum usually almost completely covered by tergite C. Cupules *ia* and *ih* small, round. Two pairs of pseudanal setae present (*ps*₂ absent). Posterior margin of posterior sternal plate entire. Leg I distinctly shorter than leg II. Tibiotarsus with well-developed claw; eupathidia *tc'-tc''* situated on clear pinnaculum; setae *s* of tibiotarsus I present. Trochanter IV anterodorsally with short spine-like process.

The genus *Unguidispus* currently includes six species distributed in the Palaearctic region: *U. stammeri*, *U. polycetenus* (Sevastianov, 1969), *U. contematosus* Sevastianov, 1981, *U. okumurai* Kurosa, 1979, *U. japonicus* Kurosa, 1979, and *U. lasii* Kurosa, 1979. All species of the genus *Unguidispus* phoretic on ants of the genera *Formica* L. and *Lasius* Fabricius (Hymenoptera: Formicinae), or inhabit their nests (Hajiqanbar and Hosseinaveh 2014; Kurosa 1979).

***Unguidispus polycatenus* (Sevastianov, 1969)**

Figs 1–4

Piniphorus polycatenus Sevastianov, 1969, p. 68, fig. 2.*Xystrorostrium polycatenus*: Mahunka 1970a: 165.*Unguidispus polycatenus*: Mahunka 1970b: 282.**Redescription. Female** Length of idiosoma 190–205, width 120–135.

Gnathosoma (Figs 1, 4E, 4F). Gnathosomal capsule beak-like, about 1.5 times longer than its width. Dorsally with two pairs of smooth subequal setae (*cha*, *chb*). Dorsal median apodeme absent. Ventral gnathosoma with one pair of subcapitular setae *m* and a pair of oval pits situated posteromedial to bases of *m*. Palps with setae *dFe* and *dGe* dorsolaterally. Setae *dGe* slightly longer than *dFe*. Ventral palpal structures not evident even on SEM photos (Fig 4F). Palps terminated with a relatively long and thin tibial claw (Fig 4F).

Idiosomal dorsum (Figs 1A, 4A). Prodorsum almost completely covered by anterior margin of tergite C, with one pair of setae *sc*₂, one pair of clavate and weakly barbed trichobothria *sc*₁ with pointed apex, and one pair of large round stigmata. All dorsal shields smooth. All dorsal setae distinctly barbed; setae *d* and *f* blunt-ended, other dorsal setae pointed. Posterior margin of tergite C straight; posterior margin of tergite H with tongue-like elongation medially. Cupules *ia* on tergite D and *ih* on tergite H small, round. Lateral shields covering lateral parts of tergite D with distinct sclerotized lines (Fig 4B). With a pair of arch-like structures anteriorly to setae *f* and a pair of oblique ridges connected to bases of setae *e* (Fig 4C). Length of dorsal setae: *sc*₂ 12–14, *c*₁ 35–38, *c*₂ 40–42, *d* 36–38, *e* 44–45, *f* 35–37, *h*₁ 40–45, *h*₂ 35–37. Distances between setae: *sc*₂–*sc*₂ 37–40, *c*₁–*c*₁ 47–50, *c*₁–*c*₂ 22–24, *d*–*d* 41–43, *e*–*f* 18–20, *f*–*f* 35–38, *h*₁–*h*₁ 19–21, *h*₁–*h*₂ 18–21.

Idiosomal venter (Figs 1B, 4D). All ventral plates smooth. All ventral setae pointed and barbed, except smooth *ps*₃. Apodemes 1 (*ap*₁) weakly developed and joined with prosternal apodeme (*appr*); apodemes 2 (*ap*₂) well developed, arch-like, fused with *appr*; prosternal and sejugal (*apsej*) apodemes well developed; apodemes 3 (*ap*₃) well sclerotized. Apodemes 4 (*ap*₄) well sclerotized and long, apodemes 5 absent. Posterior margin of posterior sternal plate slightly convex in middle part. Posterior margin of aggenital plate rounded. Anterior genital sclerite (*ags*) bell-like, posterior genital sclerite (*pgs*) very small, triangular. Length of ventral setae: *1a* 35–37, *1b* 21–23, *2a* 33–36, *2b* 36–40, *3a* 34–36, *3b* 35–37, *3c* 36–38, *4a* 36–38, *4b* 52–55, *4c* 39–41, *ps*₁ 24–26, *ps*₃ 9–11.

Legs (Figs 2–3, 4F). Leg I (Figs 2A, 4F) distinctly shorter and thinner than leg II. Setal formula: 1–3–4–16(4). Tibiotarsus not thickened, with well-developed terminal claw situated on distinct pretarsus, tip of the claw thin. Length of solenidia ω_1 11–12 = ω_2 11–12 > φ_1 6–7 = φ_2 6–7; ω_1 and ω_2 finger-shaped, φ_2 baculiform, φ_1 clavate. Setae (*u*) fused into structure opposing to tarsal claw. Leg II (Fig 2B). Setal formula: 1–3–3–4(1)–6(1). Tarsus with sickle-like, padded claws and large empodium. Solenidion ω 9–10, finger-shaped, solenidion φ 3–4 weakly clavate. Seta *dFe* distinctly blunt-ended. Leg III

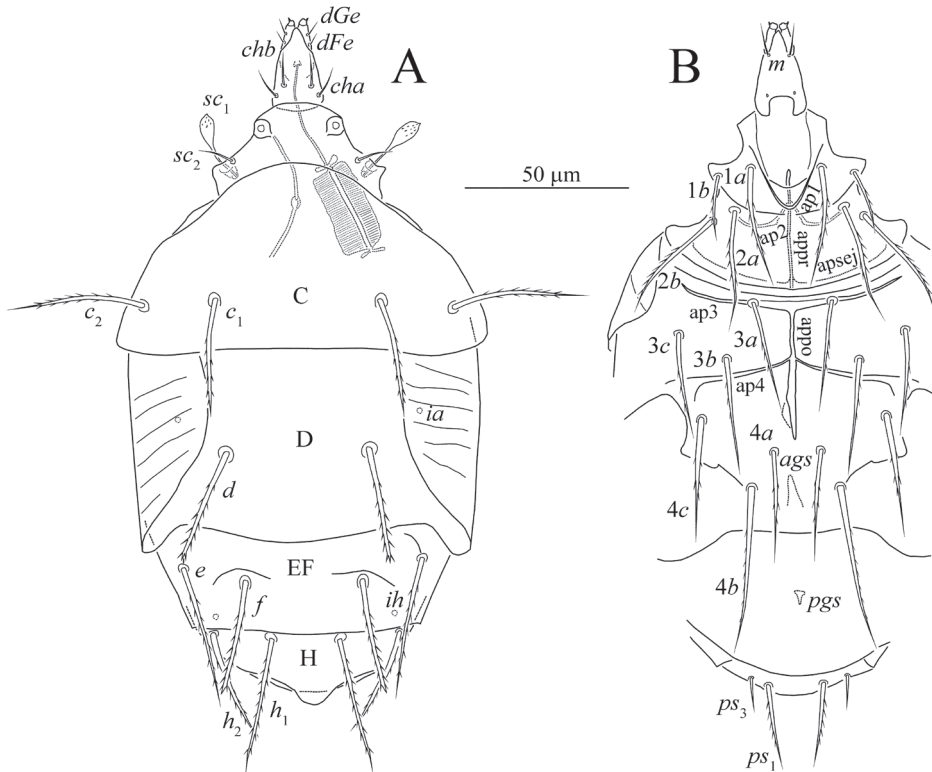


Figure 1. *Unguidispus polycetenus* (Sevastianov, 1969), female: **A** dorsum of the body **B** venter of the body.

(Fig 3A). Setal formula: 1–2–2–4(1)–6. Claws of same shape as on tarsus II. Solenidion φ 3–4 weakly clavate. Seta *dFe* distinctly blunt-ended. Leg IV (Fig 3B). Setal formula: 1–2–1–4(1)–6. Tarsus long and thin, pretarsus short, with two small simple claws and small empodium. Solenidion φ 3–4, weakly clavate. Seta *dFe* distinctly blunt-ended.

Male and larva unknown.

Material examined. Eight female paratypes, **UKRAINE**, Khmel'nitsk Province, vicinity of settlement Chemerovtsy, on ants *Formica polycetena* Forster, 23 July 1966, coll. V.D. Sevastianov; 3 females, **RUSSIA**: Tyumen Province, vicinity of Tyumen, 57°04'03"N, 65°04'12"E, on ants *Formica rufa* L., 17 August 2014, coll. A.A. Khaustov; 15 females, **RUSSIA**, Tyumen Province, vicinity of Tyumen, 57°13'43.6"N, 65°28'28.4"E, on ants *Formica polycetena*, 14 September 2014, coll. A.A. Khaustov.

Distribution and hosts. This species was described from Western Ukraine from ants *Formica polycetena* Forster (Sevastianov 1969). It was also recorded in northwestern Russia (Sevastianov 1978), Austria (Mahunka 1970b) from ants *Formica rufa* L., and in Hungary from ant nest (Mahunka 1987).

Remarks. Sevastianov (1969) placed this species in the genus *Piniphorus* Sevastianov, 1969. Mahunka (1970a) transferred it to *Xystrorostrum* Mahunka, 1968

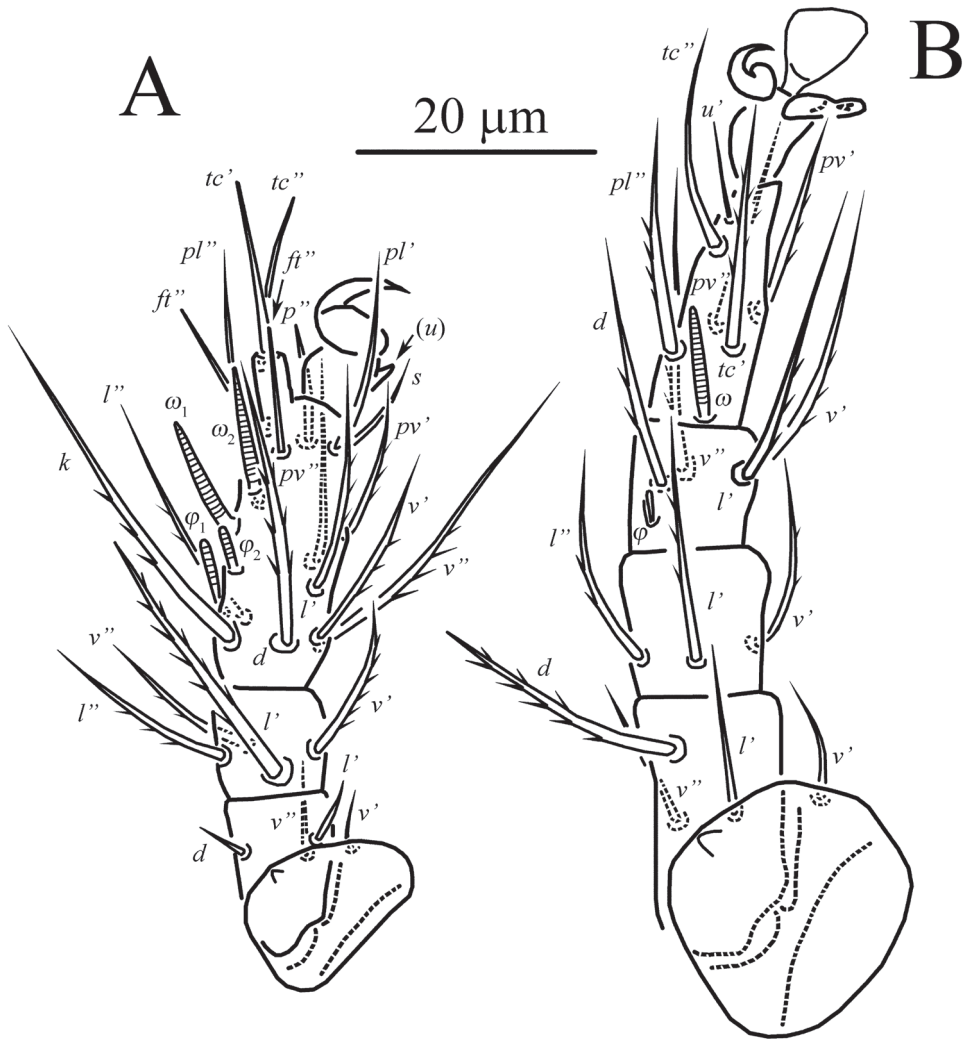


Figure 2. *Unguidispus polycytenus* (Sevastianov, 1969), female: **A** leg I **B** leg II.

(Neopygmephoridae) which he considered as a senior synonym of *Piniphorus*. The same year Mahunka (1970b) moved this species to the microdispid genus *Unguidispus* Mahunka, 1970. In spite of this, Sevastianov (1978) retained it in the neopygmephorid genus *Xystrostrum*.

The original description of *U. polycytenus* of Sevastianov (1969) is incomplete, thus I made a redescription of this species. The present redescription of *U. polycytenus* is based mainly on material from Western Siberia. The female paratypes available for this study are found in bad condition, yet sufficient to prove their identity with mite specimens from Western Siberia.

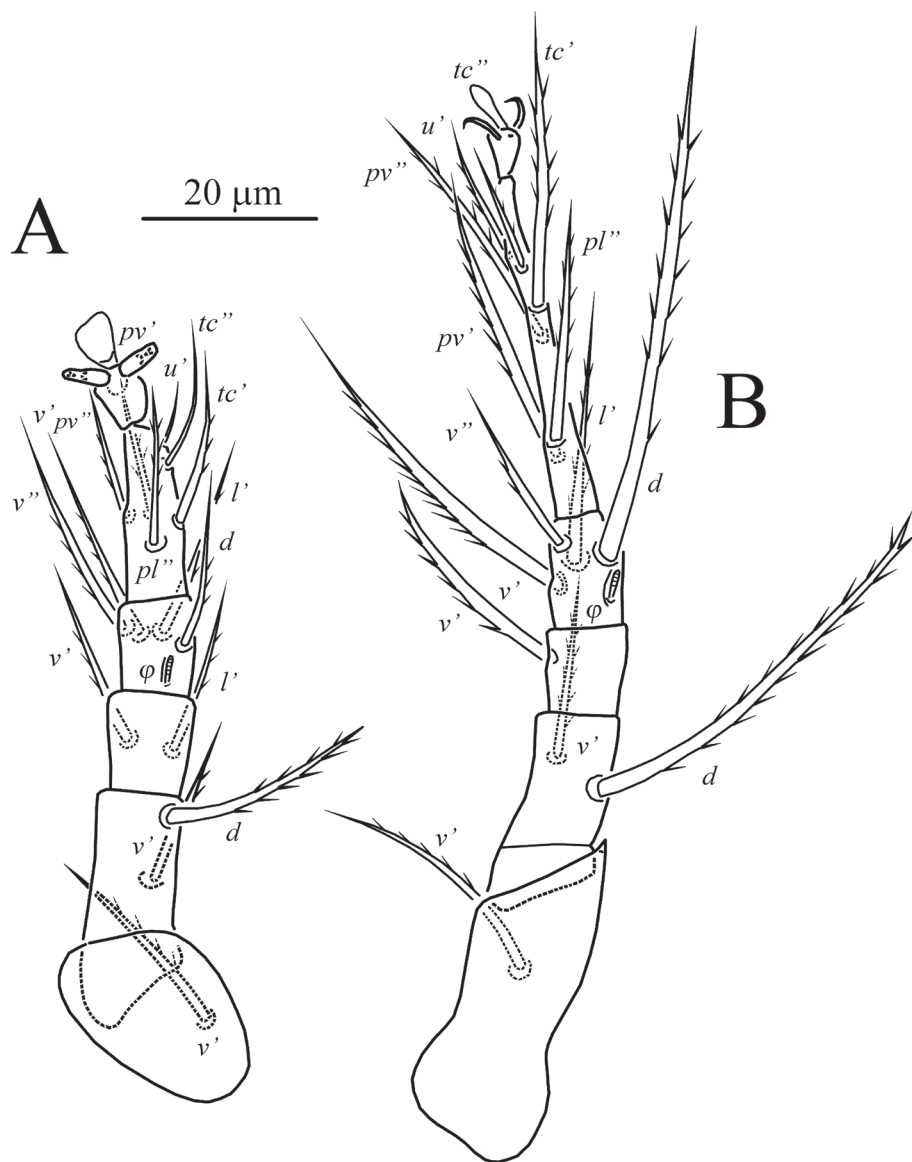


Figure 3. *Unguidispus polycatenus* (Sevastianov, 1969), female: **A** leg III **B** leg IV.

Unguidispus lasii Kurosa, 1979

Unguidispus lasii Kurosa, 1979, p. 66, figs 5–6.

Material examined. Six females, **RUSSIA:** Tyumen Province, vicinity of Tyumen, 57°04'03"N, 65°04'12"E, on ants *Lasius niger* L., 17 August 2014, coll. V.M.

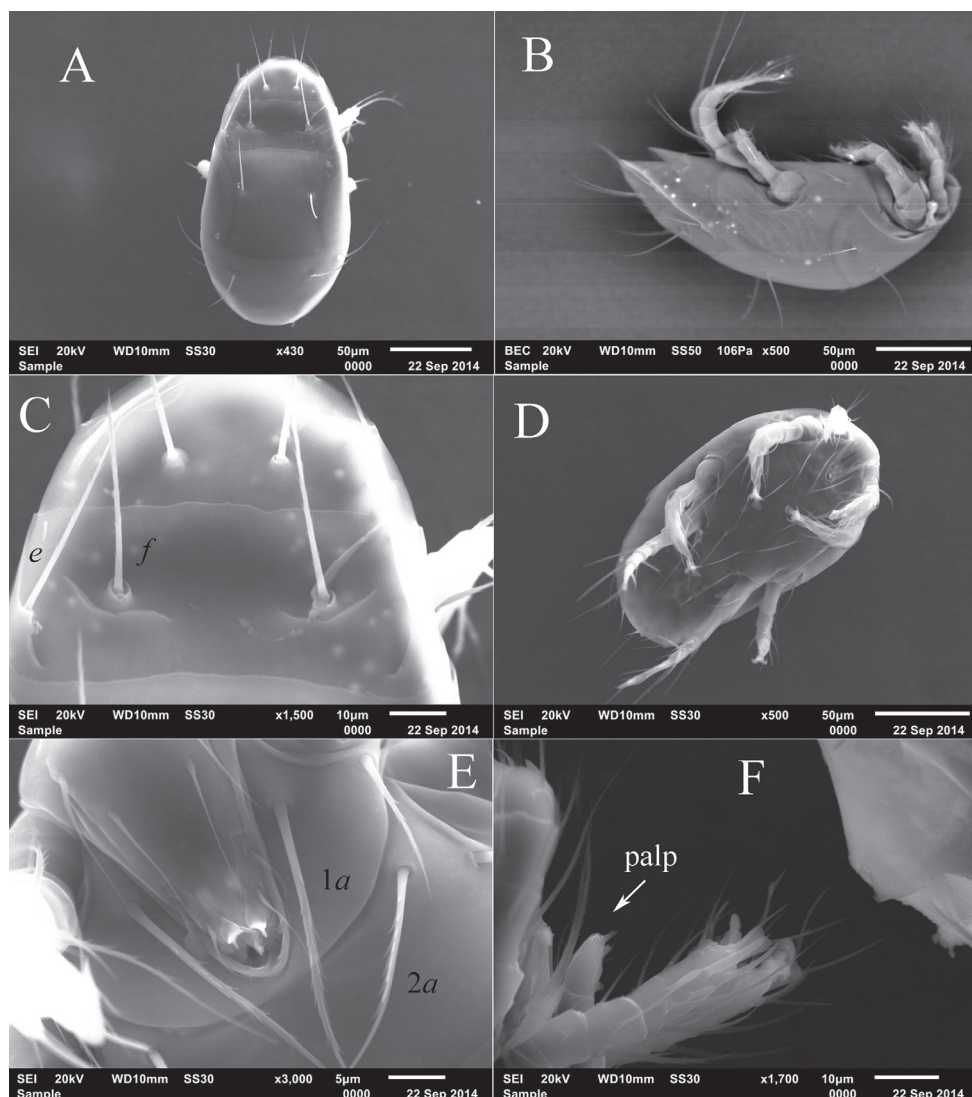


Figure 4. *Unguidispus polycetenus* (Sevastianov, 1969), female, SEM photos: **A** dorsum of the body **B** lateral view of the body **C** tergites EF and H **D** venter of the body **E** gnathosomal capsule **F** legs I and distal part of gnathosoma laterally.

Salavatulin; 5 females, Russia: Tyumen Province, vicinity of Tyumen, 57°09'55"N, 65°27'32"E, on ants *Lasius niger*, 31 August 2014, coll. A.A. Khaustov.

This species was described from Japan where it was found in the nests of ants *Lasius niger* and *L. hayashi* Yamauchi and Hayashida (Kurosa 1979). I recorded phoresy of this species on *Lasius niger* in Western Siberia. This is a new record for the fauna of Russia.

***Unguidispus japonicus* Kurosa, 1979**

Unguidispus japonicus Kurosa, 1979, p. 64, figs 1–2.

Material examined. Five females, **RUSSIA:** Tyumen Province, vicinity of Tyumen, 57°04'03"N, 65°04'12"E, on ants *Lasius niger*, 17 August 2014, coll. V.M. Salavatulin. 2 females, **RUSSIA:** Tyumen Province, vicinity of Tyumen, 57°09'55"N, 65°27'32"E, on ants *Lasius niger*, 31 August 2014, coll. A.A. Khaustov.

This species was described from Japan from the nests of ants *Lasius niger* (Kurosa 1979). I recorded phoresy of this species on *Lasius niger* in Western Siberia. This is a new record for the fauna of Russia.

Key to world species of the genus *Unguidispus* (females)

- 1 All dorsal hysterosomal setae unmodified.....2
- At least setae on tergites C and D flattened, widened distally, and heavily barbed3
- 2 Setae c_1 , d , and f thin and smooth, without arch-like ridges anteriorly to setae f***U. okumurai* Kurosa, 1979.** Japan. On *Lasius hayashi*
- All dorsal hysterosomal setae strongly barbed, with arch-like ridges anteriorly to setae f***U. polycetenus* (Sevastianov, 1969).** Ukraine, Austria, Hungary, Russia. On *Formica rufa*, *F. polycetena*
- 3 Setae h_1 flattened, widened distally and barbed4
- Setae h_1 thin, smooth, pointed***U. contematosus* Sevastianov, 1981.** Ukraine. On *Lasius fuliginosus*
- 4 Setae e distinctly thickened, subequal to or longer than f5
- Setae e not thickened, distinctly shorter than f***U. lasii* Kurosa, 1979.** Japan, Russia. On *Lasius niger*, *L. hayashi*
- 5 Setae h_2 pointed, setae d distinctly thicker than f ; trichobothria spherical.....***U. japonicas* Kurosa, 1979.** Japan, Russia. On *Lasius niger*
- Setae h_2 widened distally, setae d as thick as f , trichobothria pointed distally.....***U. stammeri* Mahunka, 1970.** Hungary. In ant nest.

Genus *Caesarodispus* Mahunka, 1977

Type species. *Caesarodispus gaius* Mahunka, 1977, by original designation.

Diagnosis. Female. Gnathosoma dorsally with two pairs of setae. Pharyngeal pumps 1 and 3 vestigial, pharyngeal pump 2 large, transversely striated. Prodorsum usually almost completely covered by tergite C. Cupules ia and ih small, usually round. Two pairs of pseudanal setae (ps_2 absent). Posterior margin of posterior sternal plate entire. Leg I distinctly shorter than leg II. Tibiotarsus without claw; pinnaculum

absent; setae *s* of tibiotarsus I present. Trochanter IV anterodorsally without spine-like process.

The genus *Caesarodispus* currently includes nine species distributed in the Holarctic region: *C. gaius*, *C. samsinaki* (Mahunka, 1967), comb. n., *C. minutus* (Sevastianov, 1981), *C. acuminatus* (Sevastianov, 1981), *C. klepzigii* Khaustov & Moser, 2008, *C. pusillus* Khaustov, 2009, *C. brevipes* Mahunka, 1986, *C. modestus* (Berlese, 1903), and *C. shandizensis* Loghmani & Hajiqaanbar, 2014. All species of the genus *Caesarodispus* phoretic on various ants, or inhabit their nests. Loghmani et al. (2014) discussed distribution and host specificity of the genus *Caesarodispus* and provided key to eight species.

***Caesarodispus samsinaki* (Mahunka, 1967), comb. n.**

Figs 5–7

Pygmephorus samsinaki Mahunka, 1967, p. 241, fig. 1.

Brennandania samsinaki: Mahunka 1972: 82.

Petalomium samsinaki: Sevastianov 1978: 37.

Redescription. Female. Length of idiosoma 220, width 135. *Gnathosoma* (Figs 5–6). Gnathosomal capsule about as long as its width. Dorsally with two pairs of smooth setae (*cha*, *chb*). Setae *cha* slightly longer than *chb*. Dorsal median apodeme absent. Ventral gnathosoma with one pair of subcapitular setae *m* and a pair of oval pits situated posteromedial to bases of *m*. Palps short, with setae *dFe* and *dGe* dorsolaterally. Setae *dGe* slightly longer than *dFe*. Ventrally with tiny solenidion and accessory setigenous structure. Palps terminated with a relatively short and thick tibial claw. Palpal tibiotarsus laterally with small triangular translucent process. Pharyngeal pumps 1 and 3 small, vestigial; pharyngeal pumps II large, transversely striated (Fig. 5A).

Idiosomal dorsum (Fig 5A). Tergite C covering only posterior part of prodorsum, which bears one pair of setae *sc*₂, one pair of spherical and weakly barbed trichobothria *sc*₁ and one pair of oval stigmata. Prodorsal shield with sparsely distributed small dimples. All hysterosomal tergites distinctly reticulated and with sparsely distributed small dimples. All dorsal setae lanceolate, sparsely barbed. Posterior margin of tergite C straight; posterior margin of tergite H with tongue-like elongation medially. Cupules *ia* on tergite D and *ih* on tergite H very small, round. Length of dorsal setae: *sc*₂ 32, *c*₁ 42, *c*₂ 44, *d* 58, *e* 47, *f* 50, *h*₁ 54, *h*₂ 46. Distances between setae: *sc*₂–*sc*₂ 43, *c*₁–*c*₁ 35, *c*₁–*c*₂ 24, *d*–*d* 31, *e*–*f* 25, *f*–*f* 30, *h*₁–*h*₁ 29, *h*₁–*h*₂ 19.

Idiosomal venter (Fig 5B). All ventral plates with small dimples. Posterior part of posterior sternal plate and aggenital plate reticulated. All ventral setae pointed and barbed. Ap1 well-developed and joined with appr; ap2 thin, arch-like, fused with appr; appr and apsej well developed; ap3 indistinct. Ap4 well sclerotized and long, apodemes 5 absent. Posterior margin of posterior sternal plate slightly convex in middle part. Posterior margin of aggenital plate rounded. Ags bell-like, pgs elongate, subtriangular.

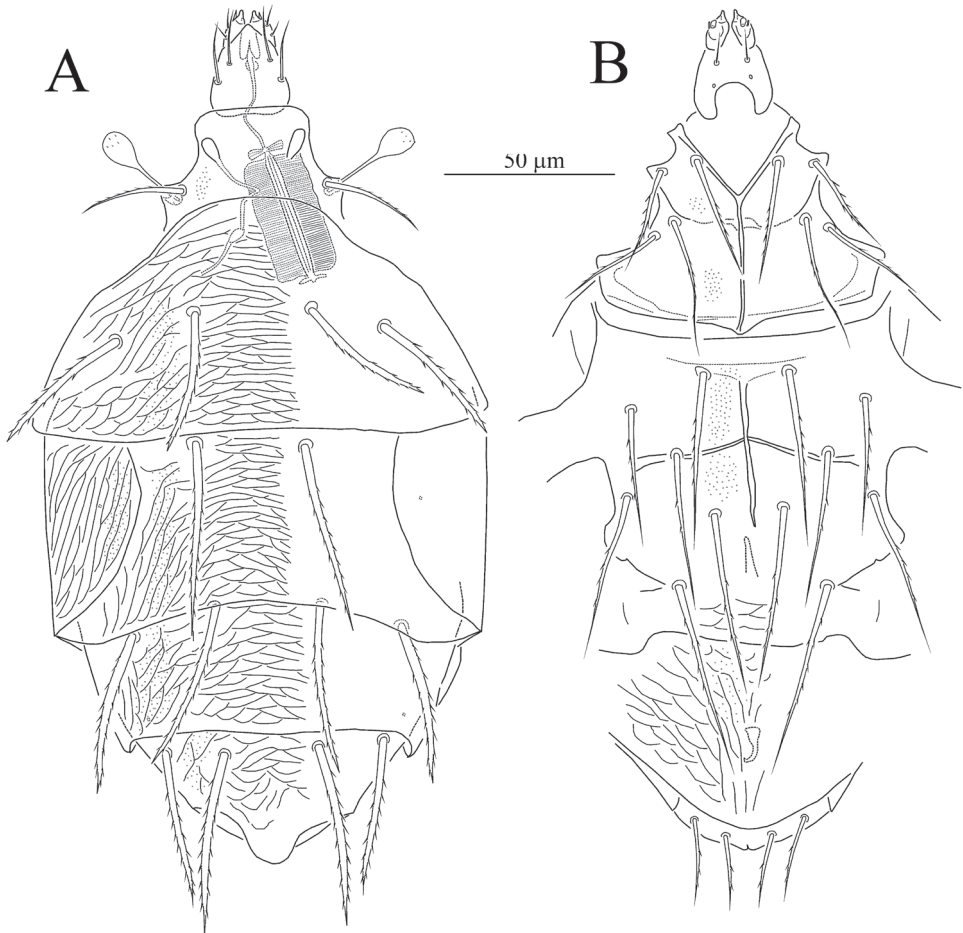


Figure 5. *Caesarodispus samsinaki* (Mahunka, 1967), comb. n., female: **A** dorsum of the body **B** venter of the body.

Length of ventral setae: $1a$ 35, $1b$ 32, $2a$ 42, $2b$ 39, $3a$ 52, $3b$ 47, $3c$ 40, $4a$ 54, $4b$ 60, $4c$ 47, ps_1 23, ps_3 24.

Legs (Figs 6–7). Leg I (Fig 6A) distinctly shorter and thinner than leg II. Setal formula: 1–3–4–16(3). Tibiotarsus not thickened, cylindrical. Length of solenidia ω_1 $11 > \varphi_1$ $5 < \varphi_2$ 10; ω_1 and φ_2 finger-shaped, φ_1 clavate, solenidium ω_2 absent. Seta k very long, slightly longer than combined genu and tibiotarsus I. Leg II (Fig 6B). Setal formula: 1–2–3–4(1)–6(1). Tarsus with sickle-like, padded claws and large empodium. Solenidium ω 8, finger-shaped, solenidium φ 4 weakly clavate. Setae v'' of femur II absent. Leg III (Fig 7A). Setal formula: 1–2–2–4(1)–6. Claws of same shape as on tarsus II. Solenidium φ 4 weakly clavate. Seta dFe blunt-ended. Leg IV (Fig 7B). Setal formula: 1–2–1–4(1)–6. Tarsus long and thin, pretarsus short, with two small simple claws and small empodium. Solenidium φ 4, weakly clavate. Seta dFe distinctly blunt-ended.

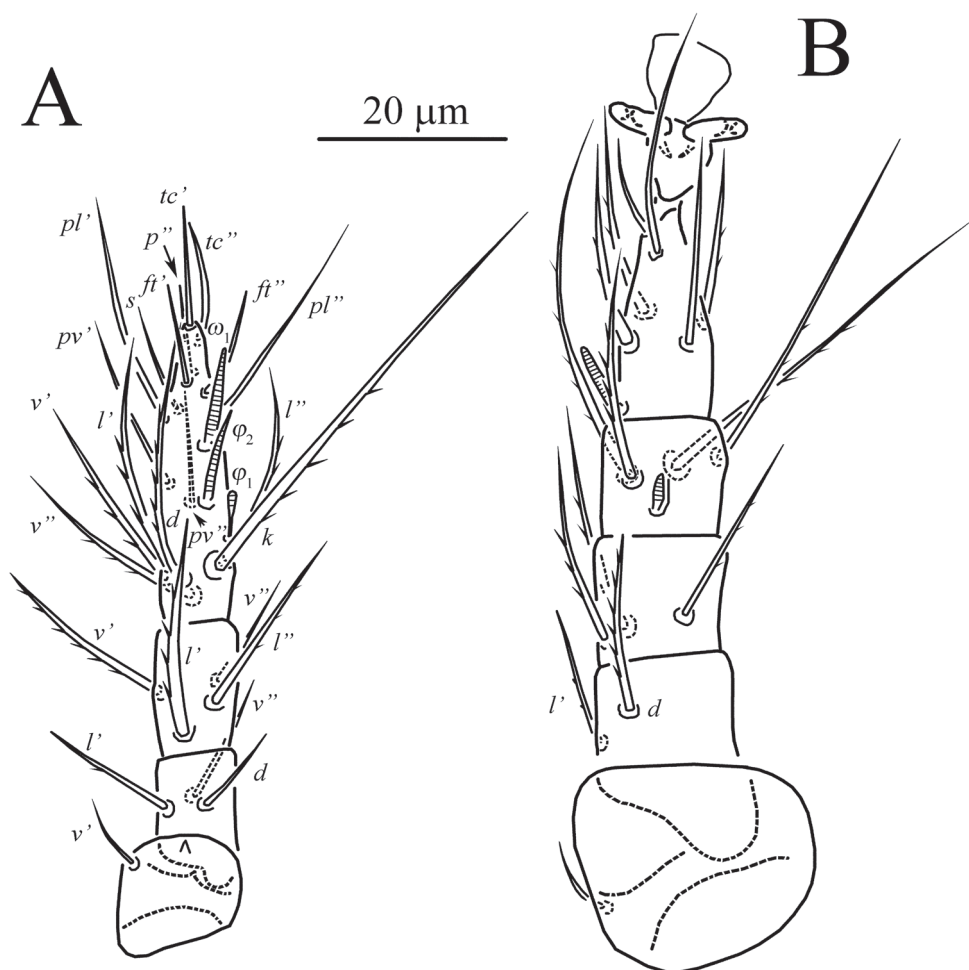


Figure 6. *Caesarodispus samsinaki* (Mahunka, 1967), comb. n., female: **A** leg I **B** leg II.

Male and larva unknown.

Material examined. One female, **RUSSIA:** Tyumen Province, vicinity of Tyumen, 57°04'03"N, 65°04'12"E, on ants *Formica rufa* L., 17 August 2014, coll. A.A. Khaustov.

Distribution and hosts. This species was originally described from the Czech Republic (Mahunka 1967) where it was collected from ants *Formica rufa*. It was also recorded from Ukraine and Belarus (Sevastianov 1978). This is a new record for the fauna of Russia.

Remarks. Mahunka (1967) described this species in the genus *Pygmephorus* Kramer (Pygmephoridae). Later on, he replaced it to the genus *Brennandania* Sasa, 1961 (Microdispidae) (Mahunka 1972). Sevastianov (1978) placed this species in the genus *Petalomium* Cross, 1965 (Neopygmephoridae).

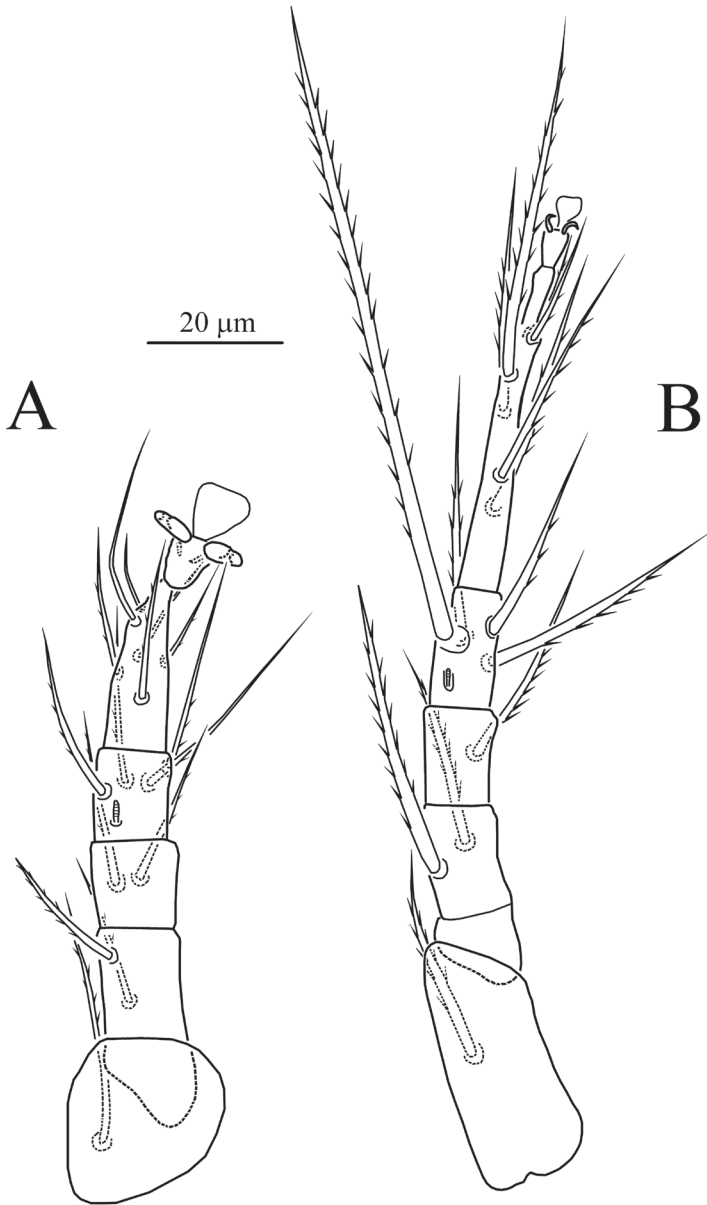


Figure 7. *Caesarodispus samsinaki* (Mahunka, 1967), comb. n., female: **A** leg III **B** leg IV.

According to key to families of the superfamily Pygmephoroidae provided by Khaustov and Ermilov (2011) this species undoubtedly belongs to the family Microdispidae by having three setae on femur I, unmodified seta *dFeI* and presence of only one pair of setae on prodorsum. I placed this species in the genus *Caesarodispus* based on the following combination of characters: 1) tibiotarsus I without claw, 2) leg I distinctly shorter and thinner than leg II, 3) seta *s* of tibiotarsus I present, 4) pharyngeal

pumps 1 and 3 vestigial, pharyngeal pump 2 large, distinctly transversely striated, 5) posterior margin of posterior sternal plate entire. All of these characters well agree with diagnosis of the genus *Caesarodispus*.

Unlike other known species of the genus *Caesarodispus*, *C. samsinaki* has only two setae on femur II (*v*" absent) and only three solenidia on tibiotarsus I (ω_2 absent). However reduction of leg chaetotaxy was also recorded in *C. klepzigii* Khaustov and Moser, 2008, which has only two setae on femur I, while other *Caesarodispus* species have three setae.

The original description of *C. samsinaki* of Mahunka (1967) is incomplete, thus I made a redescription of this species. The present redescription of *C. samsinaki* is based on material from Western Siberia. The specimens from Western Siberia are well agreed with original description of *C. samsinaki*, especially having lanceolate dorsal idiosomal setae and unique reticulated hysterosomal tergites, and undoubtedly conspecific with it.

***Caesarodispus minutus* (Sevastianov, 1981)**

Microdispus minutus Sevastianov, 1981, p. 28, fig. 5.

Caesarodispus minutus: Khaustov 2008: 390.

Material examined. Eleven females, Russia: Tyumen Province, Tyumen region, vicinity of settlement Narimanovo, 57°21'56"N, 65°08'21"E, in the nest of ants *Lasius flavus* (Fabricius), 30 July 2014, coll. V.A. Stolbov.

This species was described from Ukraine from ants *Tetramorium caespitum* L. (Sevastianov 1981). Khaustov (2009) redescribed it based on type material. It was also recorded from Iran from *Temnothorax* sp. (Loghmani et al 2014). This is a new record for the fauna of Russia.

Key to world species of the genus *Caesarodispus* (females)

- 1 Hysterosomal tergites not reticulated, femur II with three setae.....2
- Hysterosomal tergites distinctly reticulated, femur II with two setae (*v*" absent).....***C. samsinaki* (Mahunka, 1967), comb. n.** Czech Republic, Ukraine, Belarus, Russia. On *Formica rufa*.
- 2 Seta *v*' of genu I not thickened, pointed.....3
- Seta *v*' of genu I distinctly thickened, widened distally, strongly barbed.....
....***C. pusillus* Khaustov, 2009.** Crimea. In the nest of *Crematogaster schmidtii*
- 3 Seta *d* no more than 1.5 times longer than *f*.....4
- Seta *d* about 4 times longer than *f*.....
.....***C. klepzigii* Khaustov & Moser, 2008.** U.S.A. On *Solenopsis invicta*
- 4 Seta *d* of tibia IV heavily barbed, reaching beyond tip of pretarsus IV.....5
- Seta *d* of tibia IV smooth or weakly barbed, not reaching beyond tip of pretarsus IV7

- 5 Seta *d* of femur IV subequal to or longer than *tc*” of tarsus IV **6**
 – Seta *d* of femur IV more than 2 times shorter than *tc*” of tarsus IV
 ***C. gaius* Mahunka, 1977**. France. On *Myrmica sabuleti*
 6 Setae *d* and *f* lanceolate and strongly barbed
 ***C. brevipes* Mahunka, 1986**. Hungary. In ant nest
 – Setae *d* and *f* not lanceolate, weakly barbed.....
 ***C. modestus* (Berlese, 1903)**. Italy, Russia (Crimea). On *Messor* spp.
 7 Posterior part of aggenital plate smooth **8**
 – Posterior part of aggenital plate distinctly reticulated
 ***C. shandizensis* Loghmani & Hajiqanbar, 2014**. Iran. On *Temnothorax* sp.
 8 Setae *f* distinctly longer than distance *f–f*..... ***C. minutus* (Sevastianov, 1981)**.
 Ukraine, Iran, Russia. On *Tetramorium caespitum*, *Lasius flavus*, *Temnothorax* sp.
 – Setae *f* shorter than distance *f–f*.....
 ***C. acuminatus* (Sevastianov, 1981)**. Ukraine. On *Tetramorium caespitum*

Acknowledgements

The author thanks Dr. A.V. Tolstikov for valuable comments on the manuscript, Dr. V.A. Stolbov, S.A. Ivanov and V.M. Salavatulin for their help with collecting mites, D.V. Zhuravskiy (Tyumen State University, Russia) for help with SEM micrographs. This research was supported by the Ministry of Education and Science of the Russian Federation, project title “Myrmecophilous Acariform Mites (Acariformes) of the South of Western Siberia”, cooperative agreement No. 6.1933.2014/K.

References

- Berlese A (1903) Diagnosi di alcune nuove specie di Acari italiani, mirmecofili e liberi. Zoologischer Anzeiger 27: 12–28.
- Cross EA (1965) The generic relationships of the family Pyemotidae (Acarina: Trombidiformes). The University of Kansas science bulletin 45: 29–275.
- Grandjean F (1944) Observations sur les Acariens de la famille des Stigmaeidae. Archives des Sciences Physiques et Naturelles 5, 26: 103–131.
- Grandjean F (1947) L’origine pileuse des mors et la chaetotaxie de la mandibule chez les Acariens actinochitineux. Comptes rendus des séances de l’Académie des Sciences 224: 1251–1254.
- Hajiqanbar H, Hosseini-naveh F (2014) A new genus and species of the family Microdispidae (Acari: Prostigmata) associated with *Oryctes nasicornis* (Coleoptera: Scarabaeidae) and re-description of the monotypic genus *Vietodispus* Mahunka, 1975. Zoological Studies 53: 58–70. doi: 10.1186/s40555-014-0058-7
- Kaliszewski M, Athias-Binche F, Lindquist EE (1995) Parasitism and parasitoidism in Tarsonemina (Acari: Heterostigmata) and evolutionary considerations. Advances in Parasitology 35: 335–367. doi: 10.1016/S0065-308X(08)60074-3

- Khaustov AA (2004) Mites of the family Neopygmephoridae Cross, 1965 stat. n. and their position in Heterostigmata. In: Balashov YS (Ed.) VIII Russian Acarological Conference, St.-Petersburg. Zoological Institute of RAS, St.-Petersburg, 137. [in Russian]
- Khaustov AA (2008) Mites of the family Scutacaridae of Eastern Palaearctic. Akademperiodyka, Kiev, 291 pp.
- Khaustov AA (2009) New and little known species of mites of the genus *Caesarodispus* (Acari, Heterostigmata, Microdispidae) associated with ants (Hymenoptera, Formicidae) from Ukraine. Vestnik Zoologii 43: 387–393. <http://www.degruyter.com/view/j/vzoo.2009.43.issue-5/v10058-009-0017-7/v10058-009-0017-7.xml>
- Khaustov AA, Ermilov SG (2011) A new species of the genus *Siteroptes* (Acari: Heterostigmata: Pygmephoridae) from European Russia. Entomological Review 91(4): 528–532. doi: 10.1134/S0013873811040178
- Khaustov AA, Moser JC (2008) Two new species of mites of the genera *Petalomium* Cross and *Caesarodispus* Mahunka (Acari: Heterostigmata: Neopygmephoridae, Microdispidae) associated with *Solenopsis invicta* Buren (Hymenoptera: Formicidae) from the U.S.A. International Journal of Acarology 34: 115–121. doi: 10.1080/01647950808683714
- Kurosa K (1979) Three new species of *Unguidispus* (Acari, Heterostigmata, Microdispidae) from Japan. Annotationes Zoologicae Japonenses 521: 63–71.
- Lindquist EE (1986) The world genera of Tarsonemidae (Acari: Heterostigmata): a morphological, phylogenetic, and systematic revision, with a reclassification of family-group taxa in Heterostigmata. Memoirs of the Entomol. Society of Canada 136: 1–517. doi: 10.4039/entm118136fv
- Loghmani A, Hajiqanbar H, Talebi AA (2014) New species and new record of the genus *Caesarodispus* (Acari: Heterostigmata: Microdispidae) phoretic on *Temnothorax* sp. (Hymenoptera: Formicidae). Annales Zoologici 64(2): 273–278. doi: 10.3161/000345414X680627
- Mahunka S (1967) Beiträge zur Kenntnis der Tschechoslowakischen Tarsonemini-Fauna. Věstník Československé společnosti zoologické 31: 240–244.
- Mahunka S (1968) *Xystrostrum* gen. n. und eine neue *Siteroptes*-art aus Ungarn (Acari). Reichenbachia 10: 127–131.
- Mahunka S (1970a) Considerations on the systematic of the Tarsonemina and the description of new European taxa (Acari: Trombidiformes). Acta Zoologica Hungarica 16: 137–174.
- Mahunka S (1970b) Beiträge zur Kenntnis der Milbenfauna der Ötztaler Alpen. 1. Tarsoneminen-Arten aus der Umgebung von Oberurgl. Opuscula Zoologica (Budapest) 10: 271–289.
- Mahunka S (1972) Tetűtátek - Tarsonemina (Magyarország állatvilága – Fauna Hungariae 110.) – XVIII. kötet, 16. füzet (Arachnoidea). Akadémiai Kiado, Budapest, 215 pp.
- Mahunka S (1977a) Neue und interessante Milben aus dem Genfer Museum XIX. Einige Angaben zur Kenntnis der Milbenfauna der Ameisen-Nester (Acari: Acarida, Tarsonemida). Archives des Sciences Geneve 30: 91–106.
- Mahunka S (1977b) The examination of myrmecophilous tarsonemid mites based on the investigations of Dr. C. W. Rettenmeyer (Acari). Acta Zoologica Academiae Scientiarum Hungaricae 23: 99–132.
- Mahunka S (1987) Tarsonemids of the Kiskunság National park (Acari). In: Mahunka S (Ed.) The fauna of the Kiskunság National park, 1. Akadémiai Kiado, Budapest, 435–455.

- Sasa M (1961) New mites of the genus *Pygmephorus* from small mammals in Japan (Acarina: Pyemotidae). Japanese Journal of Experimental Medicine 31: 191–208.
- Sevastianov VD (1969) New genus and species of mites of the Pyemotidae (Trombidiformes) family and their position in the family. Vestnik Zoologii 3: 66–71. [in Russian]
- Sevastianov VD (1978) Tarsonemina. In: Ghilarov MS (Ed.) Opredelitel pochvoobitayushchikh kleshchey. Trombidiformes, Nauka, Moscow, 14–90. [in Russian]
- Sevastianov VD (1981) New species of mites of the family Pygmephoridae (Tarsonemina, Trombidiformes). Vestnik Zoologii 6: 25–29. [in Russian]

The Australian millipede *Dicranogonus pix* Jeekel, 1982 (Diplopoda, Polydesmida, Paradoxosomatidae): a species with and without paranota

Robert Mesibov¹

¹ Queen Victoria Museum and Art Gallery, 2 Invermay Road, Launceston, Tasmania, Australia 7248

Corresponding author: Robert Mesibov (mesibov@southcom.com.au)

Academic editor: Pavel Stoev | Received 20 September 2014 | Accepted 13 October 2014 | Published 12 November 2014

<http://zoobank.org/2CB669B1-1979-4E48-9C4E-41188F126478>

Citation: Mesibov R (2014) The Australian millipede *Dicranogonus pix* Jeekel, 1982 (Diplopoda, Polydesmida, Paradoxosomatidae): a species with and without paranota. ZooKeys 454: 29–39. doi: 10.3897/zookeys.454.8625

Abstract

Dicranogonus pix Jeekel, 1982 occurs in Victoria and Tasmania, Australia, including the islands in eastern Bass Strait between the two States. There is only slight gonopod variation across this range, but *D. pix* populations with and without paranota are separated in Bass Strait by the ca 50 km-wide gap between the Kent and Furneaux Groups of islands.

Keywords

Millipede, Diplopoda, Polydesmida, Paradoxosomatidae, Tasmania, Victoria, Bass Strait, Australia, biogeography

Introduction

Dicranogonus was erected by Jeekel (1982) for *D. pix* Jeekel, 1982, a small, dark paradoxosomatid with a simply forked gonopod. The new species had been collected two years earlier at three localities in eastern Victoria by the visiting Dutch specialist Dr C.A.W. Jeekel and his wife, A.M. Jeekel-Rijvers (Jeekel 1981).

Somewhat cryptically, Jeekel (1982: 209) wrote “The genus *Dicranogonus* has a second, as yet undescribed, species on the islands of the Furneaux group between Victoria and northeastern Tasmania”. Jeekel did not travel to the Furneaux Group

during his time in Australia, and prior to his death in 2010, Jeekel did not publish any hints regarding where he had seen specimens of a second *Dicranogonus* species, or how it differed from *D. pix*.

In 1984, Jeekel proposed that Victoria had been a centre of dispersal for *Dicranogonus*, *Pogonosternum* Jeekel, 1965 and *Somethus* Chamberlin, 1920 (Jeekel 1984: 44). At the time, Jeekel was evidently unaware of the occurrence of *Dicranogonus* on the Tasmanian mainland, writing “The distribution of *Dicranogonus* seems to indicate that migration from Victoria southward towards Tasmania along a north-eastern route was blocked south of the Furneaux Group” (Jeekel 1984: 44).

In a later publication, however, Jeekel mentioned that *Dicranogonus* also occurs in Tasmania (Jeekel 2006: 82). I am not certain whether he was referring to the Furneaux Group, which is politically part of Tasmania, or to the northeast Tasmanian mainland, from which I had earlier reported the presence of *Dicranogonus* (Mesibov and Churchill 2003).

As shown below, *Dicranogonus* occurs in two strikingly different forms: one in Victoria and northeast Bass Strait with obvious paranota, and one without paranota in southeast Bass Strait (in the Furneaux Group) and on the northeast Tasmanian mainland. In this paper I treat both forms as *D. pix*, and in the Discussion section I explain the reasons for this taxonomic decision.

Methods

All specimens I examined are in registered specimen lots in Australian repositories and are listed in the accompanying data table. Latitude/longitude figures in the table are given with the WGS84 datum together with my estimate of the spatial uncertainty (Darwin Core CoordinateUncertaintyInMeters).

Colour photomicrographs of specimens in 80% ethanol were taken with a Canon EOS 1000D digital SLR camera mounted on a Nikon SMZ800 binocular dissecting microscope equipped with a beam splitter. Colour images used in the figures are focus-stacked composites prepared with Zerene Stacker 1.04 software. Grayscale images of gonopod telopodites temporarily mounted in 1:1 glycerol:water were captured as screenshots from the output of a 1.3 megapixel digital video eyepiece camera mounted in one ocular tube of a Tasco LMSMB binocular microscope. The screenshots were edited with GIMP 2.8 software to remove background highlights and artefacts. Measurements were made in all cases to the nearest 0.1 mm with eyepiece grids and reference scales. The SEM images in Fig. 5 are of an isolated body ring which was air-dried and sputter-coated with gold before examination and image capture with an FEI Quanta 600 ESEM operated in high vacuum mode. (Another version of Fig. 5B appeared as Fig. 2B in Mesibov (2009), where the specimen was identified as “*Dicranogonus* sp.”.) Base maps were generated with ArcView 3.2 GIS software.

Abbreviations below and in the accompanying data table: AM = Australian Museum, Sydney, New South Wales, Australia; DPIPW = New Town Laboratories,

Department of Primary Industries, Parks, Water and Environment, New Town, Tasmania, Australia; NBC = Naturalis Biodiversity Center, Leiden, Netherlands; NMV = Museum Victoria, Melbourne, Victoria, Australia; NSW = New South Wales, Australia; QVM = Queen Victoria Museum and Art Gallery, Launceston, Tasmania, Australia; Tas = Tasmania, Australia; TMAG = Tasmanian Museum and Art Gallery, Hobart, Tas; Vic = Victoria, Australia.

Results

Order Polydesmida Pocock, 1887

Suborder Strongylosomatidea Brölemann, 1916

Family Paradoxosomatidae Daday, 1889

Subfamily Australiosomatinae Brölemann, 1916

Tribe Antichiropodini Brölemann, 1916

***Dicranogonus* Jeekel, 1982**

Dicranogonus: Jeekel 1982: 208; 2006: 82. Shelley et al. 2000: 97. Nguyen and Sierwald 2013: 1155.

Type species. *Dicranogonus pix* Jeekel, 1982, by original designation.

***Dicranogonus pix* Jeekel, 1982**

Figs 1–5

Dicranogonus pix Jeekel 1982: 209; Fig. 4 (p. 206). Shelley et al. 2000: 97. Mesibov 2004: 42; 2009: Fig. 2B (p. 534). Nguyen and Sierwald 2013: 1155.

Morphology. *Gonopods.* The gonopod telopodite varies only slightly in details over the *D. pix* range (Figs 1–3). There are two small tabs (Jeekel: “lappets”) on either side of the solenomere tip in the holotype, and one or both tabs (more often the basally directed one) are reduced or missing in some populations (Fig. 2). The most divergent male examined is from the northeast corner of Flinders Island in the Furneaux Group (Fig. 2C); the tip of the solenomere in this specimen is abruptly curved basally and the subapical process of the telopodite (Jeekel: “tibiotarsus”) is thinner and closer to the solenomere than in most males.

Paranota. In agreement with the original description of *D. pix*, the diplosegments of a nearly topotypical male have obvious paranota (Figs 3, 4A, 4B). Similarly well-defined paranota are present on almost all *Dicranogonus* specimens from eastern Victoria and small islands in the northeast portion of Bass Strait. In contrast, all specimens from islands in the southeast portion of Bass Strait (i.e., the Furneaux Group) and the Tasmanian mainland lack paranota (Figs 3, 4C, 4D), although the paranotal area on

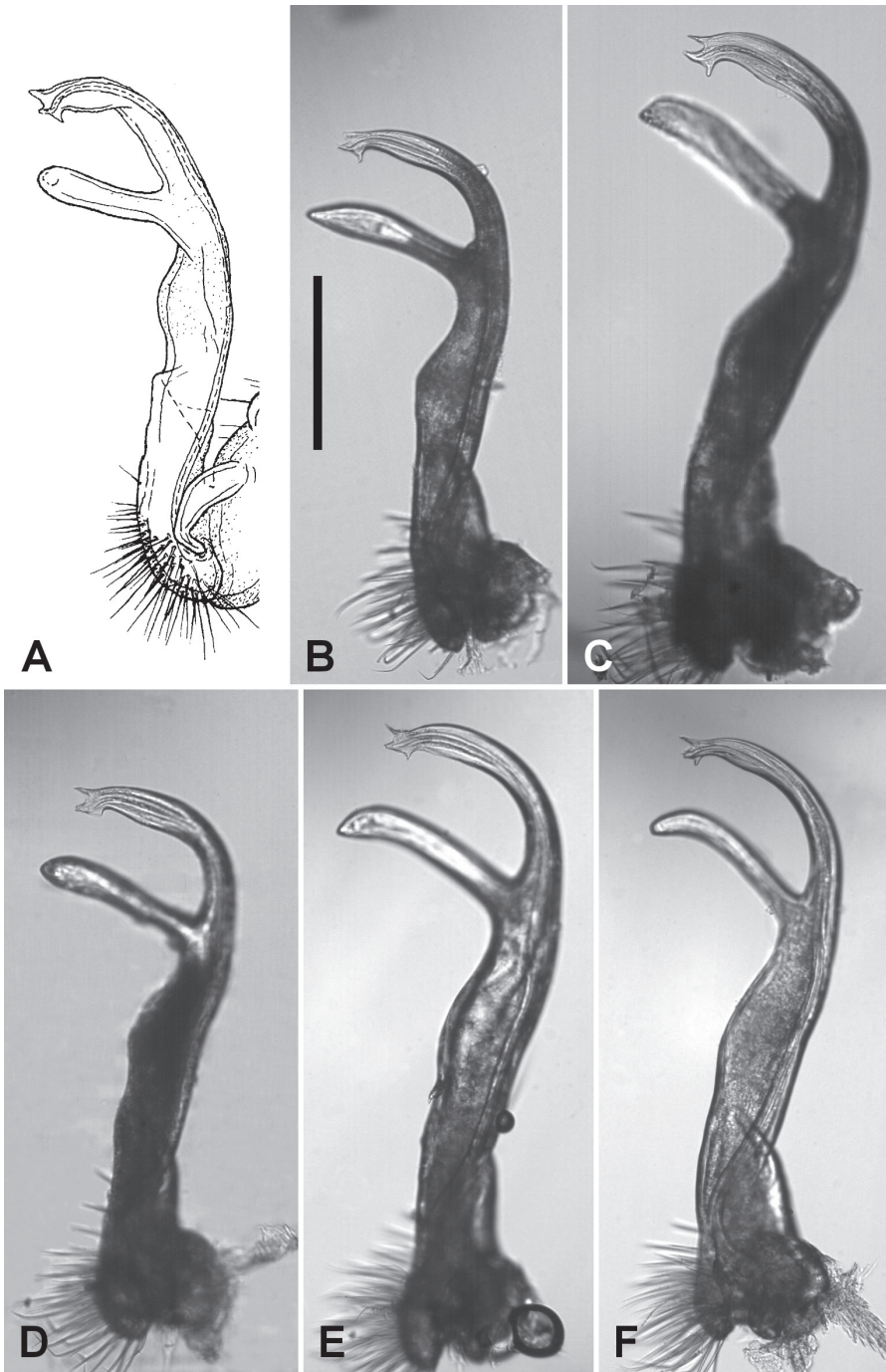


Figure 1. *Dicranogonus pix* Jeekel, 1982, right gonopod telopodite, anterior views. **A** Holotype, from Fig. 4 in Jeekel (1982), used with permission **B** NMV K-10010 **C** AM KS.105124 **D** AM KS.94201 **E** QVM 23:46456 **F** QVM 23:21876. Scale bar for **B–F** = 0.25 mm, with focus on solenomere tip. See Fig. 3A for mapped localities.

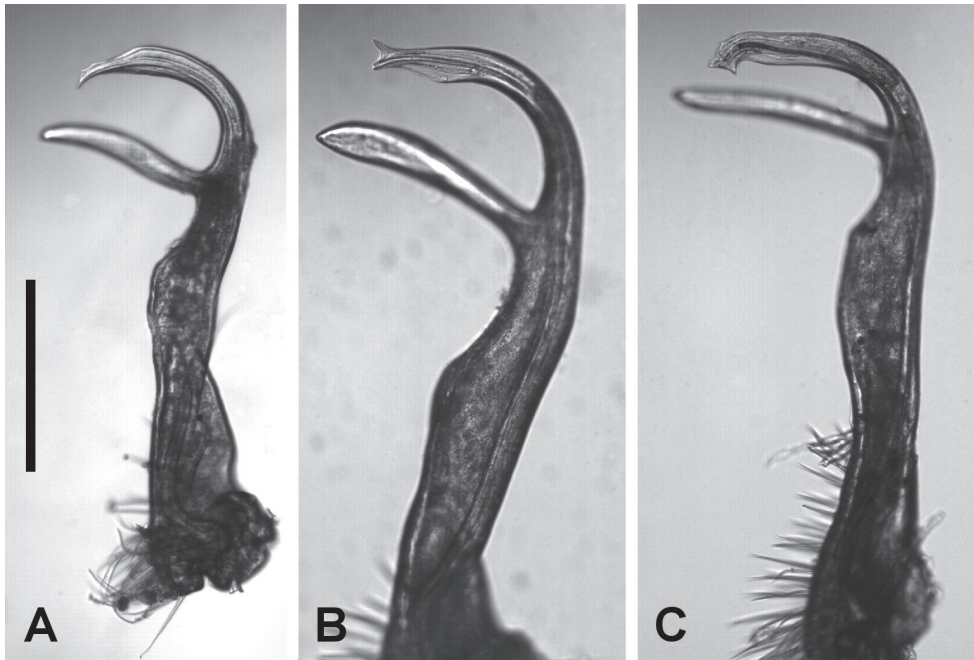


Figure 2. *Dicranogonus pix* Jeekel, 1982, right gonopod telopodite, anterior views. **A** NMV K-10011 **B** TMAG J3286 **C** QVM 23:40085. Scale bar for **A–C** = 0.25 mm, with focus on solenomere tip. See Fig. 3A for mapped localities.

diplosegments is usually marked by lighter colour, and on some rings there is a very slight lateral bulge at the level of the ozopore.

The only exceptions to this simple geographical pattern in the material examined are three males and two females lacking paranota from the Buchan district in eastern Victoria, collected in 1907 (Figs 3, 4E, 4F).

Other characters. I add here only a few minor details to the very clearly written, 1600-word description by Jeekel (1982) of the typical *D. pix*. Spiracles on diplosegments located just above and anterior to leg bases (Fig. 5A); anterior spiracle (Fig. 5B) ovoid with long axis nearly vertical, anterodorsal portion of rim extended as thin cowl and directed slightly posteriorly; posterior spiracle nearly round, rim slightly raised and rounded; anterior and posterior spiracular filters composed of numerous thin, forked tabs with blunt tips (Fig. 5B), the dorsal half of the filter produced in the posterior spiracle and emergent in the anterior spiracle. Paranota on diplosegments well-defined to ring 16, then progressively diminishing to a very slight lateral bulge on ring 19. Spinnerets in square array.

Biogeography. *D. pix* and *Notodesmus scotius* Chamberlin, 1920 are the only Polydesmida so far known to occur naturally on both sides of Bass Strait (see *N. scotius* distribution records and KML file at <http://www.polydesmida.info/millipedesofaustralia/localities.html>). The *N. scotius* material I have examined is uniform throughout the species' range in Tasmania, Victoria and southeast New South Wales, and I have not detected any morphological discontinuity in *N. scotius* in Bass Strait.

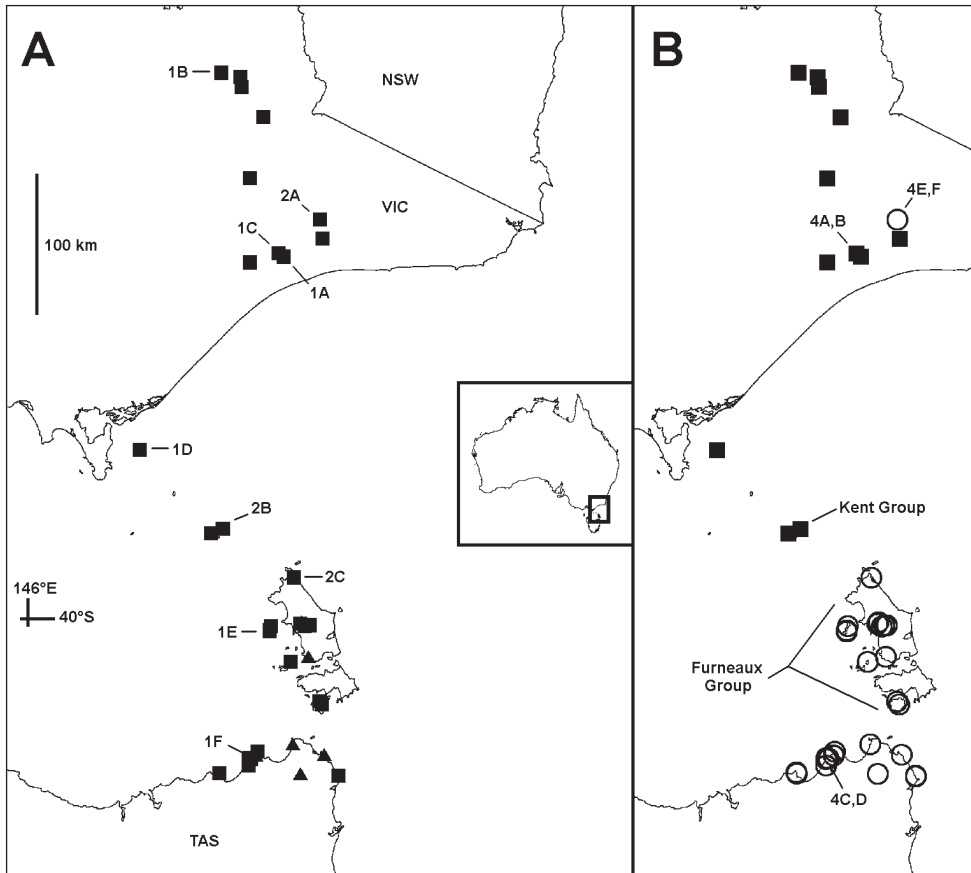


Figure 3. *Dicranogonus pix* Jeekel, 1982, known localities as of 17 September 2014. **A** Localities with males (squares) and with females only (triangles); labels indicate localities of males with gonopods imaged in Figs 1 and 2; **B** Specimens with paranota (filled squares) and without paranota (unfilled circles); labels indicate localities of specimens with midbody rings imaged in Fig. 4. Mercator projection. Inset shows Australia with map area of **A** (rectangle).

For other poorly vagile animals with trans-Bass Strait distributions, I have not yet found any documentation of discontinuities congruent with the paranota/no-paranota divide in *D. pix* between the Kent and Furneaux Groups. A possible evolutionary parallel is in the raphidophorid cricket genus *Cavernotettix* Richards, 1966. *C. flindersensis* (Chopard, 1944) is known only from the Furneaux Group, and *C. craggiensis* Richards, 1974 is known only from Craggy Island (ca 40 ha), located between the Kent and Furneaux Groups. (*Cavernotettix* records from the online *Atlas of Living Australia*, <http://www.ala.org.au>, accessed 17 September 2014.)

Within Victoria the known distribution of *D. pix* is a zone ca 150 km long and up to 60 km wide, running north from East Gippsland over the Great Dividing Range, from near sea level to ca 600 m. On the Tasmanian mainland all but one of the locality records are less than ca 2 km from the sea, the exception being a 1964 collection from

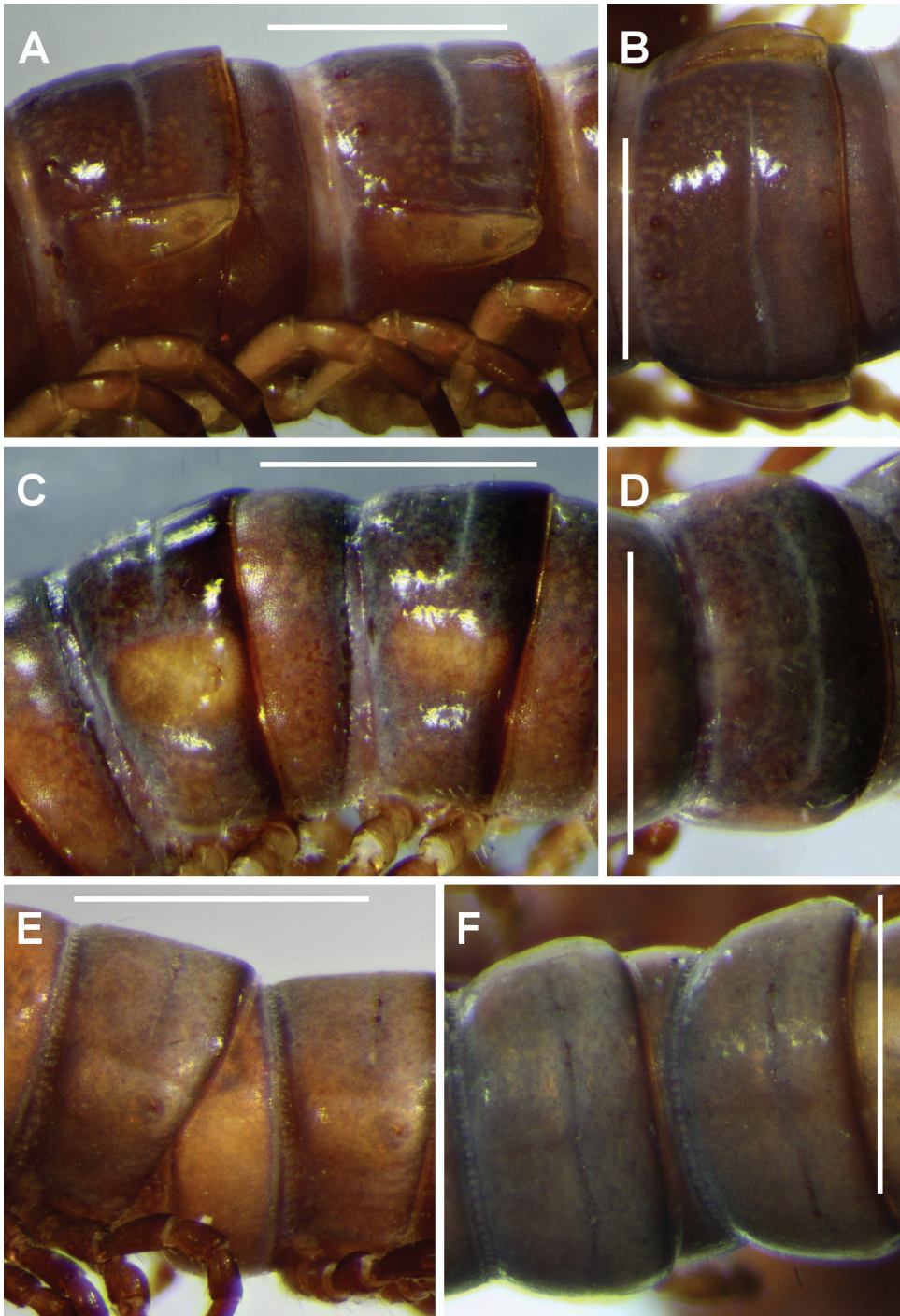


Figure 4. *Dicranogonus pix* Jeekel, 1982, males; **A, C, E** left lateral views of midbody rings **B, D, F** dorsal views of midbody rings. **A, B** AM KS.105124 **C, D** QVM 23:21875 **E, F** NMV K-10011. Scale bars = 1.0 mm. See Fig. 3B for mapped localities.

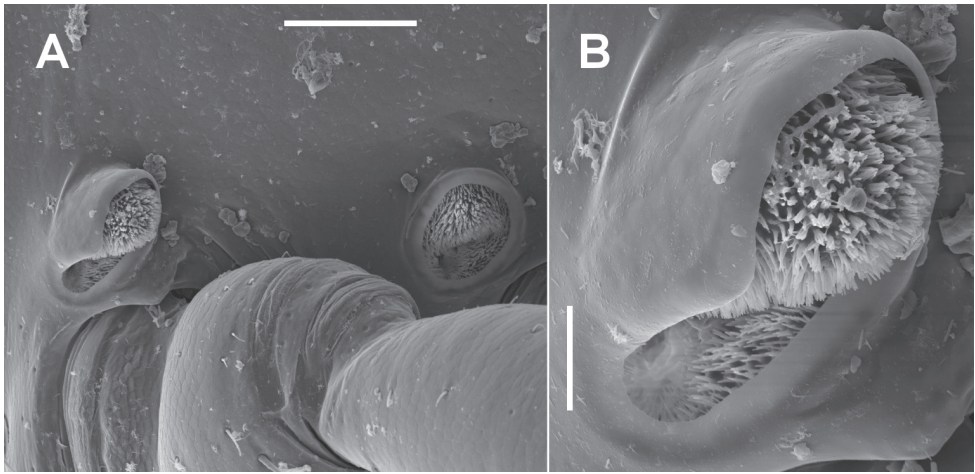


Figure 5. *Dicranogonus pix* Jeekel, 1982, male ex QVM 23:15170. **A** Left lateral view of midbody spiracles **B** Anterior spiracle. Scale bars: **A** = 0.1 mm, **B** = 0.025 mm.

Gladstone, a small town. “Gladstone”, however, may only represent the nearest named place to a coastal collecting site on Ringarooma Bay, ca 15 km distant. I have collected *N. scotius*, but not yet *D. pix*, in the dry eucalypt forests beginning ca 10 km inland from *D. pix* localities along the northeast Tasmanian coast.

Ecology. Jeekel (1982: 212) wrote of *D. pix* at the holotype and paratype localities in Victoria: “This elegant little creature was locally quite common, occurring numerously in the upper litter layer of the dry Eucalyptus forests, and, judging from the number of specimens seen, mass appearances may occasionally happen”. Adults have so far been collected in every month of the year except May, and in August 1998 I found a mixed *N. scotius*–*D. pix* ‘mating swarm’ during the day in coastal heathland near Blackmans Lagoon in northeast Tasmania.

Surprisingly, *D. pix* was missing from pitfall samples collected in coastal heathland within the *D. pix* range in northeast Tasmania in 1986–88. The sampling was carried out by T.B. Churchill, who trapped paradoxosomatids (as by-catch) in three 9 × 9 m pitfall arrays (nine evenly spaced traps per array) located at each of four 90 × 90 m sampling sites, with the traps emptied once a month for 14 months (Mesibov and Churchill 2003). The traps yielded 9754 specimens of *N. scotius* and 116 specimens of an undescribed *Pogonosternum* species.

Type specimens. Jeekel (1982: 209) lists the following type specimens for *D. pix*, all collected on 14 November 1980 by Dr Jeekel and A.M. Jeekel-Rijvers:

Holotype male: “Sta. 86. 4 km ESE Bruthen... Eucalyptus forest, State forest, under logs” [My location estimate for the type locality near Bruthen, Vic is 37°43'18"S 147°52'24"E ±1 km, probably along the Bruthen-Buchan Road.]

Paratypes: 3 males, 6 females, details as for holotype; 38 males, 29 females, “Sta. 85. 13 km SE Buchan... Eucalyptus forest, State forest, under logs” [37°36'S 148°11'E ±2 km, probably along a forest road]; 46 males, 73 females, “Sta. 87. Mt Taylor, 11 km NNW Bairnsdale...fragment of Eucalyptus forest, along roadside

between grassland, under logs and litter" [37°45'28"S 147°35'55"E ±1 km, possibly along Bullumwaal Road].

Dicranogonus samples from the three localities listed above have recently been located in the Naturalis Biodiversity Center (K. van Dorp, in litt., 17 September 2014), following a long period during which their location was uncertain. The three samples, which I have not examined, presumably contain the holotype and the published paratypes.

Discussion

The presence or absence of well-defined paranota on diplosegments is usually a genus-level character in Polydesmida. It is remarkable that both character states are found, with no obvious intermediates, in Australian paradoxosomatid specimens with no consistent, diagnosable differences in the gonopod telopodite between the forms with and without paranota (Fig. 1). The genus *Dicranogonus* (as diagnosed on gonopod form) thus offers an extreme example of the 'diphasic evolution' posited by Hoffman (1981) for Polydesmida. He observed that in many lineages, gonopods vary greatly with only minor accompanying variation in body form, while in a small minority of lineages the opposite is true.

Consistent, diagnosable gonopod variations have long been the basis of species-level taxonomy in Polydesmida. Without such variations, species delimitation on purely morphological evidence is hard to justify, especially if the taxonomist has only a limited number of specimens from an incomplete sampling of the distribution of the genus. In the case of *Dicranogonus*, however, there is abundant material from localities across the genus range. The geographical pattern for presence and absence of paranota (Fig. 3) is almost perfectly allopatric. It is tempting to delimit *Dicranogonus* species, as Jeekel may have done informally (see Introduction), on paranotal presence/absence and on geography.

However, the five specimens from Buchan (NMV K-10011; Figs 2A, 4E, 4F), in the heart of the eastern Victorian distribution of *Dicranogonus*, also lack paranota. They were collected in 1907 by the naturalist J.A. Leach (http://en.wikipedia.org/wiki/John_Albert_Leach), at the time the district inspector of schools for East Gippsland, Victoria, and I regard it as unlikely that the sample was mislabelled or that the specimens represent descendants of introduced *Dicranogonus* from Tasmania or the Furneaux Group. A more plausible interpretation is that loss of paranota has occurred at least twice in the *Dicranogonus* lineage. Loss occurred in an ancestral population which had reached the Furneaux Group or mainland Tasmania, and also in the ancestor of the paranota-less Buchan specimens.

The timing of these losses might be estimated from future genetic work on *Dicranogonus*. For current taxonomic purposes, I am satisfied that all material I examined can be assigned to *D. pix*, which is readily diagnosed on gonopod form and body size and colour.

Acknowledgements

I thank Graham Milledge (Australian Museum) and Peter Lillywhite (Museum Victoria) for the loan of specimens, and Karsten Goemann (University of Tasmania) for

assistance with SEM work. Roy Vogelpoel (in litt., 3 January 2010) kindly corrected the locality for QVM specimen lot 23:25149 from “Charter Island” to “Mt Chappell Island”, 43 years after he had collected *Dicranogonus* there. I am especially grateful to Ben Brugge (Zoological Museum, Amsterdam) and Karen van Dorp (Naturalis Biodiversity Center, Leiden) for their patience in dealing with the frustrating issue of Jeekel millipede types, and to Sancia van der Meij (Naturalis Biodiversity Center, Leiden) for permission to reproduce Fig. 4 in Jeekel (1982) as Fig. 1A (above). The manuscript was greatly improved by changes suggested by Sergei Golovatch, Pavel Stoev and an anonymous reviewer. This study was funded by the author.

References

- Hoffman RL (1981) Diphasic evolution in polydesmid millipedes. Abstract of paper presented at the 5th International Congress of Myriapodology; August 2–7, 1981, Radford, Virginia.
- Jeekel CAW (1981) Australia Expedition 1980; legit Jeekel CAW and Jeekel-Rijvers AM. List of collecting stations, together with general notes on the distribution of millipedes in eastern Australia and Tasmania. Verslagen en Technische Gegevens, Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Universiteit van Amsterdam 30: 1–59.
- Jeekel CAW (1982) Millipedes from Australia, 2: Antichiropodini from Victoria (Diplopoda, Polydesmida, Paradoxosomatidae). Bulletin Zoölogisch Museum, Universiteit van Amsterdam 8(24): 201–212.
- Jeekel CAW (1984) Millipedes from Australia, 6: Australiosomatini from Victoria (Diplopoda: Polydesmida: Paradoxosomatidae). Records of the Australian Museum 36: 19–44. doi: 10.3853/j.0067-1975.36.1984.323
- Jeekel CAW (2006) Millipedes from Australia, 18: Tasmanian Paradoxosomatidae (Diplopoda, Polydesmida) (Genera *Somethus* Chamb., *Notodesmus* Chamb. and *Aethalosoma* nov.). Myriapod Memoranda 8: 75–89.
- Mesibov R (2004) A new genus of millipedes (Diplopoda: Polydesmida: Dalodesmidae) from wet forests in southern Victoria, with brief remarks on the Victorian Polydesmida. Memoirs of Museum Victoria 61(1): 41–45. http://museumvictoria.com.au/pages/3959/61_1_Mesibov.pdf
- Mesibov R (2009) New and little-used morphological characters in Polydesmida (Diplopoda). Soil Organisms 81(3): 531–542.
- Mesibov R, Churchill TB (2003) Patterns in pitfall captures of millipedes (Diplopoda: Polydesmida: Paradoxosomatidae) at coastal heathland sites in Tasmania. Australian Zoologist 32(3): 431–438. <http://goo.gl/wfFCKV>
- Nguyen AD, Sierwald P (2013) A worldwide catalog of the family Paradoxosomatidae Daday, 1889 (Diplopoda: Polydesmida). Check List 9(6): 1132–1353. <http://www.checklist.org.br/getpdf?SL107-12>
- Shelley RM, Sierwald P, Kiser SB, Golovatch SI (2000) Nomenclator generum et familiarum Diplopodorum II. A list of the genus and family-group names in the Class Diplopoda from 1958 through 1999. Pensoft, Sofia, 167 pp.

Supplementary material I

Data table

Authors: Robert Mesibov

Data type: CSV file.

Explanation note: Known specimen lots of *Dicranogonus pix* Jeekel, 1982 as of 17 September 2014.

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

The first sexual associations in the genus *Darditilla* Casal, 1965 (Hymenoptera, Mutillidae)

David R. Luz¹, Kevin A. Williams^{1,2}

1 Laboratório de Biologia Comparada de Hymenoptera, Departamento de Zoologia, Universidade Federal do Paraná. Caixa Postal 19020, 81531-980 Curitiba, PR, Brazil **2** Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, 1911 SW 34th St., Gainesville, FL 32608, USA

Corresponding author: Kevin A. Williams (Kevin.Williams@freshfromflorida.com)

Academic editor: M. Engel | Received 5 September 2014 | Accepted 24 October 2014 | Published 13 November 2014

<http://zoobank.org/59DD67E9-ABBE-4EE2-A5DF-3AF8D02A34E8>

Citation: Luz DR, Williams KA (2014) The first sexual associations in the genus *Darditilla* Casal, 1965 (Hymenoptera, Mutillidae). ZooKeys 454: 41–68. doi: 10.3897/zookeys.454.8558

Abstract

New sex associations are proposed for four species of *Darditilla*: *D. amabilis* (Gerstaecker, 1874); *D. bejaranoi* Casal, 1968; *D. debilis* (Gerstaecker, 1874); and *D. felina* (Burmeister, 1854). *Darditilla botija* Casal, 1965, **syn. n.** is the male of *D. amabilis*; the other three males were previously unknown. *Mutilla decorosa* Kohl, 1882, **syn. n.** is conspecific with *D. felina*. Descriptions and extended diagnoses are provided for previously unknown males and for females that were not adequately described. These represent the first sex associations for the genus *Darditilla*.

Keywords

Sphaerophthalminae, Sphaerophthalmini, Pseudomethocina, velvet ants, Neotropical, *formiga feiticeira*

Introduction

The genus *Darditilla* Casal, 1965 was erected to include a single new species, *D. botija* Casal, 1965, which was known from males only (Casal 1965). In his study, Casal suggested that six described females may belong to *Darditilla*, and specifically suggested that *D. amabilis* (Gerstaecker, 1874) could be the female of *D. botija*. In 1968, Casal described 28 new *Darditilla* species or subspecies, each known only from the female,

and transferred seven described species into *Darditilla*. Subsequent authors have described new *Darditilla* species (Casal 1971, Fritz and Martinez 1974), transferred additional species into *Darditilla* (Nonveiller 1990), synonymized species or subspecies (Fritz and Martinez 1993, Quintero and Cambra 2001), and transferred species into *Pseudomethoca* Ashmead, 1899 (Quintero and Cambra 2001). Each of these subsequent publications has treated only females. As currently recognized, *Darditilla* includes 35 species known from females and one known from males.

Only seven described species of *Darditilla* occur in Brazil (Gerstaecker 1874, Nonveiller 1990, Quintero and Cambra 2001). For this study, two *Darditilla* sex associations, *D. felina* (Burmeister, 1854) and *D. bejaranoi* Casal, 1968, were made in southern and southeastern Brazil based on discovery of mating pairs. Two additional associations, *D. amabilis* and *D. debilis* (Gerstaecker, 1874), were then deduced based on overlapping ranges and morphological similarities. Only one of the males, *D. botija* syn. n. of *D. amabilis*, is known in the literature. Below, we present the first four sexual associations for the genus *Darditilla*, including the genotype. Extended diagnoses are provided for the three previously unknown males and each female studied here; the male of *D. amabilis*, as *D. botija* syn. n., was adequately described by Casal (1965). Photographs and pertinent figures are provided for each sex of each species studied herein.

Material and methods

The following acronyms are used for institutions housing the material discussed in the current study:

AMNH	American Museum of Natural History, New York, USA;
CASC	Department of Entomology, California Academy of Sciences, San Francisco, California, USA;
DZUP	Coleção de Entomologia Pe. Jesus Santiago Moure, Departamento de Zoologia da Universidade Federal do Paraná, Curitiba, Paraná, Brazil;
EMUS	Department of Biology Insect Collection, Utah State University, Logan, Utah, USA;
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina;
MLUH	Martin Luther University Halle-Wittenberg, Halle, Germany;
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil;
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil;
NHM	Natural History Museum, London, UK;
NMW	Naturhistorisches Museum Wien, Vienna, Austria;
UFES	Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brazil;
YPM	Peabody Museum of Natural History, Yale University, New Haven, USA;
ZMB	Museum für Naturkunde an der Universität Humboldt zu Berlin, Berlin, Germany.

We use the abbreviations T2, T3, etc., to denote the second, third, etc., metasomal terga while S2, S3, etc., denote the second, third, etc., metasomal sterna. To compare mesosomal length and width, the distance between the anteromedial pronotal margin (excluding the anterior collar) and the scutellar-scale apex is divided by the distance between the extreme posterolateral pronotal margins, the maximum mesosomal width. The digitus or cuspis length relative to the free paramere length is used here to quantify differences in genitalic structure. For ease of comparison and to facilitate identification without dissecting the genitalic capsule, the cuspis, digitus and paramere measurements are taken in dorsal view from the apical margin of the parapenial lobe to the apex of each respective structure. Using this method, all measurements can be taken from the dorsal view and a single anchor point can be used for all three measurements. These are not actual measurements of structure length, but an index to compare relative lengths; all provided length ratios of genitalic structures are based on these indices.

Taxonomy

Darditilla Casal, 1965

Darditilla Casal, 1965. Eos, Madrid 41: 9–18.

Type species. *Darditilla botija* Casal, 1965, by original designation.

Diagnosis. Male. Males of *Darditilla* can be separated from other South American mutillid genera by the apical row of parallel bristles on T2–4 or T2–5 (e.g. Fig. 1E) and by the ventral margin of the clypeus that is preceded by a transverse furrow (e.g. Figs. 3D, 7D) and is sometimes expanded into a broad plate-like structure over the mandibles (Fig. 1D). Additionally, *Darditilla* males have the scape bicarinate with a relatively flat or concave anterior surface between the carinae (although the dorsal carina is often obscure or obliterated); the axillae unarmed posteriorly; T1 broadly rounded into T2; the paramere downcurved apically; and the cuspis short and pad-like (e.g. Fig. 12).

Female. Females of *Darditilla* are most readily recognized by their granulate pygidium (e.g. Fig. 6E) and also have a unique combination of characters, wherein the clypeus is bidentate with the teeth slightly farther apart than the antennal tubercles (e.g. Fig. 8C); the mandible is acuminate apically and has its largest tooth situated in the basal half of the internal margin; the mesosoma is constricted anterior to the propodeal spiracles, lacks a scutellar scale, lacks a sharp dorsal tubercle directly anterior to the propodeal spiracle, and has the lateral mesonotal teeth small (e.g. Fig. 6A); T1 is broadly rounded into T2; and the metasomal setae are simple.

Species included. There are 36 species in *Darditilla* (Nonveiller 1990, Quintero and Cambra 2001).

Distribution. *Darditilla* species are known from throughout South America, putative members of *Darditilla* are known throughout Central America as well.

Remarks. Casal (1965) described the genus from a single male specimen and used some synapomorphies of that species and its relatives in his generic description. The newly associated males described here match the diagnostic features listed by Casal and other authors in keys (e.g. Brothers 2006), but in two of the species: *D. bejaranoi* and *D. debilis*, the clypeus is less strongly modified. Rather than expanding forward to cover the mandibles, the ventral clypeal margin of these species is short, yet still has the ventral margin angled anteriorly.

Darditilla is apparently closely related to *Pseudomethoca* and could be nested within that genus. Males of some Nearctic and Central American *Pseudomethoca* species have thickened setae on T2–4 that resemble the bristles of *Darditilla* and some females currently placed in *Pseudomethoca* have a granulate pygidium. Further complicating this situation, Casal's treatments of *Darditilla* focused on southern South America and the types of northern Neotropical *Pseudomethoca* species consistent with *Darditilla* were not available to him (Casal 1965, 1968a). Without phylogenetic analysis or careful study of both sexes of these species, we cannot determine which of these northern Neotropical *Pseudomethoca* should be transferred to *Darditilla*, or whether *Darditilla* is even a valid genus. We, therefore, maintain *Darditilla* using the aforementioned diagnoses and hope that this paper will facilitate the future studies needed to clarify the validity and limits of this genus.

***Darditilla amabilis* (Gerstaecker, 1874)**

Figs 1–2, 9–12

Mutilla amabilis Gerstaecker, 1874. Arch. Naturgesch. 40: 63. Lectotype female, Brasilien, Alegrette, Sello S. (ZMB, examined), presently designated.

Mutilla braconina Burmeister, 1875. Bol. Acad. Nac. Sci. Cordoba 1: 488. Holotype female, (? MACN, not examined).

Darditilla botija Casal, 1965. Eos, Madrid 41: 14. Holotype male, República Argentina, Entre Ríos, Colón, II-1961, M. A. Zelich (AMNH, examined). **syn. n.**

Diagnosis. Male. Males of *D. amabilis* have a unique clypeus (Fig. 1D), which is widely transverse, almost covering the mandibles, with the ventral margin raised broadly and medially coming to an obtuse point with a subapical brush of golden setae, and have the penis valve unidentate apically (Fig. 11).

Female. The female of *D. amabilis* can be recognized by having T1, T2, S1 and S6 entirely orange (Fig. 2A), having an arcuate transverse band of recumbent pale golden setae on the vertex, and having a pair of longitudinal pale golden stripes in the mesosomal dorsum, which extend to the anterior margin of mesonotum (Fig. 2A).

Description. Male. Body length 8.5 mm. The male was adequately described (as *D. botija*) by Casal (1965).

Extended female diagnosis. Body length 7.6 mm. *Coloration.* Body and appendages reddish-black, except T1, T2, S1 and S6 entirely orange. Tibial spurs whitish.



Figure 1. *Darditilla amabilis* (Gerstaecker), male: **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** head, anterior view **E** metasoma, dorsal view **F** T5, T6 and pygidium, dorsal view. Scale bars: 1 mm.

Vertex with dense, arcuate transverse band of recumbent pale golden setae, front and remainder of vertex with recumbent black setae; genal setae silver. Mesosomal dorsum covered with recumbent black setae, except laterally, with a pair of longitudinal pale golden stripes, extending to anterior margin of mesonotum. Posterior fringes of T1 and T2 black; T2 setae black anteriorly and posteriorly, pale golden mixed with black laterally, and reddish orange on orange integumental spots; T3–T6 clothed with black setae laterally and pale golden setae medially. *Head*. Transverse, posterior margin flat, occipital carina weak, but distinct. Head width $1.2 \times$ pronotal width. Eye slightly ovate transversely, ommatidia distinct. Front, vertex and gena densely punctate. Genal carina well-defined, terminating in slightly sharp angle posterior to hypostomal carina. Clypeus with transverse glabrous concavity, margined by dorsal and ventral carinae, between widely separated lateral teeth. Mandible slender, tapering, bidentate apically (subapical tooth minute, distant from apex and usually obliterated through wear), unarmed ventrally. Antennal scrobe with complete dorsal carina. Antennal tubercle punctate basally, with weak scratches on anterior face, glabrous dorsally. Scape simple, moderately punctate. Flagellomere 1 $1.7 \times$ pedicel length; flagellomere 2 $1.3 \times$ pedicel length. *Mesosoma*. Mesosomal length $1.4 \times$ width. Mesosomal dorsum coarsely reticulate, propodeal reticulæ broader and shallower. Lateral pronotal carina extending to epaulet, humeral angle with moderately sharp obtuse angle. Mesopleuron densely punctate and setose, posterior margin defined by vertical carina. Metapleuron and lateral face of propodeum smooth and shining dorsally with isolated fine setae, micropunctate and densely setose ventrally. In dorsal view, mesosoma broadened to anterior third, strongly narrowed at propodeal spiracle, propodeum abruptly broadened. Scutellar scale lacking. Propodeum convex, dorsal and lateral faces not obviously differentiated. *Legs*. Foreleg with a few long strong articulated spines on posterior/lateral margins of tarsomeres. Mid- and hind tibiae each with one rows of prominent spines, 5 spines in each row; apical spurs finely serrated laterally. Hind tibia with distinct secretory pore on inner/posterior surface near base of inner spur. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.6 \times$ as wide as T2; anterior face moderately punctate and setose. T2 densely punctate, punctures slightly smaller and sparser on orange spots; felt line broad, $0.5 \times$ as long as T2 laterally. T3–5 densely punctate. Pygidium broad and slightly convex, lateral margins defined by distinct weakly bowed carina, posterior margin rounded and defined by indistinct carina, finely granulate. S1 punctate, with weak darkened median longitudinal carina. S2 moderately punctate. S3–5 densely punctate. S6 moderately punctate.

Material examined. Type material. Holotype: *Darditilla botija*, 'República Argentina\Entre Ríos\Colón\II-1961\M.A. Zelich' (handwritten label) 'HOLOTYPUS' (red label) 'Darditilla [male symbol]\botija\ Casal 1965' (red label) [1 male: AMNH]; Lectotype: *Mutilla amabilis*, 'Brasilien\Alegrette\Sello S.' (handwritten label) '6611' 'Type' (red label) [1 female: ZMB]. **Other material.** 2 males and 2 females as follows: ARGENTINA: BUENOS AIRES: Bolivar, I-60 (R.J. Llano) [1 female: DZUP]; BRAZIL: RIO GRANDE DO SUL: Pelotas, 16m, $31^{\circ}44'39''\text{S}$, $52^{\circ}13'22''\text{W}$, 26.III.2004 (R.F.



Figure 2. *Darditilla amabilis* (Gerstaecker), female: **A** habitus, dorsal view **B** habitus, lateral view **C** head, anterior view **D** metasoma, dorsal view **E** T4, T5 and pygidium, dorsal view. Scale bars: 1 mm.

Krüger) [1 female: AMNH]; same locality, 16.IV.2004 (R.F. Krüger) [1 male: UFES]; Rio Grande, Taim, Mata do Nicola 32.5557°S, 52.5006°W, 10–18.XII.2011, Arm. Malaise (Krüger & Kirst) [1 male: DZUP].

Distribution. This species is widespread in Argentina and also occurs in Rio Grande do Sul, and Uruguay (Nonveiller 1990).

Host. Unknown.

Remarks. Gerstaecker (1874) described *Mutilla amabilis* based on two female specimens, one from Alegrete, Rio Grande do Sul State, Brazil and another from Paraná, Entre Ríos Province, Argentina. The specimen from Alegrete, deposited in the ZMB and bearing the labels cited above, was examined and is herein designated as a lectotype.

Casal (1965) hypothesized that *D. botija* was the male of *D. amabilis* based on geographical distribution in northern Argentina. Yet another overlapping distribution was found in Pelotas, Rio Grande do Sul State, Brazil. Only two other *Darditilla* females are known from Rio Grande do Sul: *D. debilis* and *D. infantilis* (Burmeister, 1875). The male of *D. debilis* is described below; *D. infantilis* is structurally similar to *D. bejaranoi* and has a consistently small body size, precluding it from association with *D. botija*. The newly described male of *D. felina* has similar genitalia and clypeal modifications to *D. botija*. Likewise, females of *D. felina* are similar to those of *D. amabilis* in the integumental markings of T2 and the genal carina. Distribution, similar body size, and morphological similarities to both sexes of *D. felina* support the synonymy of *D. botija* under *D. amabilis*.

Burmeister (1875) had briefly described the supposed male of *M. amabilis* from Paraná, Entre Ríos, Argentina. Later, André (1908) studied and redescribed the male that Burmeister (1875) originally associated with *M. amabilis*; he pointed out that its identity and sexual association were doubtful. This male is clearly not conspecific with the male of *D. amabilis* described above, most notably differing in its reddish basal metasomal segments. The description of this putative *D. amabilis* male is, however, consistent with some Argentinean *Pseudomethoca* males.

***Darditilla bejaranoi* Casal, 1968**

Figs 3–4, 13–16

Darditilla bejaranoi Casal, 1968. Rev. Soc. Ent. Arg. 30(1–4): 95. Holotype female, Brasil, Santa Catarina, Corupá, II-1953, A. Maller (AMNH, examined).

Diagnosis. Male. The male of *D. bejaranoi* can be recognized by having the ventral clypeal margin produced as a short transverse slightly upcurved impunctate lamella (Fig. 3D), by having the tegula truncate with a flat posterior face, and by having the bidentate penis valve teeth widely separated (Fig. 15).

Female. This female has a reddish mesosoma, with distinct black areas on the lateral pronotal dorsum and the posterior half of the pleurae (Fig. 4A, B), has lateral circular to transversely ovate silver setal spots on T2 (Fig. 4D), and has a strong hyaline median carina on S1.

Description. Male. Body length 4.5–8 mm. *Coloration.* Body and appendages black, except mandibles and metasoma dark brown apically. Tibial spurs white. Forewing slightly and uniformly infuscated between veins, veins brown; hindwing slightly infuscated. Body clothed with whitish setae, except vertex, dorsomedial portion of pronotum, axilla, scutellum, disc of T2, T6 and T7 with scattered brownish setae, mesoscutum and tegula with dark brown setae, bristles of tergal fringes pale yellowish. *Head.* Rounded posteriorly. Head width $1.1 \times$ pronotal width. Eye transversely ovate. Ocelli small; ocellocular distance $5.1 \times$ length of lateral ocellus, interocellar distance $2.3 \times$ lateral ocellus length. Occipital carina distinct, extending ventrally almost to level of oral



Figure 3. *Darditilla bejaronoi* Casal, male: **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** head, anterior view **E** metasoma, dorsal view **F** T5, T6 and pygidium, dorsal view. Scale bars: 1 mm.

fossa. Punctuation on front dense, interspaces micropunctate; gena densely punctate, interspaces with sparse micropunctures; and vertex moderately punctate, interspaces glabrous. Gena ecarinate. Antennal scrobe broadly concave to eye margin, with transverse tubercle dorsally. Clypeus densely punctate, ventral margin produced as a short transverse slightly upcurved impunctate lamella. Flagellomere 1 $1.2 \times$ pedicel length;

flagellomere 2 $1.4 \times$ pedicel length. Mandible convergent to bidentate apex, dorsal carina gradually becoming obsolete on inner tooth; edentate ventrally. *Mesosoma*. Epaulets weakly produced. Pronotal dorsum densely punctate; anterior face almost smooth; lateral face densely punctate. Tegula evenly convex anteriorly with abrupt vertical posterior face delimited by transverse dorsal carina, glabrous except with long recumbent setae anterolaterally and posteromesally. Mesoscutum with dense coarse punctures; posterolateral corner forming a small angulate lobe. Scutellum slightly convex, with coarse punctures. Axilla flat and punctate, except lateral margin with narrow vertical lamella. Metanotum surface obscured by dense shaggy mesally facing recumbent setae. Propodeum convex, broadly and deeply reticulate except smooth and shining adjacent to metapleuron. Mesopleuron moderately punctate, interspaces micropunctate. Metapleuron smooth and shining ventrally, setose and micropunctate dorsally. *Wings*. Forewing with moderate elongate sclerotized pterostigma; marginal cell broadly rounded and truncate apically; three submarginal cells, third scarcely delimited by obscure venation. *Legs*. Mid- and hind tibiae lacking strong spines, distinct apical secretory pore on inner surface near base of inner spur; spurs finely serrate on margins. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.6 \times$ width of T2, sparsely punctate; apex with fringe of simple setae or thickened bristles. T2 with coarse to moderate punctures, interspaces smooth and generally broader than punctures; apex with fringe interspersed recumbent thickened parallel bristles; felt line $0.5 \times$ lateral length of T2. T3–5 densely and finely punctate, covered with interspersed erect and recumbent setae, except fringes with row of bristles as in T2. T6 densely punctate, covered with less dense recumbent and erect setae. T7 in basal half with moderately spaced simple punctures and setae, interspaces glabrous; posterior half forming oval pygidium margined laterally and posteriorly by a strong sharp carina, apical margin rounded, surface flat, microgranulate with numerous large irregular transverse rugae. S1 punctate and setose, with medial longitudinal carina extending from base to apex. S2 moderately punctate. S3–6 moderately and finely punctate, with fairly sparse erect and recumbent setae. Lateral margins of S2–5 sometimes with similar bristles to those of T2–6. S7 transversely rectangular. Hypopygium smooth, moderately punctate, posteromedial margin with two approximate weak teeth medially. *Genitalia* (Figs 13–16). Paramere tapering apically, gradually curved ventrally, apices diverging slightly, dense setal brush on basoventral lateral margin, scattered setae along inner and lateral margins. Cuspis acute angulate apically, extending $0.2 \times$ free length of paramere, with densely setose oblique ventral surface. Digitus laterally compressed and rounded apically, extending $0.2 \times$ free length of paramere, asetose. Penis valve asetose, bidentate apically, basoventral margin expanded apically as blunt tooth, basodorsal margin with slight tubercle.

Extended female diagnosis. Body length 4.1–4.6 mm. *Coloration*. Head and metasoma black. Mesosoma reddish with variable blackish areas on lateral portion of pronotum and lateral face of mesosoma in posterior half. Appendages reddish, except mandible, flagellum, femora, and tibiae often darkened apically. Tibial spurs whitish. Front and vertex clothed with recumbent golden setae; genal setae silver. Mesosomal



Figure 4. *Darditilla bejaronoi* Casal, female: **A** habitus, dorsal view **B** habitus, lateral view **C** head, anterior view **D** metasoma, dorsal view **E** T5 and pygidium, dorsal view. Scale bars: 1 mm.

dorsum with sparse erect black setae, except often with silver setae laterally on pronotum and pale yellow setae dorsomedially on pronotum and posteriorly on propodeum. Posterior fringes of T1 and T2 black; T2 with lateral circular to transversely ovate silver setal spots; T3–6 clothed with silver setae. *Head*. Transverse, posterior margin flat, occipital carina obscure. Head width $1.4 \times$ pronotal width. Eye slightly ovate transversely, ommatidia distinct. Front and vertex densely punctate; gena moderately punctate. Genal carina well-defined, extending nearly to hypostomal carina. Clypeus with shallow transverse glabrous concavity, margined by dorsal and ventral carinae, between widely separated lateral teeth. Mandible slender, tapering, bidentate apically (subapical tooth minute, distant from apex and usually obliterated through wear), unarmed ventrally. Antennal scrobe with complete dorsal carina. Antennal tubercle punctate basally and

laterally. Scape simple, moderately punctate. Flagellomere 1 $1.5 \times$ pedicel length; flagellomere 2 $1.4 \times$ pedicel length. *Mesosoma*. Mesosomal length $1.8 \times$ width. Mesosomal dorsum coarsely reticulate, propodeal reticulae broader and shallower. Lateral pronotal carina extending to epaulet, humeral angle shallowly obtusely angulate. Mesopleuron densely punctate and setose, posterior margin defined by vertical carina. Metapleuron and lateral face of propodeum smooth and shining dorsally with isolated fine setae, micropunctate and densely setose ventrally. In dorsal view, mesosoma broadened to anterior third, strongly narrowed at propodeal spiracle, propodeum abruptly broadened. Scutellar scale lacking. Propodeum convex, dorsal and lateral faces not obviously differentiated. *Legs*. Foreleg with a few long strong articulated spines on posterior/lateral margins of tarsomeres. Mid- and hind tibiae each with two rows of prominent spines, 2–4 spines in each row; apical spurs finely serrated laterally. Hind tibia with distinct secretory pore on inner/posterior surface near base of inner spur. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.5 \times$ as wide as T2; anterior face moderately punctate and setose. T2 densely punctate and setose, punctures slightly larger and sparser anterolaterally; felt line broad, $0.4 \times$ as long as T2 laterally. T3–5 densely punctate. Pygidium broad and slightly convex, lateral margins defined by distinct weakly bowed carina, posterior margin rounded and defined by indistinct carina, granulate, posterior granulae often more sparse, anterior granulae often merging to obscure striae or rugae. S1 punctate, with strong hyaline median carina. S2 moderately punctate. S3–5 densely punctate. S6 moderately punctate.

Material examined. Type material. Holotype: ‘Brasil\Santa Catarina\Corupá\II-1953\A. Maller’ (handwritten label) ‘HOLOTYPUS’ (red label) ‘Darditilla [female symbol]\bejaronoi\ Casal 1968’ (red label) [1 female: AMNH]. **Other material.** 18 males and 49 females as follows: ARGENTINA: CORRIENTES: Ytuzaingo, III.1982 (M.A. Fritz) [1 female, 1 male: AMNH]; ENTRE RÍOS: Colón, Parque Nacional, X.1974 (M.A. Fritz) [1 female: AMNH]; same locality, III.1982 (M.A. Fritz) [1 female: AMNH]; same locality, date unknown (M.A. Fritz) [1 female: AMNH]; same locality, XII.1973 (M.A. Fritz) [1 male: AMNH]; same locality, I.1974 (M.A. Fritz) [1 male: AMNH]; BRAZIL: MINAS GERAIS: Belo Horizonte, Museu de História Natural, 22.III.1998 (G.A.R. Melo) [1 female: DZUP]; 16 km S de Berizal, Serra do Anastácio, 18.XII.2012 (G.A.R. Melo) [1 male: DZUP]; 7 km S Itanhandu, 14.XI.2005 (L.R.R. Faria Jr.) [1 female: DZUP]; near Timoteo, 1–14.II.1999 (E.R. DePaula) [1 female: EMUS]; PARANÁ: Piraquara, Mananciais da Serra, 27.III.2003 (E.Q. Garcia) [1 female: DZUP]; Ponta Grossa, Parque Estadual da Vila Velha, 23.XI.2001 (G.A.R. Melo) [1 female: DZUP]; same locality, 15.XI.2003 (G.A.R. Melo & R.B. Gonçalves) [1 female: DZUP]; same locality, 5.IV.2013 (K.A. Williams) [10 females: DZUP]; same locality, 6.IV.2013 (K.A. Williams) [11 females: DZUP]; RIO DE JANEIRO: Mendes, 23.IV.1936 (Borgmeier) [1 pair *in copula*: MNRJ]; Petrópolis, Alto da Serra, 18.II.1962 (H. Cesar) [1 male: MNRJ]; km 47, estrada Rio-São Paulo, 24.X.1944 (Wygodzinsky) [1 female: MNRJ]; SANTA CATARINA: Corupa, various dates [5 females: MNRJ]; Galheta, P. Mole, 5.X.1988 (C.R.F. Brandão) [1 female: MZSP]; SÃO PAULO: Barueri, V.1958 (K. Lenko) [1 female: MNRJ]; Botucatu, Cerrado, Armadilha Solo,

19.III.1987 (L.C. Forti & I.M.P. Rinaldi) [1 female: MZSP]; Cajuru, Fazenda Rio Grande, 18.XII.1999–10.I.2000 (G.A.R. Melo & Nascimento) [2 males: DZUP]; same locality, 10.I–1.II.2000 (G.A.R. Melo & Nascimento) [3 males: DZUP]; same city, Fazenda Santa Carlota, 17.XI–2.XII.1999 (G.A.R. Melo & Nascimento) [4 males: DZUP]; Campo Limpo, 20.II.1966 (W.W. Kempf) [2 females: MZSP]; Caraguata, Reserva Florestal, 40m, II.1963 (F. Werner, U. Martins, & L. Silva) [1 female: MZSP]; Cosmópolis, 22.I.1974 (J.G. Rozen et al.) [2 females: AMNH]; Ribeirão Grande, P.E. Intervalles, ponto 5, 24°16'23"S, 48°25'22"W, 22.XII.2009 (N.W. Perito) [1 male: MZSP]; Ribeirão Preto, Campus da USP, 12.XI.1998 (G.A.R. Melo) [1 female: DZUP]; Rio Claro, Floresta Estadual Edmundo Navarro de Andrade, 10.IX–1.X.2005 (A.P. Aguiar & J.T. Dias) [1 male: MZSP]; São Jose dos Campos, 8–14.III.1999 (E.R. DePaula) [1 female: EMUS]; same locality, 22–29.IX.1999 [1 female: EMUS]; São Paulo, 10.XI.1972 (G.E. Bohart) [1 male: EMUS].

Distribution. This species is known from the Atlantic Rainforest of Brazil and surrounding areas of Argentina.

Host. Unknown.

Remarks. The sexes of *Darditilla bejaranoi* are associated based on a mating pair found in the MNRJ. Additionally, M.A. Fritz collected males and females in the same locality twice in Argentina. The male and female are similar in size and geographical distribution.

Females vary in mesosomal coloration, with some specimens having only a small dark brown patch on the pronotal dorsum and others having the mesosomal dorsum and pleurae extensively darkened. The setal spots of T2 also vary slightly in shape, from perfectly circular to transversely ovate. In Casal's key (1968a) specimens with transversely ovate setal spots will run to couplet 25, where they can be separated from *D. bachmanni* Casal, 1968 and *D. nelidae* Casal, 1968 by the entirely black fringe of T1 (T1 with extensive white setae in *D. bachmanni* and *D. nelidae*) and geographical distribution (*D. bachmanni* from Bolivian Amazon and *D. nelidae* from central Argentina).

***Darditilla debilis* (Gerstaecker, 1874)**

Figs 5–6, 17–20

Mutilla debilis Gerstaecker, 1874. Arch. Naturgesch. 40: 60. Holotype female, Brasil. mer, Sello. (ZMB, examined).

Diagnosis. Male. Males are similar to *D. bejaranoi*, but have a simply convex tegula, have the ventral impunctate lamella of the clypeus less produced than the preceding species (Fig. 5D), and have the apical and preapical teeth of the penis valve coalescent (Fig. 19).

Female. The female of *D. debilis* is similar to *D. bejaranoi*, but can be recognized by its reddish mesosoma, at most having reduced dark stains laterally (Fig. 6A); by its pygidium, which is densely granulate throughout (Fig. 6E); and by its S1, which has a weak darkened median longitudinal carina.



Figure 5. *Darditilla debilis* (Gerstaecker), male: **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** head, anterior view **E** metasoma, dorsal view **F** T5, T6 and pygidium, dorsal view. Scale bars: 1 mm.

Description. Male. Body length 5.7–8.4 mm. *Coloration.* Body and appendages black, except mandibles and metasoma dark brown apically. Tibial spurs white. Forewing slightly and uniformly infuscated between veins, veins brown; hindwing slightly

infuscated. Body clothed with whitish setae, except disc of T2 and T7 with scattered brownish setae, mesoscutum, tegula, and T6 with dark brown setae, bristles of tergal fringes silver to pale yellowish. *Head*. Rounded posteriorly. Head width $1.0 \times$ pronotal width. Eye transversely ovate. Ocelli small; ocellocular distance $7.1 \times$ length of lateral ocellus, interocellar distance $3.1 \times$ lateral ocellus length. Occipital carina distinct, extending ventrally almost to level of oral fossa. Punctuation on front dense, interspaces micropunctate; gena densely punctate, interspaces with sparse micropunctures; and vertex moderately punctate, interspaces glabrous. Gena ecarinate. Antennal scrobe broadly concave to eye margin, with transverse tubercle dorsally. Clypeus densely punctate, ventral margin produced as a short slightly upcurved transverse impunctate lamella. Flagellomere 1 $1.4 \times$ pedicel length; flagellomere 2 $1.6 \times$ pedicel length. Mandible convergent to bidentate apex, dorsal carina gradually becoming obsolete on inner tooth; edentate ventrally. *Mesosoma*. Epaulets weakly produced. Pronotal dorsum densely punctate; anterior face almost smooth; lateral face densely punctate. Tegula evenly convex, glabrous except with long recumbent setae anterolaterally and posteromesally. Mesoscutum with dense coarse punctures; posterolateral corner forming a small angulate lobe. Scutellum slightly convex, with coarse punctures. Axilla flat and punctate, except lateral margin with narrow vertical lamella. Metanotum surface obscured by dense shaggy mesally facing recumbent setae. Propodeum convex, broadly and deeply reticulate except smooth and shining adjacent to metapleuron. Mesopleuron moderately punctate, interspaces micropunctate. Metapleuron smooth and shining ventrally, setose and micropunctate dorsally. *Wings*. Forewing with moderate elongate sclerotized pterostigma; marginal cell broadly rounded and truncate apically; three submarginal cells, third scarcely delimited by obscure venation. *Legs*. Mid- and hind tibiae lacking strong spines, distinct apical secretory pore on inner surface near base of inner spur; spurs finely serrate on margins. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.6 \times$ width of T2, sparsely punctate; apex with fringe of simple setae or thickened bristles. T2 with coarse to moderate punctures, interspaces smooth and generally broader than punctures; apex with fringe interspersed recumbent thickened parallel bristles; felt line $0.5 \times$ lateral length of T2. T3–5 densely and finely punctate, covered with interspersed erect and recumbent setae, except fringes with row of bristles as in T2. T6 densely punctate, covered with less dense recumbent and erect setae. T7 coarsely and densely punctate, punctures uneven medially, appearing rugose; posterior half forming oval pygidium margined laterally and posteriorly by a strong sharp carina, apical margin rounded, surface flat, microgranulate with numerous large irregular transverse rugae. S1 punctate and setose, with medial longitudinal carina extending from base to apex. S2 moderately punctate. S3–6 moderately and finely punctate, with fairly sparse erect and recumbent setae. Lateral margins of S2–5 sometimes with similar bristles to those of T2–6. S7 transversely rectangular. Hypopygium coarsely punctate, posteromedial margin with two approximate weak teeth medially. *Genitalia* (Figs 17–20). Paramere tapering apically, slightly curved ventrally on basal half, dense setal brush on basoventral lateral margin, scattered setae along inner and lateral margins. Cuspis acute angulate apically, extending ~ 0.3



Figure 6. *Darditilla debilis* (Gerstaecker), female: **A** habitus, dorsal view **B** habitus, lateral view **C** head, anterior view **D** metasoma, dorsal view **E** T5 and pygidium, dorsal view. Scale bars: 1 mm.

\times free length of paramere, with densely setose oblique ventral surface. Digitus laterally compressed and rounded apically, extending $\sim 0.3 \times$ free length of paramere, asetose. Penis valve asetose, bidentate apically with apical and preapical tooth, basoventral margin slightly expanded apically as blunt tooth, basodorsal margin with slight tubercle.

Extended female diagnosis. Body length 4.8–10 mm. *Coloration.* Head and metasoma black. Mesosoma reddish, rarely with dark stains laterally. Appendages blackish, often reddish basally. Tibial spurs whitish. Vertex with arcuate transverse band of recumbent silver to golden setae, front and remainder of vertex with recumbent black setae; genal setae silver. Mesosomal dorsum with sparse erect black setae, except anterior margin pronotum with pale yellow setae. Posterior fringes of T1 and T2 black; T2 with lateral circular silver setal spots; T3–6 clothed with black setae ba-

sally and silver setae apically. *Head*. Transverse, posterior margin flat, occipital carina obscure. Head width $1.3 \times$ pronotal width. Eye slightly ovate transversely, ommatidia distinct. Front and vertex densely punctate; gena moderately punctate. Genal carina well-defined, extending nearly to hypostomal carina. Clypeus with transverse glabrous concavity, margined by dorsal and ventral carinae, between widely separated lateral teeth. Mandible slender, tapering, bidentate apically (subapical tooth minute, distant from apex and usually obliterated through wear), unarmed ventrally. Antennal scrobe with complete dorsal carina. Antennal tubercle punctate basally, with weak scratches on anterior face, glabrous dorsally. Scape simple, moderately punctate. Flagellomere 1 $1.9 \times$ pedicel length; flagellomere 2 $1.8 \times$ pedicel length. *Mesosoma*. Mesosomal length $1.3 \times$ width. Mesosomal dorsum coarsely reticulate, propodeal reticulae broader and shallower. Lateral pronotal carina extending to epaulet, humeral angle with sharp obtuse angle. Mesopleuron finely densely punctate and setose, posterior margin defined by vertical carina. Metapleuron and lateral face of propodeum smooth and shining dorsally with isolated fine setae, micropunctate and densely setose ventrally. In dorsal view, mesosoma broadened to anterior third, strongly narrowed at propodeal spiracle, propodeum abruptly broadened. Scutellar scale lacking. Propodeum convex, dorsal and lateral faces not obviously differentiated. *Legs*. Foreleg with a few long strong articulated spines on posterior/lateral margins of tarsomeres. Mid- and hind tibiae each with two rows of prominent spines, 2–4 spines in each row; apical spurs finely serrated laterally. Hind tibia with distinct secretory pore on inner/posterior surface near base of inner spur. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.6 \times$ as wide as T2; anterior face moderately punctate and setose. T2 densely punctate and setose, punctures slightly larger and sparser anterolaterally; felt line broad, $0.4 \times$ as long as T2 laterally. T3–5 densely punctate. Pygidium broad and slightly convex, lateral margins defined by distinct weakly bowed carina, posterior margin rounded and defined by indistinct carina, densely granulate throughout. S1 punctate, with weak darkened median longitudinal carina. S2 densely punctate. S3–5 densely punctate. S6 moderately punctate.

Material examined. Type material. Holotype: ‘Brasil. mer\Sello.’ (green label partially handwritten) ‘6648’ ‘Type’ (red label) ‘Lectotypus\C.E. Mickel’ (red label partially handwritten) [1 female: ZMB]. **Other material.** 92 males and 101 females as follows: ARGENTINA: ENTRE RÍOS: XII.1996 (Liebig, Zelich) [4 females, 4 males: AMNH]; MISSIONES: Dos de Mayo, XII.1989 (Foerster) [1 male: AMNH]; Puerto Esperanza, XII.1976 (M.A. Fritz) [3 males: AMNH]; XII.1973 (M.A. Fritz) [19 males: AMNH]; BRAZIL: MINAS GERAIS: Belo Horizonte, Museu de História Natural, 22.III.1998 (G.A.R. Melo) [1 female: DZUP]; 9 km E de Catas Altas, Serra da Caraca, 12.I.2012 (G.A.R. Melo) [1 female: DZUP]; 8 km S de Ouro Preto, Lago do Custódio, 20.I.2012 (G.A.R. Melo) [3 females: DZUP]; Serra do Caraca, S. Barbara, I.1970 (F.M. Oliveira) [1 male: EMUS]; Viçosa, M. do Paraíso, 5.I.1995 (G.A.R. Melo) [1 female: DZUP]; same city, XII.1944 (Wygodzinsky) [1 female: MNRJ]; PARANÁ: Capitão Leônidas Marques, Salto Caxias, 6–13.X.2004 (Soares, E.D.G.) [3 males: DZUP]; same locality, 13–20.X.2004 (Soares, E.D.G.) [5 males: DZUP]; same

locality, 3–10.XI.2004 (Soares, E.D.G.) [12 males: DZUP]; Fazenda do Jordão, Posto Florestal, Salto Segredo, 6–10.X.2004 (Soares, E.D.G.) [1 male: DZUP]; Jaguatirica, Rio Capivari, 1.III.2003 (G.A.R. Melo) [1 male: DZUP]; Piraquara, Mananciais da Serra, 13.XII.2002 (Garcia, E.Q.) [2 males: DZUP]; same locality, 13.XII.2002 (Garcia, E.Q.) [1 female: DZUP]; same locality, 23.I.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 2.II.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 5.II.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 8.II.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 19.II.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 26.II.2003 (Garcia, E.Q.) [3 females: DZUP]; same locality, 27.II.2003 (Garcia, E.Q.) [2 females: DZUP]; same locality, 14.III.2003 (Garcia, E.Q.) [3 females: DZUP]; same locality, 3.IV.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 27.I.2001 (G.A.R. Melo) [5 males: DZUP]; Ponta Grossa, Parque Estadual da Vila Velha, 5.IV.2013 (K.A. Williams) [12 females: DZUP]; same locality, 6.IV.2013 (K.A. Williams) [10 females: DZUP]; same locality, 11.XII.2000 (Ganho & Marinoni) [1 female: DZUP]; same locality, 25.XII.2000 (Ganho & Marinoni) [1 female: DZUP]; same locality, 11.III.2002 (Ganho & Marinoni) [1 female: DZUP]; Prudentópolis, 8.II.1970 (J.S. Moure) [1 female: DZUP]; Tibagi, XII.1952 (Justus) [1 female: DZUP]; RIO DE JANEIRO: Itatiaia: Faz. Penedo, II.1943 (Wygodzinsky) [1 female: MNRJ]; same city, 700m, XII.1954 (W. Zikan) [1 female: MNRJ]; Petrópolis, IV.1952 (C. Novais) [1 female: MNRJ]; RIO GRANDE DO SUL: Arroio Grande, 101m, 32°13'S, 53°12'W, 9.IV.2004 (R.F. Kruger) [1 male: UFES]; SANTA CATARINA: Criciúma, Campus da UNESC, 16.XI.2002 (G.A.R. Melo) [1 male: DZUP]; Nova Teutonia, XI.1968 (F. Plaumann) [1 female: EMUS]; same locality, various dates (F. Plaumann) [16 females: MNRJ]; same locality, various dates (F. Plaumann) [3 females: YPM]; same locality, XI.1968 (F. Plaumann) [2 males: YPM]; same locality, XII.1968 (F. Plaumann) [1 male: YPM]; same locality, XI.1980 (F. Plaumann) [1 female: DZUP]; SÃO PAULO: Barueri, various dates (K. Lenko) [3 females: CASC]; same locality, V.1958 (K. Lenko) [1 female: MNRJ]; Batatais, I.1946 (J.S. Moure) [1 female: DZUP]; Cajuru, Fazenda Rio Grande, 2–18.XI.1999 (G.A.R. Melo & Nascimento) [2 males: DZUP]; same locality, 17.XI–2.XII.1999 (G.A.R. Melo & Nascimento) [3 males: DZUP]; same locality, 18.XII.1999–10.I.2000 (G.A.R. Melo & Nascimento) [3 males: DZUP]; same locality, 10.I–1.II.2000 (G.A.R. Melo & Nascimento) [4 males: DZUP]; Caraguatatuba, 1.III.1967 (M.E. Irwin) [1 female: CASC]; Cosmópolis, 22.I.1974 (J.G. Rozen et al.) [3 females: EMUS]; Est. Biol. Boracéia, 850m, 27.II.1967 (M.E. Irwin) [2 females: CASC]; Estação Ecológica de Jataí, Luís Antônio, 22.IV.1999 (G.A.R. Melo) [1 female: DZUP]; same locality, 16.X.1999 (G.A.R. Melo) [3 females: DZUP]; Riberão Grande, P.E. Intervalos: ponto 2, 24°16'29"S, 48°25'17"W, 22.I.2010 (Perioto, N.W.) [2 males: MZSP]; same locality, 22.II.2010 (Perioto, N.W.) [1 male: MZSP]; same locality, 22.XII.2010 (Perioto, N.W.) [3 males: MZSP]; same locality, ponto 5, 24°16'23"S, 48°25'22"W, 22.I.2010 (Perioto, N.W.) [2 males: MZSP]; same locality, 22.IV.2010 (Perioto, N.W.) [2 males: MZSP]; same locality, 22.XII.2010 (Perioto, N.W.) [2 males: MZSP]; same locality, 22.XI.2010 (Perioto, N.W.) [1 male: MZSP]; Parque Ainhanguera, 28.II.1986 (C. Costa) [1

female: MZSP]; São Jose dos Campos, XII.1934 (H.S. Lopes) [1 female: MNRJ]; same locality, 5–20.V.1999 (E.R. DePaula) [1 male: EMUS]; Teodoro Sampaio, P.E. Morro do Diabo, Estrada do Angelim, 16.II.1999 (G.A.R. Melo) [1 female: DZUP]; PARAGUAY: ALTO PARANA: Estancia Dimas, 25°33'S, 55°13'W, 28–30.XI.2005 (U. Dreschel) [1 female: EMUS]; CANINDEYÚ: Tava Yopoi, 24°22'S, 55°53'W, 26.X-4.XI.2007 (U. Dreschel) [1 female: EMUS]; PARAGUARÍ: La Rosada, 28–30.IV.2006 (U. Dreschel) [1 female: EMUS]; SAN PEDRO: Rio Ypane, Cororo, various dates (Fritz) [2 females, 2 males: AMNH, EMUS]; URUGUAY, Río NEGRO: Arroyo Negro, 15 km S Paysandu, 27–31.XII.1962 (R.G. Van Gelder) [3 males: AMNH].

Distribution. This species apparently occurs throughout the forest and grassland regions of southern South America: Argentina, Brazil, Paraguay and Uruguay.

Host. Unknown.

Remarks. *Darditilla debilis* is a widely distributed and common species. Over 200 additional specimens were examined in MZSP and others were studied from various North American collections.

Males are associated with *D. debilis* based on morphological similarity to *D. bejarranoi* males and overlapping distribution with the females of *D. debilis*, including five localities where both sexes were collected.

Darditilla felina (Burmeister, 1854)

Figs 7–8, 21–24

Mutilla felina Burmeister, 1854. Abh. naturf. Ges. Halle 2: 26. Holotype female, Brazil, Novo-Friburgo (MLUH, not examined).

Mutilla parasitica Smith, 1879: 213. Holotype female, Brazil, Constanica (NHM, examined), synonymized by Mickel (1964: 166).

Mutilla decorosa Kohl, 1882. Holotype female, Brasilia (NMW, examined through photographs). **syn. n.**

Mutilla decorosa Kohl: Nonveiller 1990: 113, ♀ (*incertae sedis*).

Diagnosis. Male. The male of *D. felina* is easily recognized by having a unique clypeus, with the ventral margin, often hyaline, raised broadly lamellate (Fig. 7D), and the penis valve, which is unidentate apically (Fig. 23).

Female. This female can be separated from all other southern and southeastern Brazillian *Darditilla* by the large, coalescing lateral orange spots of T2 (Fig. 8D), and the large coalescing lateral patches of silver to pale golden setae on the propodeum (Fig. 8A).

Description. Male. Body length 5.8–9.4 mm. **Coloration.** Body and appendages black, except mandibles and metasoma dark brown apically and ventral margin of clypeus often hyaline. Tibial spurs white. Forewing slightly and uniformly infuscated between veins, veins brown; hindwing slightly infuscated. Body clothed with whitish setae, except dorsoposterior portion of pronotum, axilla, scutellum, disc of T2, T6 and



Figure 7. *Darditilla felina* (Burmeister), male: **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** head, anterior view **E** metasoma, dorsal view **F** T5, T6 and pygidium, dorsal view. Scale bars: 1 mm.

T7 with scattered brownish setae, mesoscutum and tegula with dark brown setae, bristles of tergal fringes silver to pale yellowish. *Head*. Rounded posteriorly. Head width $1.2 \times$ pronotal width. Eye transversely ovate. Ocelli small; ocellocular distance $7.1 \times$ length of lateral ocellus, interocellar distance $2.6 \times$ lateral ocellus length. Occipital cari-

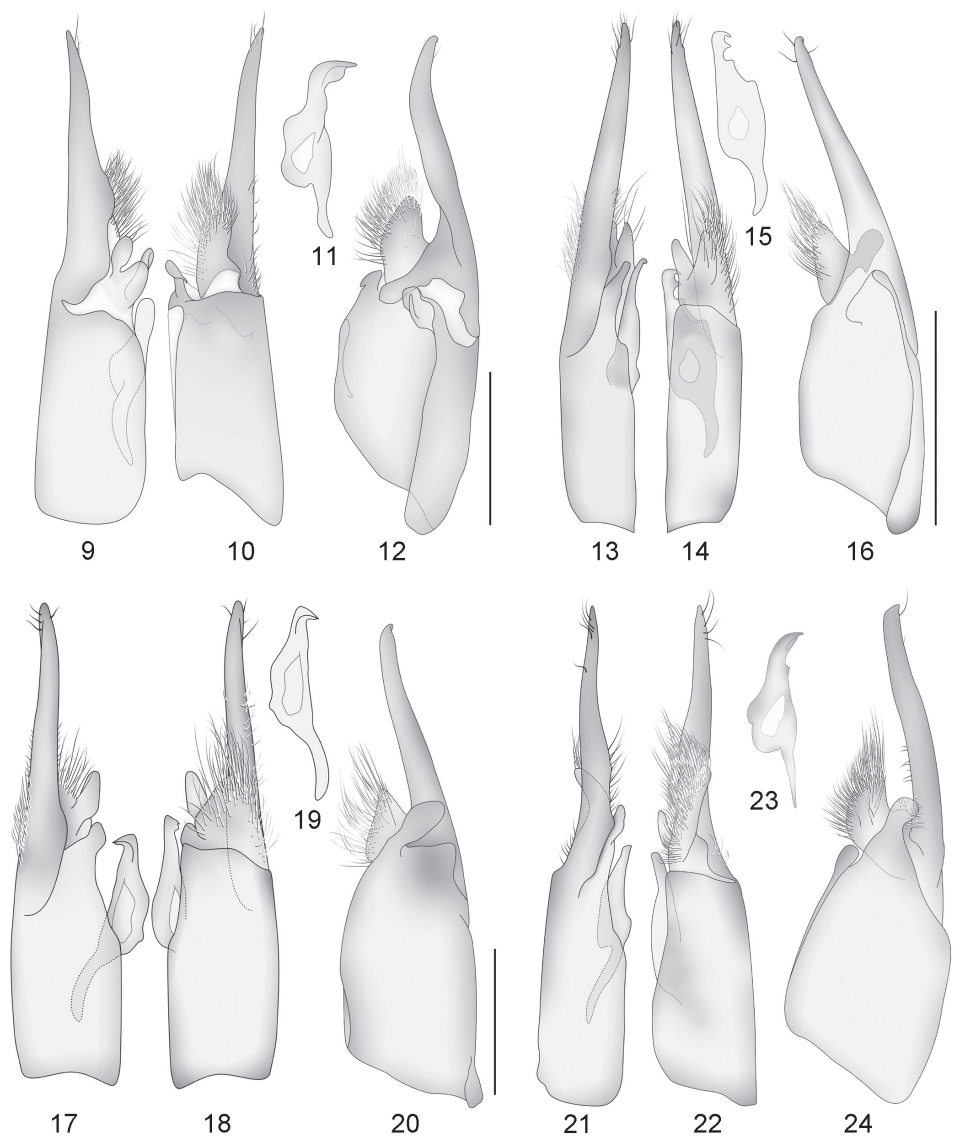
na distinct, extending ventrally almost to level of oral fossa. Punctuation on front dense, interspaces micropunctate; gena densely punctate, interspaces with sparse micropunctures; and vertex moderately punctate, interspaces glabrous. Gena ecarinate. Antennal scrobe broadly concave to eye margin, lacking dorsal carina or tubercle. Clypeus densely punctate, with small median concavity and raised broadly bilobate lamellate ventral margin. Scape unicarinate ventrally. Flagellomere 1 $1.3 \times$ pedicel length; flagellomere 2 $1.6 \times$ pedicel length. Mandible convergent to bidentate apex, dorsal carina gradually becoming obsolete near inner tooth; edentate ventrally. *Mesosoma*. Epaulets weakly produced. Pronotal dorsum densely punctate; anterior face obscurely punctate laterally and smooth medially; lateral face densely punctate. Tegula evenly convex, glabrous except with long recumbent setae anterolaterally and posteromesally. Mesoscutum with dense coarse punctures; posterolateral corner forming a small angulate lobe. Scutellum slightly convex, with coarse punctures. Axilla flat and punctate, except lateral margin with narrow vertical lamella. Metanotum surface obscured by dense shaggy mesally facing recumbent setae. Propodeum convex, broadly and deeply reticulate except smooth and shining adjacent to metapleuron. Mesopleuron moderately punctate, interspaces micropunctate. Metapleuron smooth and shining ventrally, setose and micropunctate dorsally. *Wings*. Forewing with moderate elongate sclerotized pterostigma; marginal cell broadly rounded; three submarginal cells, third scarcely delimited by obscure venation. *Legs*. Mid- and hind tibiae lacking strong spines, distinct apical secretory pore on inner surface near base of inner spur; spurs finely serrate on margins. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.5 \times$ width of T2, sparsely coarsely punctate; apex with fringe of simple setae or thickened bristles. T2 with coarse to moderate punctures, interspaces smooth and generally broader than punctures; apex with fringe interspersed recumbent thickened parallel bristles; felt line $0.5 \times$ lateral length of T2. T3–5 densely and finely punctate, covered with interspersed erect and recumbent setae, except fringes with row of bristles as in T2. T6 densely punctate, covered with less dense recumbent and erect setae. T7 in basal half with densely and coarsely punctures; posterior half forming oval pygidium margined laterally by a strong sharp carina, apical margin rounded, microgranulate with numerous large irregular rugae. S1 punctate and setose, with low medial longitudinal carina extending from base to apex. S2 moderately punctate. S3–6 moderately and finely punctate, with fairly sparse erect and recumbent setae. Lateral margins of S2–5 sometimes with similar bristles to those of T2–6. S7 transversely rectangular. Hypopygium coarsely punctate, posterior margin straight with small medial emargination. *Genitalia* (Figs 21–24). Paramere tapering apically, moderately curved ventrally on basal half, scattered setae along inner and lateral margins. Cuspis angulate apically, extending $\sim 0.3 \times$ free length of paramere, with densely setose oblique ventral surface. Digitus laterally compressed and rounded apically, extending $\sim 0.2 \times$ free length of paramere, asetose. Penis valve asetose, unidentate apically, basoventral margin with two minute teeth, basodorsal margin with slight tubercle.

Extended female diagnosis. Body length 5.7–11.9 mm. *Coloration*. Body entirely black, except T2 with large, coalescing lateral orange spots and S2 often orange



Figure 8. *Darditilla felina* (Burmeister), female: **A** habitus, dorsal view **B** habitus, lateral view **C** head, anterior view **D** metasoma, dorsal view **E** T5 and pygidium, dorsal view. Scale bars: 1 mm.

basomedially. Appendages variable, ranging from entirely black to entirely orangish. Tibial spurs whitish. Head with sparse erect black setae. Mesosoma with sparse erect black setae, except propodeum with coalescing large lateral patch of silver to pale golden setae. Posterior fringes of T1 and T2 black; T2 setae black anteriorly and posteriorly, pale golden laterally, and reddish orange on orange integumental spots; T3–6 clothed with silver to golden setae. *Head*. Transverse, posterior margin flat, occipital carina obscure. Head width $1.5 \times$ pronotal width. Eye slightly ovate transversely, ommatidia distinct. Front, vertex and gena densely punctate. Genal carina well-defined, terminating in sharp angle posterior to hypostomal carina. Clypeus with transverse glabrous concavity, margined by dorsal and ventral carinae, between widely separated



Figures 9–24. Male genitalia of *Darditilla* species: dorsal view (left), ventral view (middle), lateral view of penis valve (above), and lateral view with penis valve removed (right). **9–12** *Darditilla amabilis* **13–16** *D. bejaronoi* **17–20** *D. debilis* **21–24** *D. felina*. Scale bars: 0.5 mm.

lateral teeth. Mandible tapering to apex, with tooth in basal third and in apical third, unarmed ventrally. Antennal scrobe with complete dorsal carina. Antennal tubercle punctate basally and on anterior face, glabrous dorsally. Scape simple, moderately punctate. Flagellomere 1 $2.0 \times$ pedicel length; flagellomere 2 $1.25 \times$ pedicel length. *Mesosoma*. Mesosomal length $1.4 \times$ width. Mesosomal dorsum densely reticulate, propodeal reticulæ broader. Lateral pronotal carina extending to epaulet, humeral

angle obtusely angulate. Mesopleuron densely punctate and setose, posterior margin defined by vertical carina. Metapleuron and lateral face of propodeum smooth and shining dorsally with isolated fine setae, micropunctate and densely setose ventrally. In dorsal view, mesosoma broadened to anterior third, strongly narrowed at propodeal spiracle, propodeum abruptly broadened. Scutellar scale lacking. Propodeum convex, dorsal and lateral faces not obviously differentiated. *Legs*. Foreleg with a few long strong articulated spines on posterior/lateral margins of tarsomeres. Mid- and hind tibiae each with one rows of prominent spines, 5 spines in each row; apical spurs finely serrated laterally. Hind tibia with distinct secretory pore on inner/posterior surface near base of inner spur. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.5 \times$ as wide as T2; anterior face moderately punctate and setose. T2 densely punctate, punctures slightly larger and sparser anterolaterally on orange spots; felt line broad, $0.6 \times$ as long as T2 laterally. T3–5 densely punctate. Pygidium broad and slightly convex, lateral margins defined by distinct weakly bowed carina, posterior margin rounded and defined by indistinct carina, granulate. S1 punctate, with obscure blackish median carina. S2 moderately punctate. S3–6 densely punctate.

Material examined. Type material. Holotypes: *Mutilla parasitica*, ‘CONSTANCIA\Jan 1857.\H.Clark’ ‘Mutilla\parasitica\ (Type) Sm’ (handwritten label) ‘Type’ (round, red-edged label) ‘B.M. TYPE\HYM.\15.871’ [1 female: NHM]; *Mutilla decorosa*, ‘Wthm.’ ‘6648’ ‘Brasilia\Macalú’ (handwritten label) ‘decorosa Kohl\Type’ (handwritten label) ‘decorosa\Type. Kohl’ (handwritten label) ‘HT decorosa’ (handwritten label) ‘Pseudomethoca\decorosa (Kohl)\det.R.Cambra 2012’ (handwritten label) [1 female: NMW]. **Other material.** 143 males and 36 females as follows: BRAZIL: MATO GROSSO DO SUL: Aquidauana, malaise 09, 20°26'07"S, 55°39'33"W, 11-26.X.2011 (Lamas & Nihei) [2 males: MZSP]; PARANÁ: Capitão Leônidas Marques, Salto Caxias, 3-10.XI.2004 (E.D.G. Soares) [18 males: DZUP]; Fazenda do Jordão, Posto Florestal, Salto Segredo, 6-10.X.2004 (E.D.G. Soares) [5 males: DZUP]; same locality, 13-20.X.2004 (E.D.G. Soares) [3 males: DZUP]; Piraquara, Mananciais da Serra, 2.XII.2005 (L.C. Rocha-Filho) [1 female: DZUP]; same locality, 2.I.2006 (L.C. Rocha-Filho) [1 female: DZUP]; same locality, 30.XI.2005 (L.C. Rocha-Filho) [2 males: DZUP]; same locality, 10.I.2001 (G.A.R. Melo) [2 females: DZUP]; same locality, 27.I.2001 (G.A.R. Melo) [1 male: DZUP]; same locality, 9.III.2002 (Garcia, E.Q.) [1 female: DZUP]; same locality, 24.IV.2002 (Garcia, E.Q.) [1 female: DZUP]; same locality, 12.XII.2002 (Garcia, E.Q.) [1 female: DZUP]; same locality, 5.II.2003 (Garcia, E.Q.) [2 females: DZUP]; same locality, 1.II.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 8.II.2003 (Garcia, E.Q.) [1 female: DZUP]; same locality, 26.II.2003 (Garcia, E.Q.) [2 females: DZUP]; same locality, 27.II.2003 (Garcia, E.Q.) [2 females: DZUP]; same locality, 14.III.2003 (Garcia, E.Q.) [1 female: DZUP]; Ponta Grossa, Lageado, II.1957 (Justus) [1 female: DZUP]; Parque Estadual Vila Velha, 25.X.1999 (Ganho & Marinoni) [3 males: DZUP]; same locality, 1.XI.1999 (Ganho & Marinoni) [11 males: DZUP]; same locality, 8.XI.1999 (Ganho & Marinoni) [7 males: DZUP]; same locality, 15.XI.1999 (Ganho & Marinoni) [1 female, 6 males: DZUP]; same locality, 22.XI.1999 (Ganho & Marinoni) [10 males: DZUP]; same lo-

cality, 29.XI.1999 (Ganho & Marinoni) [2 males: DZUP]; same locality, 6.XII.1999 (Ganho & Marinoni) [2 males: DZUP]; same locality, 20.XII.1999 (Ganho & Marinoni) [1 female, 1 male: DZUP]; same locality, 27.XII.1999 (Ganho & Marinoni) [1 male: DZUP]; same locality, 23.X.2000 (Ganho & Marinoni) [4 males: DZUP]; same locality, 30.X.2000 (Ganho & Marinoni) [1 male: DZUP]; same locality, 6.XI.2000 (Ganho & Marinoni) [3 males: DZUP]; same locality, 13.XI.2000 (Ganho & Marinoni) [4 males: DZUP]; same locality, 20.XI.2000 (Ganho & Marinoni) [1 male: DZUP]; same locality, 27.XI.2000 (Ganho & Marinoni) [4 males: DZUP]; same locality, 4.XII.2000 (Ganho & Marinoni) [1 female, 3 males: DZUP]; same locality, 1.I.2001 (Ganho & Marinoni) [1 female: DZUP]; same locality, 29.X.2001 (Ganho & Marinoni) [1 female: DZUP]; same locality, 29.X.2001 (Ganho & Marinoni) [4 males: DZUP]; same locality, 5.XI.2001 (Ganho & Marinoni) [1 female: DZUP]; same locality, 12.XI.2001 (Ganho & Marinoni) [6 males: DZUP]; same locality, 26.XI.2001 (Ganho & Marinoni) [11 males: DZUP]; same locality, 3.XII.2001 (Ganho & Marinoni) [2 males: DZUP]; same locality, 26.XI.2001 (Ganho & Marinoni) [2 females: DZUP]; same locality, 24.XII.2001 (Ganho & Marinoni) [1 female: DZUP]; same locality, 28.I.2002 (Ganho & Marinoni) [1 female: DZUP]; same locality, 18.III.2002 (Ganho & Marinoni) [1 female: DZUP]; São José dos Pinhais, 17-27.XII.1984 (C.I.I.F.) [1 male: DZUP]; same locality, 22-29.X.1984 (C.I.I.F.) [1 male: DZUP]; same locality, 17-27.XII.1984 (C.I.I.F.) [1 male: DZUP]; RIO DE JANEIRO: Itatiaia, 6 km NW de Itatiaia, PN Itatiaia, 28.X.2011 (D.R. Luz) [1 female, 1 pair *in copula*: DZUP]; Novo Friburgo, I.2013 (P.C. Grossi) [1 male: DZUP]; Represa Rio Grande, 20.V.1967 (F.M. Oliveira) [1 female: DZUP]; Teresopolis, P.N. Serra das Orgãos, 22°26'S, 42°56'W, 31.X-5.XI.2004 (A.L.B.G. Peronti) [1 male: UFES]; SANTA CATARINA: Corupa, I.1954 (A. Maller) [1 female: MNRJ]; same locality, II.1954 (A. Maller) [2 females: MNRJ]; SÃO PAULO: Americo Brasiliense Clube Nautico, Cerrado, 25-29.IX.1999 (M.T. Tavares) [1 male: UFES]; Cajuru, Fazenda Santa Carlota, 17.XI-2.XII.1999 (G.A.R. Melo & Nascimento) [2 males: DZUP]; Campos do Jordão, XI.1957 (K. Lenko) [1 female: DZUP]; Eug. Lefevre, 1.XI.1937 (Travassos, Lopes e Oiticica) [1 female: MNRJ]; Riberão Grande, P.E. Intervalles: ponto 2, 24°16'29"S, 48°25'17"W, 22.XII.2009 (N.W. Perioto) [3 males: MZSP]; same locality, ponto 3, 24°16'28"S, 48°25'19"W, 23.XI.2009 (N.W. Perioto) [6 males: MZSP]; same locality, 22.I.2010 (N.W. Perioto) [2 males: MZSP]; same locality, 22.XI.2010 (N.W. Perioto) [2 males: MZSP]; same locality, ponto 4, 24°16'29"S, 48°25'21"W, 20.XII.2010 (N.W. Perioto) [2 males: MZSP]; PARAGUAY: SAN PEDRO: Rio Ypane, Cororo, XII.1983 (M.A. Fritz) [1 male: AMNH]; same locality, 24-27.XI.1983 (M. Wasbauer) [1 male: EMUS].

Distribution. This species is distributed throughout the Atlantic Rainforest of Brazil and Paraguay.

Host. Unknown.

Remarks. The sexes of *D. felina* were associated based on collection of a mating pair in the *Parque Nacional do Itatiaia* in Rio de Janeiro state. DRL discovered the male and female together, already *in copula*, on leaf litter in a trail through the forest.

The male that Burmeister (1854) originally associated with *D. felina* was recognized as *Ephuta inaurata* (Smith, 1855) by Mickel (1964).

Both sexes of *D. felina* have been examined from throughout the Atlantic Rainforest. The subspecies, *D. felina agatas* Casal, 1968 differs from typical females of *D. felina* in setal coloration and is known from two specimens from the Chaco region of Bolivia. It is unclear whether this is a valid species, valid subspecies, or a synonym of *D. felina* without study of further specimens.

Females that key (Casal 1968a) to *D. felina* have been examined from Rondônia. Although these females match *D. felina* in coloration, their genal carina is different. *Darditilla felina* has the genal carina extending from the posterior head margin to below the eye, where it terminates at an angle; this putative new species has the genal carina extending nearly to the hypostomal carina where it gradually terminates. We refrain from describing the species at this time because the focus of this manuscript is southern and southeastern Brazilian *Darditilla* and the male is yet unknown.

Females show extensive variation in coloration of the legs. Many specimens have the legs entirely orange, while other specimens, including the female from the mating pair, have the legs partially darkened or entirely black. In an unpublished key to female *Pseudomethoca* types, Mickel separated *D. felina* from *Mutilla decorosa* (Kohl, 1882) on the basis of leg color. Photographs of the type of *M. decorosa* were provided by Dominique Zimmermann (NMW) and it is a perfect match for the orange-legged form of *D. felina*. As such, we place *M. decorosa* as a junior synonym of *D. felina*.

Discussion

These are the first valid species-level sex associations in *Darditilla*. The sex associations presented here support Casal's (1965, 1968a) initial genus-level associations. Because his male diagnosis, however, was based on a single species, it needed to be altered, as provided above. Seven additional South American genera are recognized from both sexes, but do not yet have any published species-level associations: *Calomutilla* Mickel, 1952 (Quintero and Cambra 1996, Quintero and Cambra 2001); *Limaytilla* Casal, 1964 (Brothers 2006); *Neomutilla* Reed, 1898 (Quintero and Cambra 2001); *Pertyella* Mickel, 1952 (Quintero and Cambra 1996); *Suarezitilla* Casal, 1968 (Casal 1968b); *Tobantilla* Casal, 1965 (Williams et al. 2011); and *Vianatilla* Casal, 1962 (Quintero and Cambra 1996). Discovery of species-level sex associations in these genera will likely lead to broader diagnoses for the genera and can verify, or potentially invalidate, these genus-level associations.

The initial sex associations for this project came from a field observation of a mating pair (*D. felina*) and from a mating pair in a museum (*D. bejaranoi*). These rare events provided the data needed for further discoveries. The male morphology analyzed from the first two sex associations was compared to other male mutillids and allowed us to associate the sexes of two other species (*D. amabilis* & *D. debilis*). There remain 31 *Darditilla* species known only from females (Nonveiller 1990). Data pre-

sented here could be vital for recognizing the males. Instead of relying on rare events, further progress can be made in mutillid sex associations by systematic study of the distribution and morphology of museum specimens.

Acknowledgements

We are grateful to the collection managers and curators that provided specimens and photographs for this research, including: Gabriel Melo (DZUP), Carlos Brandão (MZSP), Christine LeBeau (AMNH), Felipe Vivallo (MNRJ), James Pitts (EMUS), Gavin Broad (NHM), Dominique Zimmermann (NMW), Celso Azevedo (UFES), Frank Koch (ZMB) and Raymond Pupedis (YPM). The authors would also like to thank CNPq for financial support: DRL (process number 143491/2011-3) and KAW (process number 370106/2013-0). This is Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Entomology Contribution 1272.

References

- André E (1908) Étude sur les Mutillides du Musée National d'Histoire naturelle de Buénos Aires. *Anales del Museo Nacional de Buenos Aires* (Ser. 3a) 10: 169–214.
- Brothers DJ (2006) Familia Mutillidae. In: Fernandez F, Sharkey MJ (Eds) *Introducción a los Hymenoptera de la Región Neotropical*. Sociedad Colombiana de Entomología & Universidad Nacional de Colombia, Bogotá DC, 577–594.
- Burmeister HCC (1854) Uebersicht der brasilianischen Mutillen. *Abhandlungen der Naturforschenden Gesellschaft zu Halle* 2: 19–29.
- Burmeister HCC (1875 [“1874”]) Mutillae Argentinae. *Boletín de la Academia Nacional de Ciencias Exactas existente en la Universidad de Córdoba* 1: 461–502.
- Casal OH (1965) *Darditilla* nuevo género neotropical de Sphaerotherminae [sic!] (Hym. Mutillidae). *Eos, Revista Española de Entomología*, Madrid 41: 9–18.
- Casal OH (1968a) Aportaciones para el conocimiento de las Mutillidae de la Republica Argentina. I. – Las hembras del genero *Darditilla* (Hymenoptera). *Revista de la Sociedad Entomológica Argentina* 30(1/4): 83–96.
- Casal OH (1968b) Comentarios sobre *Reedomutilla* Mickel, 1964 con la descripción de *Suarezitilla* gen. nov. (Hymenoptera, Mutillidae). *Neotropica (La Plata)* 14(44): 75–80.
- Casal OH (1971) Dos nuevas especies de *Darditilla* Casal (Hymenoptera, Mutillidae). *Anales del Museo de Historia Natural de Valparaíso* 4: 251–254.
- Fritz MA, Martínez A (1974) Notas sobre Mutillidae, II. (Hymenoptera). *Studia Entomologica* 17(1/4): 313–316.
- Fritz MA, Martínez A (1993) Notas sinonimicas de Mutillidae neotropicales (Hymenoptera). *Revista Chilena de Entomología* 57: 9–11.
- Gerstaecker A (1874) Mutillarum Americae meridionalis indigenarum synopsis systematica et synonymica. *Archiv für Naturgeschichte* 40: 41–77, 299–328.

- Kohl FF (1882) Neue Hymenopteren in den Sammlungen des k. k. zoolog. Hof-Cabinetes zu Wien. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 32: 475–498.
- Mickel CE (1964) Synonymical notes on Neotropical Mutillidae (Hymenoptera). Proceedings of the Royal Entomological Society of London (B) 33(9/10): 163–171.
- Nonveiller G (1990) Catalogue of the Mutillidae, Myrmosidae and Bradynobaenidae of the Neotropical Region including Mexico (Insecta, Hymenoptera). Hymenopterorum Catalogus (Nova Editio), 18. SPB Academic Publishing, Den Haag, 150 pp.
- Quintero D, Cambra RA (1996) Contribución a la sistemática de las Mutílidas (Hymenoptera) del Perú, en especial las de la Estación Biológica BIOLAT, Río Manu, Pakitza. In: Wilson DE, Sandoval A (Eds) Manu: The Biodiversity of Southeastern Peru. Smithsonian Institution Press, Washington, D.C., 327–357.
- Quintero D, Cambra RA (2001) On the identity of *Scaptopoda* F. Lynch Arribálzaga, new taxonomic changes and new distribution records for Neotropical Mutillidae (Hymenoptera), with notes on their biology. Transactions of the American Entomological Society 127(3): 291–304.
- Smith F (1879) Descriptions of new species of Hymenoptera in the collection of the British Museum. British Museum, London, 240 pp.
- Williams KA, Brothers DJ, Pitts JP (2011) New species of *Tobantilla* Casal, 1965 and a new genus and species, *Gogoltilla chichikovi* gen. et sp. nov., from Argentina (Hymenoptera: Mutillidae). Zootaxa 3064: 41–68.

Du'an Karst of Guangxi: a kingdom of the cavernicolous genus *Dongodytes* Deuve (Coleoptera, Carabidae, Trechinae)

Mingyi Tian¹, Haomin Yin¹, Sunbin Huang¹

¹ Department of Entomology, College of Natural Resources and Environment, South China Agricultural University, 483 Wushan Road, Guangzhou, 510642, China

Corresponding author: Mingyi Tian (mytian168@aliyun.com)

Academic editor: T. Assmann | Received 16 February 2014 | Accepted 17 October 2014 | Published 14 November 2014

<http://zoobank.org/9A22E524-BD38-402F-ABDC-506BC238CF94>

Citation: Tian MY, Yin HM, Huang SB (2014) Du'an Karst of Guangxi: a kingdom of the cavernicolous genus *Dongodytes* Deuve (Coleoptera, Carabidae, Trechinae). ZooKeys 454: 69–107. doi: 10.3897/zookeys.454.7269

Abstract

Recent cave biodiversity surveys carried out in Du'an County and its adjacent areas of northwestern Guangxi, China, have revealed some exciting scientific findings. In a very limited area seven new species of the cavernicolous trechine genus *Dongodytes* Deuve, 1993 were found and are described: *Dongodytes* (*s. str.*) *elongatus* **sp. n.**, *D. (s. str.) troglodytes* **sp. n.**, *D. (s. str.) lani* **sp. n.**, *D. (Dongodytodes) brevipenis* **sp. n.**, *D. (Dongodytodes) jinzhensis* **sp. n.**, *D. (Dongodytodes) inexpectatus* **sp. n.** and *D. (Dongodytodes) yaophilus* **sp. n.** Diagnoses and notes on the genus, subgenera, and two known species in Du'an Karst, *Dongodytes* (*s. str.*) *baxian* Tian, 2011 and *D. (Dongodytodes) deharvengi* Tian, 2011, are also given. A key to subgenera and all species of *Dongodytes* is provided. To date, *Dongodytes* becomes one of the richest in species genera of subterranean carabid trechines in China with 12 species which are arranged into two subgenera. *Dongodytes* (*s. str.*) Deuve is composed of seven species, four of which from Du'an County, each of other three from Bama, Fengshan and Tian'e Counties, respectively. All species of the subgenus *Dongodytodes* Tian, 2011 are recorded from Du'an Karst. By having 10 species (nine *Dongodytes* and one *Libotrechus* Uéno, 1998), Du'an Karst holds the richest specific diversity of cavernicolous Trechinae in China. *Dongodytes* species are distributed in a very limited area of the river Hongshui He drainages in northwestern Guangxi, and the river acts as a natural barrier of *Dongodytes* dispersal at only a specific level. However, all members of *Dongodytodes* are recorded from the eastern or northern bank of Hongshui He.

Keywords

Ground beetles, anophthalmic, troglobitic, new species, specific diversity, China

Introduction

Although troglobitic trechine species were not reported from Mainland China before 1991 (Uéno and Wang 1991), China has become one of the most fascinating countries for subterranean trechines in the world, having more than 30 genera and about 90 species so far (Tian and Clarke 2012). All of the known cave-dwelling trechines in Mainland China are recorded from the southern provinces or regions, viz. Guizhou, Guangxi, Yunnan, Sichuan, Chongqing, Hunan, Hubei, Jiangxi and Zhejiang (Deuve et al. 1999; Deuve 2002; Uéno 1998b, 2007; Uéno and Clarke 2007; Deuve and Tian 2008, 2009, 2011; Tian 2010, 2011; Tian and Yin 2013).

Dongodytes Deuve, 1993 is one of the morphologically most modified cavernicolous genera within the subfamily Trechinae and represents a very peculiar lineage (Deuve 1993; Vigna Taglianti 1997; Uéno 1998a). It was established by Deuve (1993) to comprise the species *D. fowleri* Deuve, 1993, known by only a single male specimen at that time which was collected in a limestone cave in Bama County of northwestern Guangxi. Then, Uéno (1998a) discovered two more specimens of *D. fowleri* in the same cave and described the second species *D. grandis* from a cave in Fengshan County. Seven years later, Uéno (2005) reported the third species, *D. giraffa* from a cave in southern Tian'e County, northern Guangxi, which is the most modified species in *Dongodytes*, having a very long and elongate head and prothorax, and serrate humeral shoulders. According to material collected from two caves in Du'an County, Tian (2011) added two species to the genus, one belonging to the nominate subgenus *Dongodytes* (*s. str.*), the other to the newly established subgenus *Dongodytodes* Tian, 2011.

Administratively, Du'an Yao Autonomous County belongs to Hechi Prefecture, northwestern Guangxi Zhuang Autonomous Region (Fig. 1). This county is located on the transition zones between Yunnan-Guizhou Plateau and Guangxi Basin. Karstic landscape covers 77.9% of the whole terrestrial areas in Du'an (Hu et al. 2012), creating numerous mountains, hills and caves (Figs 2–5). However, the subterranean fauna in Du'an is still not well-known. The only exception is the fauna of cave fishes. In total, nine species of cave fishes are recorded in Du'an, including three anophthalmic species (Lan et al. 2013). On the contrary, only three troglobitic carabid beetles have been reported from this county so far: a clivinine *Guiodytes cavicola* Tian, 2013 (Tian 2013, 2014) and two trechines, *Dongodytes* (*s. str.*) *baxian* Tian, 2011 and *D. (Dongodytodes) deharvengi* Tian, 2011. All above mentioned ground beetles were part of the findings of the China-France Biospeleological Expedition 2010 in Guangxi, which was led by Dr. Louis Deharveng, a well known biospeleologist of Muséum National d'Histoire Naturelle, Paris, and organized by the Biodiversity Conservation Office, Forestry Department of Guangxi Regional Government and financed by the World Bank, GEF.

In 2013, Du'an Karst was surveyed to study the cave fauna as part of a biodiversity conservation project, sponsored mainly by Nanjing Institute of Environmental Sciences, Ministry of Environmental Protection. Three biospeleological surveys had been carried out in May, June and December of 2013 in Du'an and the adjacent karstic

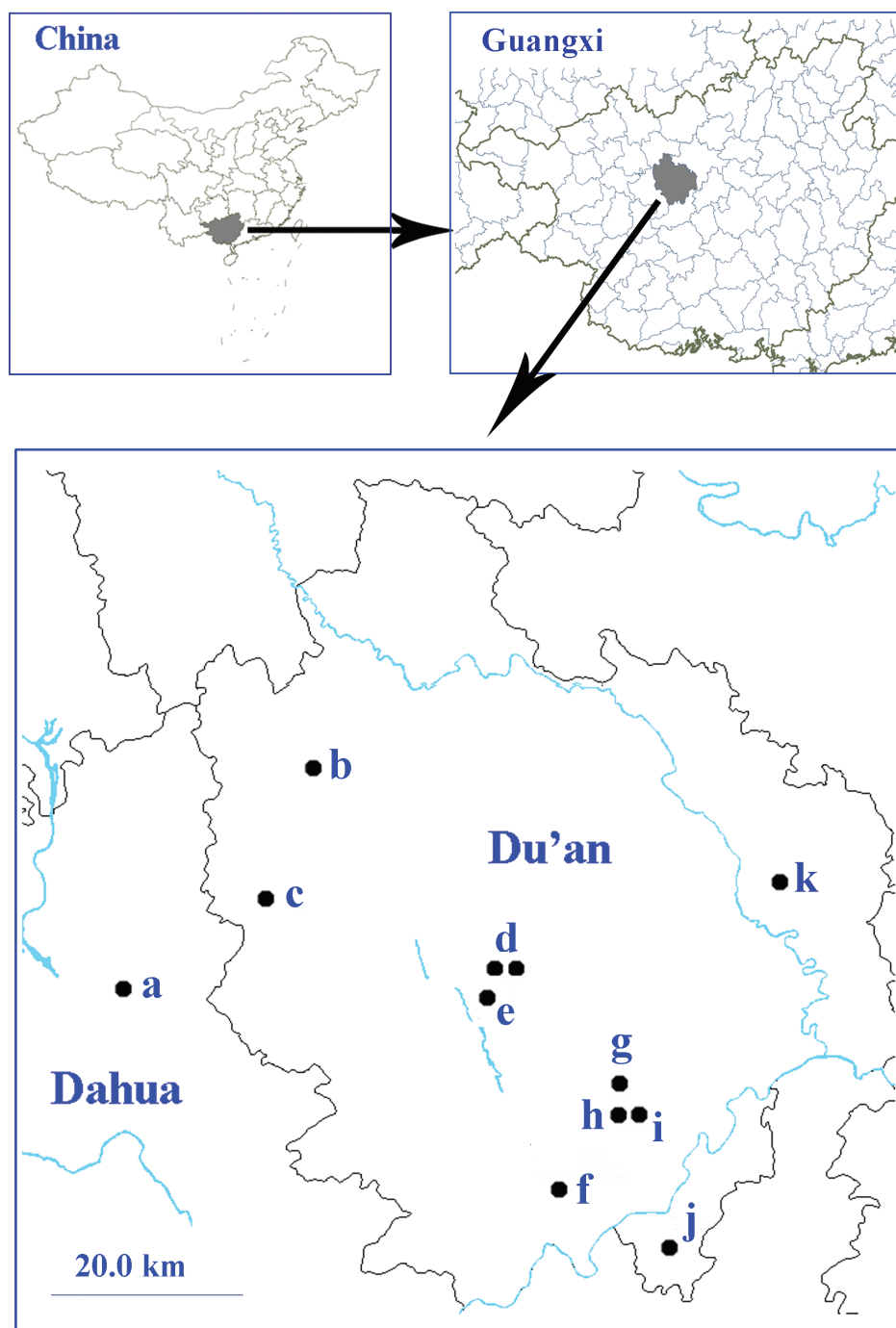


Figure 1. Surveyed caves in Du'an Karst from which trechine beetles were discovered. **a** Qiaoxu Dong (Qibainong) **b** Lubian Dong (Xia'ao) **c** Shuiyuan Dong (Longfu) **d** Jinzhu Dong I and Jinzhu Dong II **e** Nongguanshang Dong II **f** Baxian Dong (Chengjiang) **g** Diaomao Dong (Chengjiang) **h** Nongzhong Dong I (Chengjiang) **i** Nongqu Dong (Longwan) **j** Longhuan Dong (Longwan) **k** Lapo Dong I (Lalie).



Figures 2–5. Karstic landscapes in Du'an County. **2** hills near Gushan, on the road to Lalie **3** a cave entrance near Gushan, on the road to Lalie **4–5** beautiful deposits in Qinqi Dong of Longwan.

areas, and led to important discoveries. Seven new species of *Dongodytes* were found: three belonging to *Dongodytes* (*s. str.*), and four to the subgenus *Dongodytodes*. In addition, another new species of the genus *Libotrechus* Uéno, 1998 was also found in cave Shuiyuan Dong in Longfu (Lin and Tian 2014). This extremely rich anophthalmic trechine fauna, of 10 species, makes Du'an Karst the “hottest” spot of cavernicolous trechines in China. It is probably that additional *Dongodytes* species or other eyeless trechines will be discovered in Du'an Karst.

Materials and methods

During the biospeleological surveys in 2013, we visited and collected in 48 caves in Du'an and its adjacent areas. In total, 95 specimens of *Dongodytes* were found in 12 caves, all of

them are in Du'an County except the cave Qiaoxu Dong which is in Dahua County but belongs also to Du'an Karst (Fig. 1a).

The beetles were collected by hand or by using an aspirator, and kept in 55% ethanol before study. Dissections and observations were made under a Leica MZ75 dissecting microscope. Dissected genital pieces, including the median lobe and parameres of aedeagus, were glued on small paper cards and then pinned under the specimen from which they were removed. Digital pictures were taken using a Canon EOS 5D Mark III camera, and then processed by means of Adobe Photoshop CS5 software. Distributional map was prepared using Mapinfo 8.5 SCP software.

Length of body is measured from apex of right mandible (in opened position) to elytral apex.

Abbreviations of other measurements used in the text are as following.

HL	length of head, from apex of right mandible to occipital suture;
HW	maximum width of head;
PL	length of pronotum, along the median line;
PW	maximum width of pronotum;
PTW	maximum width of prothorax;
PAW	width of pronotum at front;
PBW	width of pronotum at base;
EL	length of elytra, from base of scutellum to elytral apex;
EW	maximum width of combined elytra.

Abbreviations for the specimens' depository are as following.

IOZ	National Museum of Zoology, Institute of Zoology, Chinese Academy of Sciences, Beijing;
MNHN	Muséum National d'Histoire Naturelle, Paris;
SCAU	South China Agricultural University, Guangzhou;
ZUBM	Biological Museum of Zhongshan University, Guangzhou.

Systematics

Genus *Dongodytes* Deuve

Dongodytes Deuve, 1993: 292

Type species. *D. fowleri* Deuve, 1993: 292

Type locality. Jiabao Dong, in Bama County, northwestern Guangxi (Uéno 1998).

Diagnostic characters of the genus. Members of *Dongodytes* share the following combined characters: elytra remarkably elongate though much wider than prothorax and without shoulders; eyes completely effaced and depigmented; body especially head and

prothorax strongly elongate; frontal furrows very short, mandibles long and slender, right mandible bidentate, palps and antennae very elongate and thin; propleura strongly tumid, visible from above; pronotum much longer than wide; elytra depressed medially on humeral parts, anterior and preapical dorsal pores present or not, humeral set of marginal umbilicate pores not aggregated, 1st pore widely located from 2nd and 3rd which are close to each other, 1st to 3rd more or less adjoining marginal gutter, 4th distinctly dorsal wards located and far from marginal gutter; 5th and 6th of middle set are close to each other; legs thin and very long, tarsi slender; protarsi not distinctly modified in male.

Male genitalia are strongly diversified in *Dongodytes* and could be important character states for phylogenetic analysis of the genus. Three types of the median lobe can be recognized. Type I, species of the subgenus *Dongodytes* (*s. str.*) which are known only from Du'an Karst, the median lobe is very short and stout, basal orifice very large, but with a very small, sometimes indistinct, sagittal aileron, and the parameres are broader (Figs 33–38); Type II, species of the subgenus *Dongodytodes*, which are all known from Du'an Karst, the median lobe is very elongate and thin, basal orifice comparatively small, but with a large sagittal aileron, and slender parameres (Figs 39–46); Type III, species of *Dongodytes* (*s. str.*) which are all known from other counties rather than Du'an: the median lobe is intermediately shaped between the two patterns described above, moderately elongate, rather stout, and with a large sagittal aileron; in particular, the median lobe distinctly curved at apex (Deuve 1993: Fig. 2; Uéno 1998: Figs 1–4).

Systematic position of *Dongodytes*. *Dongodytes* is one of the most modified troglobiomorphic genera of trechines in the world. To determine the taxonomic position of *Dongodytes* within the tribe Trechini remains a challenge. Vigna Taglianti (1997) and Uéno (1998) suggested it may be allied to the European *Aphaenops* series, contrary to Deuve (1993) who compared *Dongodytes* with *Sinaphaenops* Uéno & Wang, 1991. Because recent study based on molecular phylogenetic analysis have clearly demonstrated that the *Aphaenops* series in the widest and traditional sense are restricted to the Pyrenean lineage (Faille et al. 2010, 2013), we agree with Deuve's opinion. *Dongodytes* seems to be allied to its Chinese congeners such as *Sinaphaenops* and *Pilosaphaenops* Deuve & Tian, 2008. For example, by having very short frontal furrows, very elongate genae and slender neck constriction, the head structures of *Dongodytes* are more or less similar to those of *Sinaphaenops* and *Pilosaphaenops*. Furthermore, all of the above genera have similar prothorax although latero-marginal setae are always absent in *Sinaphaenops* and *Pilosaphaenops*.

Geographical distribution. Endemic to northwestern Guangxi (Fig. 73). Members of *Dongodytes* are recorded from several counties of Hechi Prefecture. However, only a single species is known in each of Bama, Fengshan, Tian'e and Dahua Counties, respectively. On the other hand, majority of the species (eight) are distributed in Du'an County. Thus, it is clear that, from the present knowledge, all species of *Dongodytes* are distributed in a very limited area of the river Hongshui He drainages in northwestern Guangxi. The river acts as a natural barrier for dispersal of *Dongodytes* at only a specific level. The nominate subgenus *Dongodytes* (*s. str.*) covers a larger distribution range than the subgenus *Dongodytodes* which is restricted to Du'an Karst in the eastern or northern bank of Hongshui He.

Taxonomic treatment. Species of *Dongodytes* are divided into two subgenera, *Dongodytes* (*s. str.*) Deuve and *Dongodytodes* Tian. Both subgenera can be separated each other by shape of head, length of antennae, body pubescent or not, and chaetotaxal pattern on head, pronotum, elytra, and abdominal ventrite VII of male (Tian 2011). See the following key for details.

Key to subgenera and species of *Dongodytes* Deuve

- 1 Antennae very long, extending over elytral apex (Figs 8–10), head more elongate, gradually narrowed posteriad, neck constriction long (Figs 16–19), posterior supraorbital setae present or not, head and pronotum glabrous or covered with sparse long and erected setae; elytra glabrous in most species (except for *D. elongatus* sp. n.), anterior dorsal pore of 3rd elytral stria present (Fig. 6); ventrite VII in male with two pairs of paramedian setae (Fig. 25) (subgenus *Dongodytes* Deuve)..... **2**
- Antennae short, not extending over elytral apex (Figs 11–15), head less elongate, suddenly constricted posteriad before neck constriction which is short (Figs 20–24), posterior supraorbital setae always present, whole body pubescent, covered with dense, erected short setae, anterior dorsal pore of 3rd elytral stria absent (Fig. 7); ventrite VII in male with a pair of paramedian setae (Fig. 26) (subgenus *Dongodytodes* Tian) **8**
- 2 Fore body extremely elongate especially on head, head (excluding mandibles) plus prothorax as long as elytra, propleura slightly expanded (Tian'e: cave Bahao Dong) ***D. (s. str.) giraffa* Uéno**
- Fore body less elongate, head (excluding mandibles) plus prothorax shorter than elytra, propleura strongly expanded **3**
- 3 Posterior latero-marginal setae of pronotum absent **4**
- Posterior latero-marginal setae of pronotum present **5**
- 4 Elytra pubescent, with three dorsal pores on 3rd stria (Du'an: Lalie: cave Lapo Dong I) ***D. (s. str.) elongatus* sp. n.**
- Elytra smooth and glabrous, with two dorsal pores on 3rd striae, the preapical one absent (Du'an: Longwan: cave Longhuan Dong) ... ***D. (s. str.) lani* sp. n.**
- 5 Hind latero-marginal setae of pronotum distant from hind angles, pronotum glabrous, ventrites IV–VI each with two pairs of paramedian setae, median lobe of aedeagus distinctly curved at apex **6**
- Hind latero-marginal setae close to hind angles, pronotum covered by sparse and long setae, ventrites IV–VI each with only a pairs of paramedian setae, median lobe of aedeagus not curved at apex..... **7**
- 6 Lateral borders of pronotum invisible from above in apical fifth, pronotum shorter (PL/PW=2.0) (Bama: cave Jiabao Dong).... ***D. (s. str.) fowleri* Deuve**
- Lateral borders of pronotum visible from above in apical fifth, pronotum longer (PL/PW=2.1) (Fengshan: cave Yuanyang Dong)..... ***D. (s. str.) grandis* Uéno**

- 7 Head and pronotum covered with sparser, long and erected setae, head broader, suddenly constricted before neck constriction (Fig. 16), hind angles of pronotum sharp, lateral sides of elytra near base nearly straight (Fig. 27) (Du'an: Chengjiang: cave Baxian Dong)..... ***D. (s. str.) baxian* Tian**
- Head and pronotum covered with denser, long and erected setae, head elongate, gently and gradually narrowed before neck constriction (Fig. 19), hind angles of pronotum blunt, lateral sides of elytra near base slightly sinuate (Fig. 30) (Du'an: Longfu: cave Shuiyuan Dong)..... ***D. (s. str.) troglodytes* sp. n.**
- 8 Body stout, pronotum with only a pair of latero-marginal setae close to hind angles..... **9**
- dle and a little before hind angles respectively **10**
- 9 Head strongly expanded (Fig. 21), clypeus sexsetose, elytra elongate (Fig. 11) (Du'an: Gaoling: caves Jinzhu Dong I and Jinzhu Dong II) ***D. (Dongodytodes) jinzhuensis* sp. n.**
- Head elongate (Fig. 22), clypeus 10-setose, elytra more ovate (Fig. 12) (Gaoling: cave Nongguanshang Dong II) ***D. (Dongodytodes) inexpectatus* sp. n.**
- 10 Head broader, sides nearly paralleled in median part (Fig. 20), lateral sides of pronotum almost straight or weakly sinuate before hind angles (Fig. 31) (Du'an: Xia'ao: cave Lubian Dong) ***D. (Dongodytodes) deharvengi* Tian**
- Head slender, sides not paralleled in median part, lateral sides of pronotum distinctly sinuate before hind angles..... **11**
- 11 Small, propleura more expanded, elytra shorter, base of elytra broader (Figs 13–14), elytra with only preapical dorsal pore, median lobe of aedeagus stout and much shorter (Figs 43–44) (Du'an: Longwan: cave Nongqu Dong I; Chengjiang: caves Diaomao Dong and Nongzhong Dong I) ***D. (Dongodytodes) brevipenis* sp. n.**
- Large, propleura less expanded, elytra more elongate, base of elytra narrowed (Fig. 13), elytra with middle and apical dorsal pores, median lobe of aedeagus much slender (Figs 45–46) (Dahua: Qibainong: cave Qiaoxu Dong) ***D. (Dongodytodes) yaophilus* sp. n.**

Subgenus *Dongodytes* (s. str.) Deuve, 1993

Dongodytes Deuve, 1993: 292

Type species. *D. fowleri* Deuve, 1993: 292.

Type locality: Bama County: cave Jiabao Dong.

Diagnostic characters. Body shiny and polished, antennae very long, extending over elytral apex, head elongate, genae gradually narrowed posteriad, not expanded medially, neck constriction long, posterior supraorbital setae present or not, head and pronotum glabrous or covered with sparse long and erected setae, elytra glabrous in most species (except for *D. elongatus* sp. n. which is wholly pubescent), anterior dorsal

pore on 3rd stria present (Fig. 6); legs very elongate, more slender than in *Dongodytodes*; ventrite VII in male with two pairs of paramedian setae in both sexes (Fig. 25).

Distribution. Northwestern Guangxi (Du'an, Bama, Fengshan and Tian'e Counties) (Fig. 73). *Dongodytes* (*s. str.*) is composed of six species. Three of them are recorded from Du'an County, and a single species is known in each of Bama, Fengshan and Tian'e Counties, respectively. Each species of *Dongodytes* (*s. str.*) is only known from a single limestone cave.

***Dongodytes* (*s. str.*) *baxian* Tian, 2011**

Figs 1f, 16, 27, 73j

Dongodytes (*s. str.*) *baxian* Tian, 2011: 62

Diagnosis. Middle sized, head and pronotum sparsely covered with erected setae, elytra glabrous; head (Fig. 16) extremely elongate though comparatively stout, and gradually narrowed towards neck constriction; only anterior pair of supraorbital setae present; clypeus quadrisetose; head (excluding mandibles) plus prothorax distinctly shorter than elytra; pronotum with two pairs of latero-marginal setae, posterior ones at a little before hind angles; lateral borders near front angles clearly visible from above, hind angle rectangular and sharp (Fig. 27); 3rd elytral stria with three dorsal pores, at about 2/7, 1/2 and 1/7 from base, respectively; marginal umbilicate pores: distance from 2nd to 3rd longer than half from 1st to 2nd, distance from 4th to 3rd as long as that from 3rd to 5th; male genitalia stout, nearly straight, base orifice very wide, with a small sagittal aileron, dorsally apical lobe broadly rounded; each paramere with four long setae at apex.

Material examined. Only the male holotype (Tian 2011).

Distribution. Guangxi (Du'an). Known only from the limestone cave called Baxian Dong, Chengjiang (Figs 1f and 73j).

Baxian Dong remains its natural state in some degree though it is located in Baxian Park close to Chengjiang. However, the species *D. (s. str.) baxian* is very rare. We visited the cave twice in June and December, 2013 respectively, but failed to collect any additional specimens. Major parts of the big cave are too dry, except for a small area at about 40 m from the upper entrance where water droppings create a suitable habitat for trechines.

***Dongodytes* (*s. str.*) *elongatus* sp. n.**

<http://zoobank.org/9C648AB1-6334-44AA-B22F-966B67FDA7FD>

Figs 1k, 8, 17, 28, 33–34, 47–49, 73l

Description. Length: 8.1–8.5 mm (mean 8.3 mm); width: 1.9–2.4 mm (mean 2.1 mm). Habitus as in Fig. 8.

Colour: Light yellowish brown to brown, dull, palps pale.

Macrosculpture: Head including underside surface and pronotum smooth and rather polish, sparsely covered with rather long and erected setae (except the tumid propleura), elytra and prosternum wholly covered with long setae; legs and abdominal ventrites pubescent.

Microsculpture: Engraved meshes clearly and strongly transverse on head and pronotum, faintly isodiametric on elytra.

Head (Fig. 17) much longer than wide, $HL/HW=2.7-3.5$ (mean 3.0); head excluding mandibles distinctly longer than pronotum, 1.3–2.3 times (mean 1.8), with a long and gradually narrowed neck constriction; widest at a little behind antennal articulations, two pairs of supraorbital setae present in holotype and three paratypes, setae on posterior pores shorter, asymmetrically sited, left one a little more behind than the right; right posterior pore absent in a female paratype; a pair of suborbital pores present, long, not far from the ring-shaped base, more or less asymmetrically sited; clypeus transverse, quadrisetose, sparsely covered with six additional short setae; labrum transverse, sexsetose; front shallowly emarginated; palps thin and very elongate, penultimate palpomeres longer than the apical ones; 2nd labial palp bisetose on inner margin; mentum and submentum partly fused, labial suture shortly traceable at sides; mentum bisetose basally, mental tooth simple, mental pits fine but distinct; submentum octosetose (but 12-setose in one female paratype, and 13-setose in one male paratype); antennae filiform, extending over elytral apex, all antennomeres pubescent, 1st as long as 2nd, 3rd 1.84 times longer than 2nd, each of 3rd–5th subequal in length, then gradually shortened towards apex, 10th as long as 11th, slightly longer than 1st.

Prothorax comparatively short (though much longer than wide) and narrow, slightly wider than head, $PW/HW=0.7-1.1$ (mean 0.9); front much narrower than base, $PAW/PBW=0.4-0.7$ (mean 0.6); propleura strongly tumid, much wider than pronotum, $PW/PTW=0.8-0.9$ (mean 0.8); pronotum rather short, lateral borders invisible from above at about 1/6 of apical parts (but visible in a male paratype), hind angles (Fig. 28) nearly rectangular, but obtuse, posterior lateral setae absent.

Elytra very elongate (but abnormally ovate in a male paratype), $EL/EW=1.8-2.1$ (mean 2.0), much wider than prothorax, $EW/PTW=2.0-2.1$ (mean 2.0); moderately convex; base comparatively thick (Fig. 28), humeral parts nearly straight, apex round; widest at about 2/3 from base; elytra slightly longer than head (excluding mandibles) plus prothorax; striae shallow, 2nd and 3rd traceable, others vague; 3rd elytral stria with three dorsal pores at about 1/3, 4/7 and 6/7 from base, respectively; chaetotaxal pattern of the marginal umbilicate pores similar in *D. baxian*, but distance from 1st to 2nd pores over twice as long as that from 2nd to 3rd (less than twice in *D. baxian*); distance from 3rd to 4th pores much longer than that from 4th to 6th (almost as long as in *D. baxian*).

Male genitalia (Figs 33–34): Median lobe of aedeagus stout, slightly sinuate before apex, apical part very short and broad, basal part wide and larger, basal orifice large, with margin distinctly protruding ventrally; ventral margin arcuate ventrad; sagittal aileron very small; inner sac armed with a broad and long copulatory piece which covered with scale structures on surface, as long as 1/3 of the median lobe; in dorsal, apical

lobe very broad, and rounded at apex; parameres wide and rather long, right and left ones with four and three long apical setae respectively.

Remarks. This species is a peculiar representative within *Dongodytes* (*s. str.*) because of its wholly pubescent elytra and comparatively shorter antennae in which only 10–11th segments extending over elytra. It is rather similar to *D. baxian* in appearance, but easily distinguished from the latter by its larger body size, slenderer and more elongate head, more expanded of propleura, without posterior latero-marginal setae, and stouter aedeagus.

Etymology. This new species is named referring to its very slender and elongate body.

Material examined. Holotype: male, Guangxi: Du'an: Lalie: Fuyan: Jianong: cave Lapo Dong I, 24°11.987N, 108°20.378E, 140 m, 2013-VI-23, leg. Mingyi Tian, Weixin Liu, Haomin Yin & Sunbin Huang; Paratypes: 2 males and 2 females, *ibid.* All are deposited in SCAU.

Distribution. Guangxi (Du'an). Known only from the type locality, cave Lapo Dong I in Lalie (Figs 1k and 73l).

The species was found close to the entrance of Lapo Dong (Figs 47–49). Deeper parts of the cave were not accessible during our visit. It was said that the cave is about 400 m long. There is no pool in the cave, but it is wet and muddy, and covered with guano. Other cave-dwelling animals living in this cave are crickets, mosquitoes, pseudoscorpions, spiders, millipedes, snails and bats.

***Dongodytes* (*s. str.*) *troglodytes* sp. n.**

<http://zoobank.org/63074B01-10B2-4531-96D3-90DECF2DAB95>

Figs 1c, 9, 19, 30, 37–38, 50–52, 73f

Description. Length: 7.0–7.5 mm (mean 7.3 mm); width: 1.9–2.4 mm (mean 2.1 mm). Habitus as in Fig. 9.

Colour: Light yellowish brown, palps pale.

Macrosculpture: Surface smooth, polish and strongly shiny; head including underside surface and prothorax sparsely covered with rather long and erected setae except the tumid propleura, elytra glabrous; prosternum with a row of 6–8 setae on each side; legs and abdominal ventrites pubescent.

Microsculpture: Engraved meshes faint, densely and strongly transverse on head and pronotum, without clear meshes on elytra.

Head (Fig. 19) nearly reverse triangular shaped, much longer than wide, HL/HW=3.1–3.7 (mean 3.4); slightly less elongate than in *D. elongatus* sp. n., but more slender than in *D. baxian*; head excluding mandibles slightly longer than pronotum, with mandibles much longer than pronotum (1.9–2.0 times, mean 1.9); gradually narrowed posteriad, forming a collar-like neck, neck constriction distinct, about half as wide as head; two pairs of supraorbital setae present, at about 1/3 and 2/3 from apex respectively; setae of anterior pores long and distinct, of posterior pores short and indistinct, only slightly longer than other erected setae nearby; frontal furrows

short, deeply impressed and narrow; clypeus transverse, sexsetose; labrum similar in *D. baxian*, but less emarginated apically; palps thin and very elongate, 3rd maxillary palpomere as long as 4th; 2nd labial palpomere distinctly longer than 3rd, and bisetose on inner margin; mentum and submentum not fused, labial suture distinct; mentum bisetose basally, mental tooth simple, blunt apically, a pair of basal pits small but distinct; submentum octosetose but 12-setose in one female paratype, and 14-setose in one male paratype; antennae filiform, wholly pubescent, extending over elytral apex, as long as in *D. baxian*; 1st antennomere as long as 2nd, 10th, and 11th, respectively, 3rd longest, about twice as long as 2nd, then gradually shortened towards apex.

Prothorax short though much longer than wide and narrow, slightly wider than head, propleura strongly tumid, PW/PTW=0.8, front narrower than base, PAW/PBW=0.7–0.8 (mean 0.8); pronotum narrower than head, PW/HW=0.8–1.0 (mean 0.9); lateral borders of pronotum invisible from above at 1/6 of apical parts (but visible in a male paratype); hind angles nearly rectangular, but obtuse (Fig. 30), posterior latero-marginal setae present, with location as in *D. (s. str.) baxian*.

Elytra very elongate, much longer than wide, EL/EW=1.8–2.0 (mean 2.0); slightly longer than head (excluding mandibles) plus prothorax, twice as wide as prothorax, EW/PTW=2.0–2.2 (mean 2.1); base thin (Fig. 30); humeral parts slightly and widely sinuate, apex round; widest at about 3/5 from base; disc strongly convex; striae shallow and vague though 2nd and 3rd traceable; 3rd stria with three dorsal pores at about 1/3, 1/2 and 5/6 from base, respectively; chaetotaxal pattern of marginal umbilicate pores similar in *D. baxian*.

Male genitalia (Figs 37–38): Median lobe of aedeagus short and rather slender, ventral margin strongly arcuate, not sinuate before apex, bisinuate dorsally; apical part short and blunt, basal part very wide and long, basal orifice very large; sagittal aileron very small; inner sac armed with a broad and long copulatory piece which covered with scale structures on surface, about 1/3 as long as the median lobe; in dorsal, apical lobe very broad, and more rounded at apex than other species; parameres wide and rather long, each of right and left parameres with two long setae at apex.

Remarks. *D. troglodytes* sp. n. is similar to *D. baxian*. It differs from the latter by the following characters: head more elongate, narrower, gently and gradually constricted towards neck constriction (stouter and quickly constricted before neck constriction in *D. baxian*); hind angles of pronotum blunt (sharp in *D. baxian*); head and pronotum covered with denser setae (sparser in *D. baxian*); elytra narrower, but more convex (broader but rather flat in *D. baxian*); and marginal borders at humeral parts slightly sinuate (nearly straight in *D. baxian*).

Etymology. Referring to its cave-adapted morphological characters.

Materials examined. Holotype: male, Guangxi: Du'an: Longfu: Shangme: cave Shuiyuan Dong, 24°11.335N, 107°49.865E, 509 m, 2013-VI-28, leg. Mingyi Tian, Wei Lin, Weixin Liu, Haomin Yin & Sunbin Huang, in SCAU; Paratypes: 9 males, 22 females, *ibid*; 11 females, 2013-V-2, leg. Mingyi Tian, Weixin Liu, Feifei Sun & Haomin Yin, in SCAU, MNHN, IOZ and ZUBM, respectively.

Distribution. Guangxi (Du'an) (Fig. 73f). Known only from the type locality, a cave called Shuiyuan Dong in Longfu (Figs 1c and 73f).

Shuiyuan Dong (Figs 50–52) is composed of two layers. The lower layer is an underground river which provides water source for the local people and it is impossible to entre. The upper part is a short passage, one to one and half metres high, two to four metres wide, and about 15 m long. All of the specimens of *D. troglodytes* sp. n. were collected in the upper part of the cave. Apart from *Dongodytes*, another anophthalmic trechine, belonging to the genus *Libotrechus* Uéno, 1998, was also collected in the cave (Lin and Tian 2014). Other cave animals found in Shuiyuan Dong are crickets, millipedes, isopods, moths, spiders, mosquitoes, snails, bats and cave fishes.

***Dongodytes* (s. str.) *lani* sp. n.**

<http://zoobank.org/9F7B7024-FF9F-45E3-B775-ECBE05133275>

Figs 1j, 6, 10, 18, 25, 29, 35–36, 53–55 and 73k

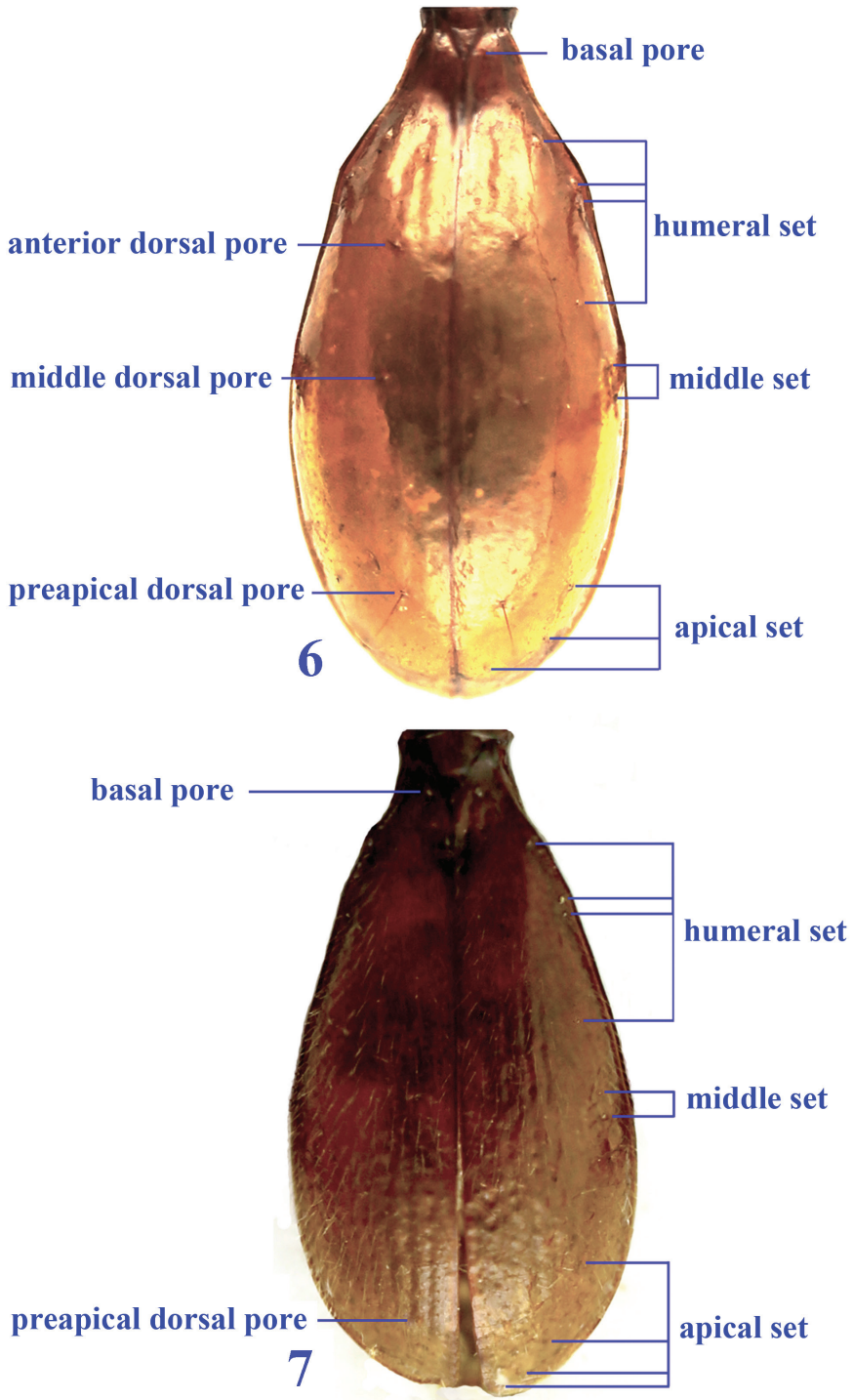
Description. Length: 6.8–7.3 mm (mean 7.1 mm); width: 1.9–2.1 mm (mean 2.0 mm). Habitus as in Fig. 10.

Colour: Light yellowish brown, palps pale.

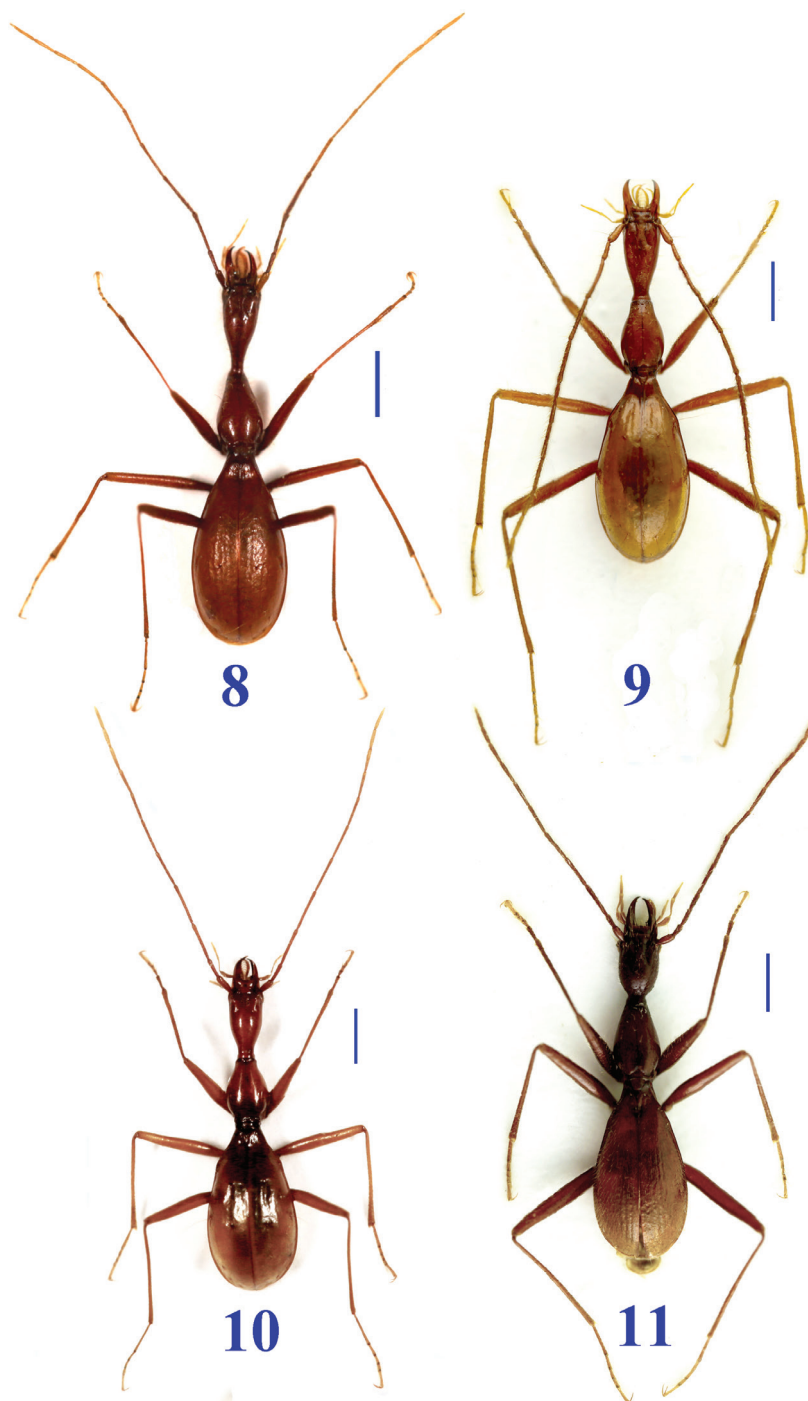
Macrosculpture: Surface smooth, polish and strongly shiny; head including underside surface and pronotum sparsely covered with rather long and erected setae (except the tumid propleura), elytra glabrous; prosternum with a row of 4–5 setae on each side; legs and abdominal ventrites pubescent.

Microsculpture: Engraved meshes densely and strongly transverse on head and pronotum, less transverse and faint on elytra.

Shape of the head (Fig. 18) intermediate between *Dongodytes* (s. str.) and *Dongodytodes*, genae more elongate than in *Dongodytodes* but more expanded posteriorly than in other *Dongodytes* (s. str.), widest at middle part; much longer than wide, HL/HW=3.0–3.5 (mean 3.2), excluding mandibles distinctly longer than pronotum (1.6–1.8 times, mean 1.7); neck constriction shorter but broader, about half as wide as head; two pairs of supraorbital setae present, at about 1/3 and 2/3 from apex respectively; setae of anterior pores long and distinct, of posterior pores short and indistinct, slightly longer than other erected setae nearby, and asymmetrically sited; frontal furrows short, deeply impressed and narrow, not parallel medially; clypeus transverse, sexsetose; labrum transverse, distinctly emarginated apically; a pair of suborbital setae present; palps thin and very elongate, 3rd maxillary palpomere slightly longer than 4th; 2nd labial palpomere distinctly longer than 3rd, and bisetose on inner margin; ligula bisetose, but multi-setose at apex with adnated paraglosae; mentum and submentum well separated by clear labial suture; mentum bisetose medially, mental tooth simple, broad apically, a pair of basal pits small but distinct; submentum octosetose; antennae wholly pubescent, as long as in *D. baxian*, extending over elytral apex; 1st antennomere distinctly longer than 2nd which is as long as 10th and shorter than 11th, 3rd as long as 5th



Figures 6–7. Elytral chaetotaxal patterns in *Dongodytes*. **6** *D. (s. str.) lani* sp. n. **7** *D. (Dongodytodes) jinzhuensis* sp. n.



Figures 8–11. Habitus of *Dongodytes* species. **8** *D. (s. str.) elongatus* sp. n. female, paratype **9** *D. (s. str.) troglodytes* sp. n. male, holotype **10** *D. (s. str.) lani* sp. n. female, paratype **11** *D. (Dongodytodes) jinzhuensis* sp. n. female, paratype, from Jinzhu Dong I. Scale bar: 1.0 mm.

and slightly shorter than 4th which is the longest, 3rd nearly twice as long as 2nd, from 5th gradually shortened towards 10th.

Prothorax short and stout though much longer than wide, distinctly wider than head, widest at about 2/5 from base; propleura strongly tumid; PAW/PBW=0.7–0.9 (mean 0.8), PW/PTW=0.7–0.8 (mean 0.7); pronotum narrow, slightly narrower than head, PW/HW=0.8–1.0 (mean 0.9), lateral borders invisible from above at about 1/6 of apical parts; widest at about middle, as wide as head; only a pair of latero-marginal setae present (posterior ones absent), at about middle, lateral sides strongly sinuate before hind angles which are bluntly acute (Fig. 29).

Elytra (Fig. 6) very elongate ovate, almost as long as head (excluding mandibles) plus prothorax; EW/PTW=2.0–2.2 (mean 2.1), EL/EW=1.9; base thin, sides at humeral parts slightly and widely sinuate, forming very faint shoulders (Fig. 29), where borders indistinct; apex rounded; comparatively long, distinctly longer than head (including mandibles) plus prothorax, widest at about 2/3 from base; striae shallow and vague, though 1st and 2nd are traceable; two dorsal pores present on areas of 3rd stria, at about 1/3 and 4/7 from base respectively; preapical dorsal pore absent; chaetotaxal pattern of marginal umbilicate pores similar in *D. baxian*, but 1st pore of the humeral set closer to marginal gutter, and far from 2nd, distance of them three times as long as from 2nd and 3rd.

Male genitalia (Figs 35–36): Median lobe of aedeagus very short, distinctly stouter than that of *D. baxian* and *D. elongatus* sp. n., ventral margin slightly and gently arcuate, slightly sinuate before apex which is broadly rounded, basal part very wide and long, nearly straight ventrally, basal orifice large; sagittal aileron very small and indistinct; inner sac armed with a large and long copulatory piece which covered with scale structures on surface, about 2/5 as long as the median lobe; in dorsal, apical lobe is slender, distinctly narrower than other congeners; parameres wide and broad, each of right and left parameres with three long apical setae respectively.

Remarks. *D. lani* sp. n. is also a peculiar species in *Dongodytes* (s. str.) by having peculiar structures of head and aedeagus. Compared to *D. elongatus* sp. n. for which the posterior latero-marginal setae on pronotum are also lacking, *D. lani* sp. n. has stouter but shorter body, smooth and glabrous elytra, its genae more expanded posteriorly, and elytra without preapical dorsal pore (present in *D. elongatus* sp. n.).

Etymology. Dedicated to Prof. Jiahu Lan (Du'an Fishery Technique Popularization Station, Guangxi), a well-known cave fish specialist in China, for thanking his various assistances and efficient cooperation during our biospeleological surveys in Du'an Karst.

Material examined. Holotype: male, Guangxi: Du'an: Longwan: cave Longhuan Dong, 23°49.5213N, 108°14.4792E, 248 m, 2013-XII-24, leg. Mingyi Tian, Weixin Liu, Haomin Yin & Xiaozhu Luo, in SCAU; Paratypes: 1 male and 4 females, ibid, in SCAU.

Distribution. Guangxi (Du'an). Known only from the type locality, a cave called Longhuan Dong in Longwan (Figs 1j and 73k).

Longhuan Dong (Figs 53–55) is about 100 m long, one to two metres wide and one to two metres high. There is a pool at the end of the passage, which is the water source for the local people. Part of the main passage is an artificial tunnel and very dry. The blind beetles were collected under pieces of decayed woods in a wet area just close to the pool. Other animals living in the cave are crickets, diplurans, isopods, millipedes, scutigera and snails.

Subgenus *Dongodytodes* Tian, 2011

Dongodytes (*Dongodytodes*) Tian, 2011: 57.

Type species. *D. (D.) deharvengi* Tian, 2011.

Type locality. a limestone cave called Lubian Dong in Xia'ao, Du'an.

Diagnostic characters. Body pubescent, covered with dense, erected short pubescence; antennae short, not extending over elytral apex; head stout and expanded posteriorly, suddenly constricted before neck constriction which is very short, posterior supraorbital setae always present; anterior dorsal pore on 3rd elytral stria absent, preapical pore present (Fig. 7); legs thin and elongate, but slightly stouter than in *Dongodytes* (*s. str.*), ventrite VII in male with a pair of paramedian setae (Fig. 26).

Distribution. Northwestern Guangxi (Du'an and Dahua Counties) (Fig. 73). *Dongodytodes* is composed of five species, all of them are occurring in Du'an Karst, and at the eastern (or northern) bank of the river Hongshui He. Each species is recorded from a single cave except *D. jinzhuensis* sp. n. (from two caves which are close to each other in Gaoling) and *D. brevipennis* sp. n. (from three caves which are very close to one another in Longwan and Chengjiang).

Dongodytes (*Dongodytodes*) *deharvengi* Tian, 2011

Figs 1b, 20, 31, 73e

Diagnosis. Small sized, dark reddish brown, whole surface covered with dense and short bristly setae; head stout though rather elongate (Fig. 20), head excluding mandibles slightly longer than prothorax; genae distinctly expanded posteriorly, then suddenly constricted before the collar-shaped neck, posterior supraorbital setae present and close to neck constriction; mentum and submentum well separated by labial suture; antennae long, extending at about apical 1/6 of elytra; clypeus transverse, sex-setose; prothorax much longer than wide though propleura distinctly tumid, widest at about 1/3 from base; pronotum narrow, lateral borders almost parallel-sided but feebly expanded at about 1/3 basally, slightly sinuate before hind angles (Fig. 31); front angles right, hind angles obtuse; two pairs of latero-marginal setae present, at about 2/5 from base and a little before hind angles respectively; elytra as long as head with mandibles and pronotum combined, widest at about apical 2/5 of elytra, lateral

sides near base straight (Fig. 31); two (middle and preapical) dorsal pores present on 3rd elytral stria, at about middle and apical 1/6 respectively; median lobe of aedeagus slender, widely and evenly arcuate, sagittal aileron moderately sized, each of parameres with four long apical setae.

Material examined. Apart from the type series (Tian 2011), two additional specimens were studied: 1 male and 1 female, cave Lubian Dong, same cave of the type locality, 310 m, Du'an: Xia'ao, 2013-V-02, leg. Mingyi Tian, Weixin Liu, Feifei Sun and Haomin Yin, in SCAU.

Distribution. Guangxi (Du'an). Known only from the cave called Lubian Dong which was pointed out as an anonymous cave in the original description (Tian 2011), in Xia'ao, northern Du'an (Figs 1b and 73e). We visited this cave four times in 2013, but collected only two specimens more during the first visit in early May. The reason is probably that the beetle's habitats had been partly changed after the huge collapse in the cave during the summer raining season.

***Dongodytes (Dongodytodes) brevipenis* sp. n.**

<http://zoobank.org/1D24FECA-BB71-4A22-979E-593FE59F5BB2>

Figs 1j, h, i, 13–14, 23, 43–44, 56–60, 73i

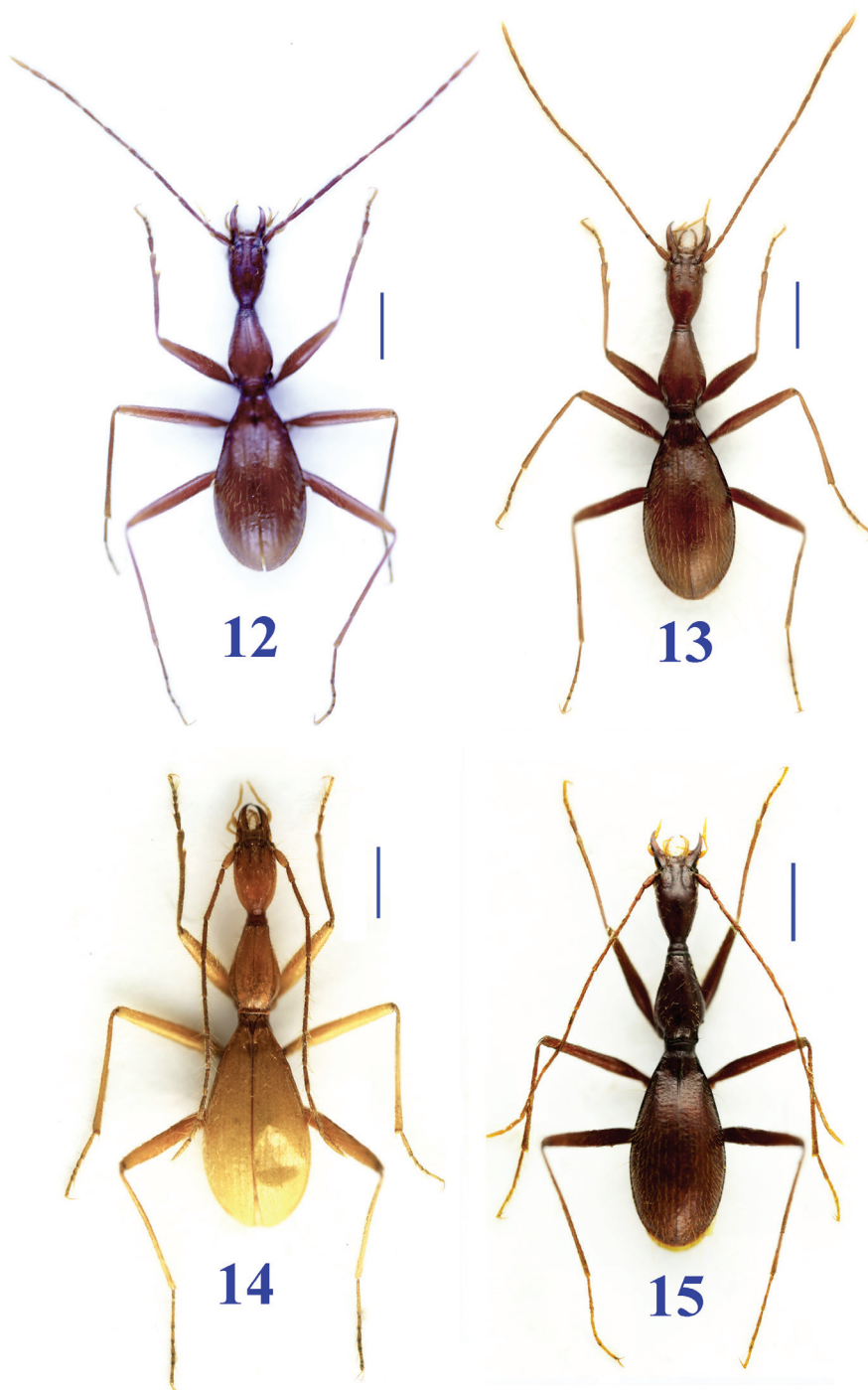
Description. Length: 6.8–7.1 mm (mean 6.9 mm); width: 1.7–2.0 mm (mean 1.8 mm). Habitus as in Figs 13–14, and 58–60.

Colour: Yellowish to light dark brown, palps pale.

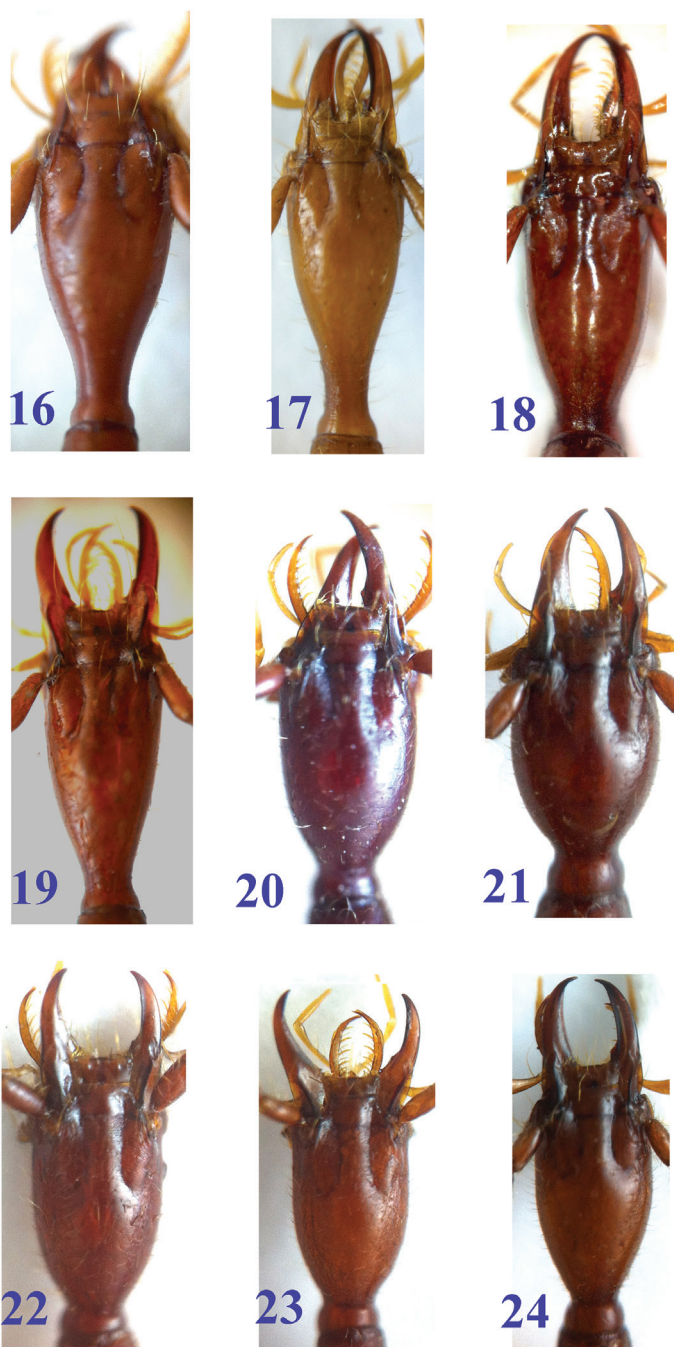
Macrosculpture: Head and pronotum smooth, elytra vaguely punctate, body moderately shiny and wholly pubescent.

Microsculpture: Similar in *D. deharvengi*.

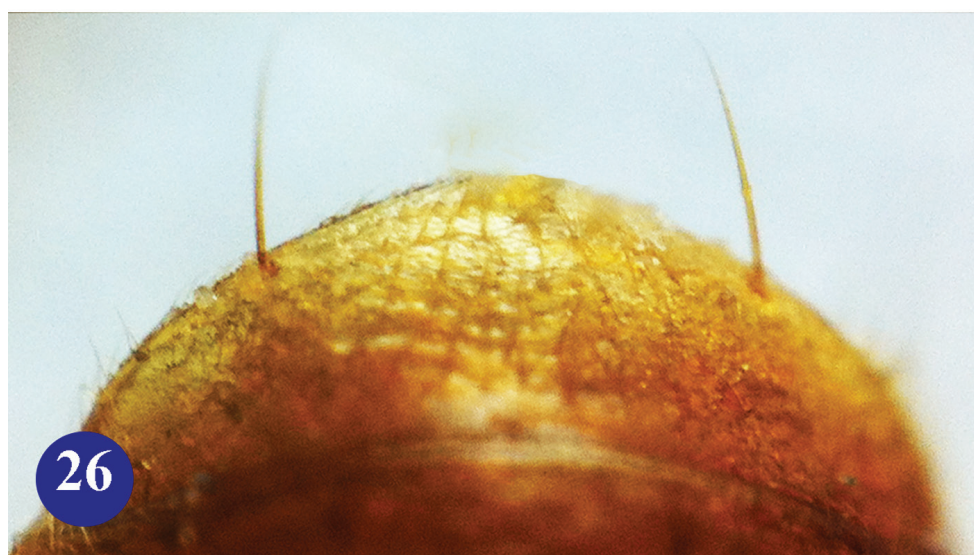
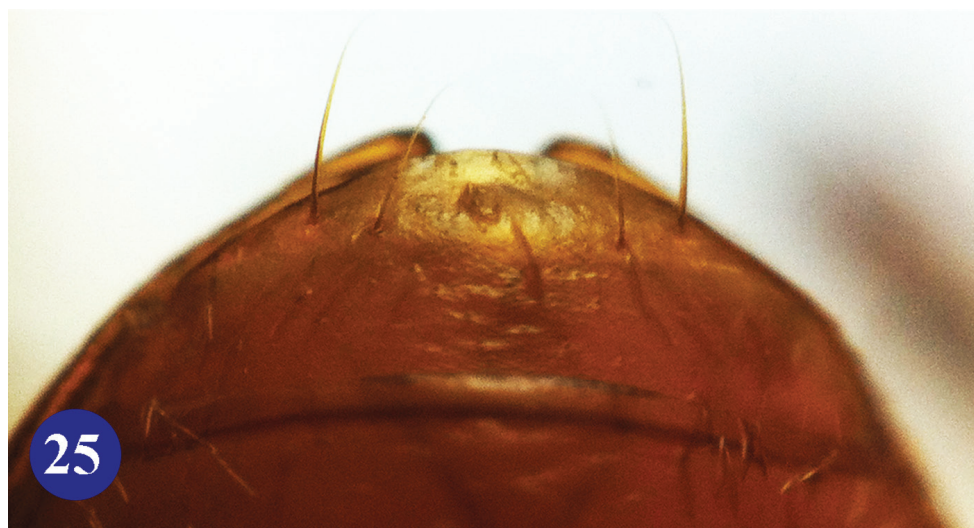
Head (Fig. 23) elongate, much longer than wide, HL/HW=2. 7–3.0 (mean 2.9); widest at about middle (from labrum), excluding mandibles as long as prothorax, including mandibles much longer than pronotum (1.4–1.6 times, mean 1.5); head (including mandibles) plus prothorax as long as elytra; head rather slender, genae less expanded laterally and posteriad, nearly parallel-sided medially; collar-shaped neck distinct, about 3/7 as wide as head; two pairs of supraorbital setae present, anterior ones far from each other, posterior ones close to each other; a pair of suborbital setae present, a pair of mental pits present; mental tooth bluntly bifid at apex; 2nd labial palpomere bisetose on inner margin; clypeus transverse, sexsetose; ligula multi-setose; mentum and submentum fused partly, labial suture indistinct in median part; mentum sexsetose, apart from a pair of median setae beneath mental tooth, a pair of long basal setae present, and each accompanied by a short seta at front; submentum 10-setose; antennae extending at about apical 1/6 of elytra; 1st antennomere strongly dilated, much more wider than others, distinctly longer than 2nd which is the shortest, 3rd longest, about twice as long as 2nd, and slightly longer than 4th, then gradually shortened towards 10th which is slightly longer than 1st but shorter than 11th.



Figures 12–15. Habitus of *Dongodytes* species. **12** *D. (Dongodytodes) inexpectatus* sp. n. male, holotype **13** *D. (Dongodytodes) brevipenis* sp. n. male, paratype, from Longwan: Nongqu Dong **14** *ibid*, from Chengjinag: Diaomao Dong **15** *D. (Dongodytodes) yaophilus* sp. n. female, paratype. Scale bar: 1.0 mm.

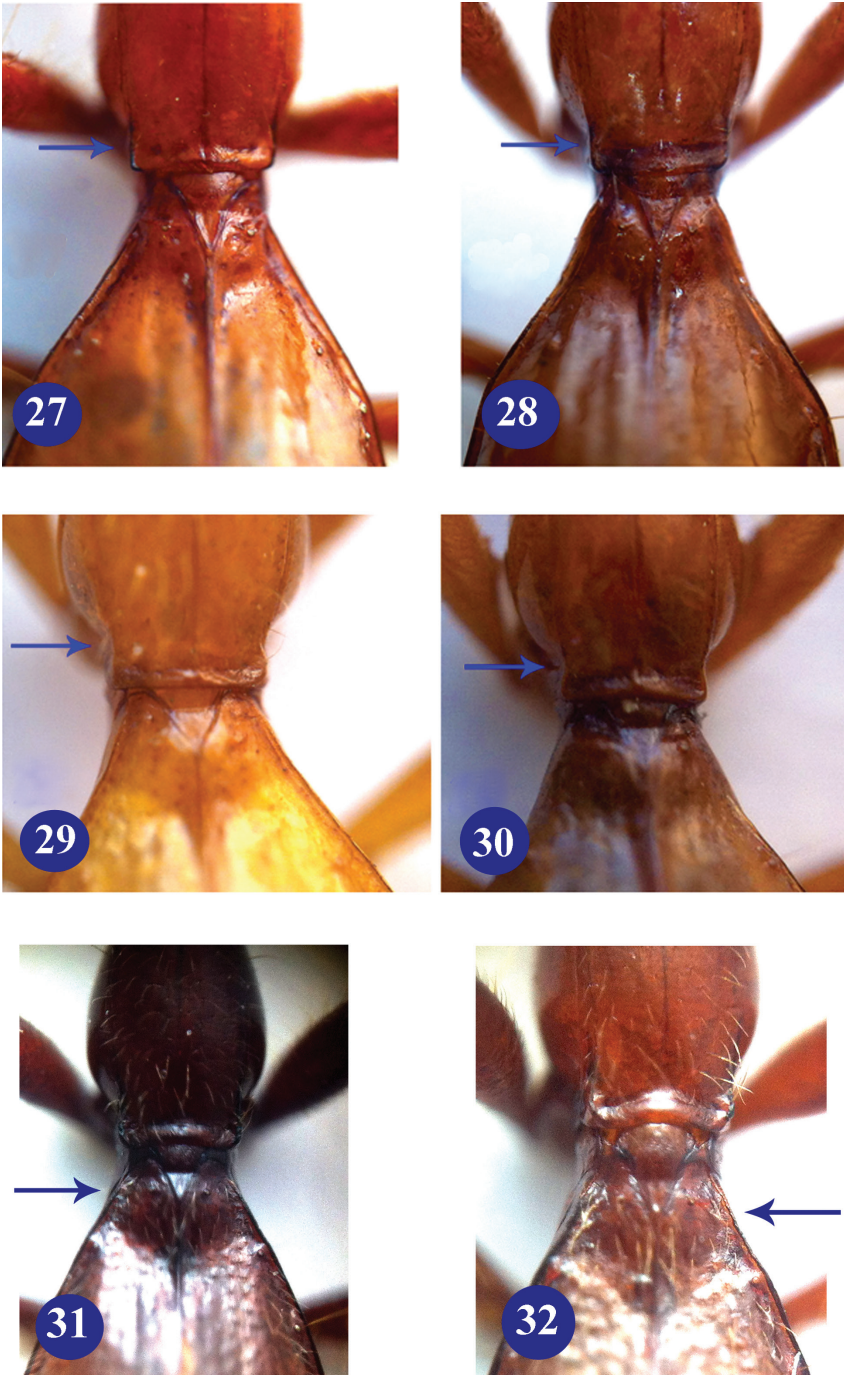


Figures 16–24. Head of *Dongodytes* species. **16** *D. (s. str.) baxian* M, male, holotype **17** *D. (s. str.) elongatus* sp. n. male, holotype **18** *D. (s. str.) lani* sp. n. male, holotype **19** *D. (s. str.) troglodytes* sp. n. male, holotype **20** *D. (Dongodytodes) deharvengi*, male, holotype **21** *D. (Dongodytodes) jinzhbuensis* sp. n. female, paratype **22** *D. (Dongodytodes) inexpectatus* sp. n. male, holotype **23** *D. (Dongodytodes) brevipenis* sp. n. male, holotype **24** *D. (Dongodytodes) yaophilus* sp. n. male, holotype.

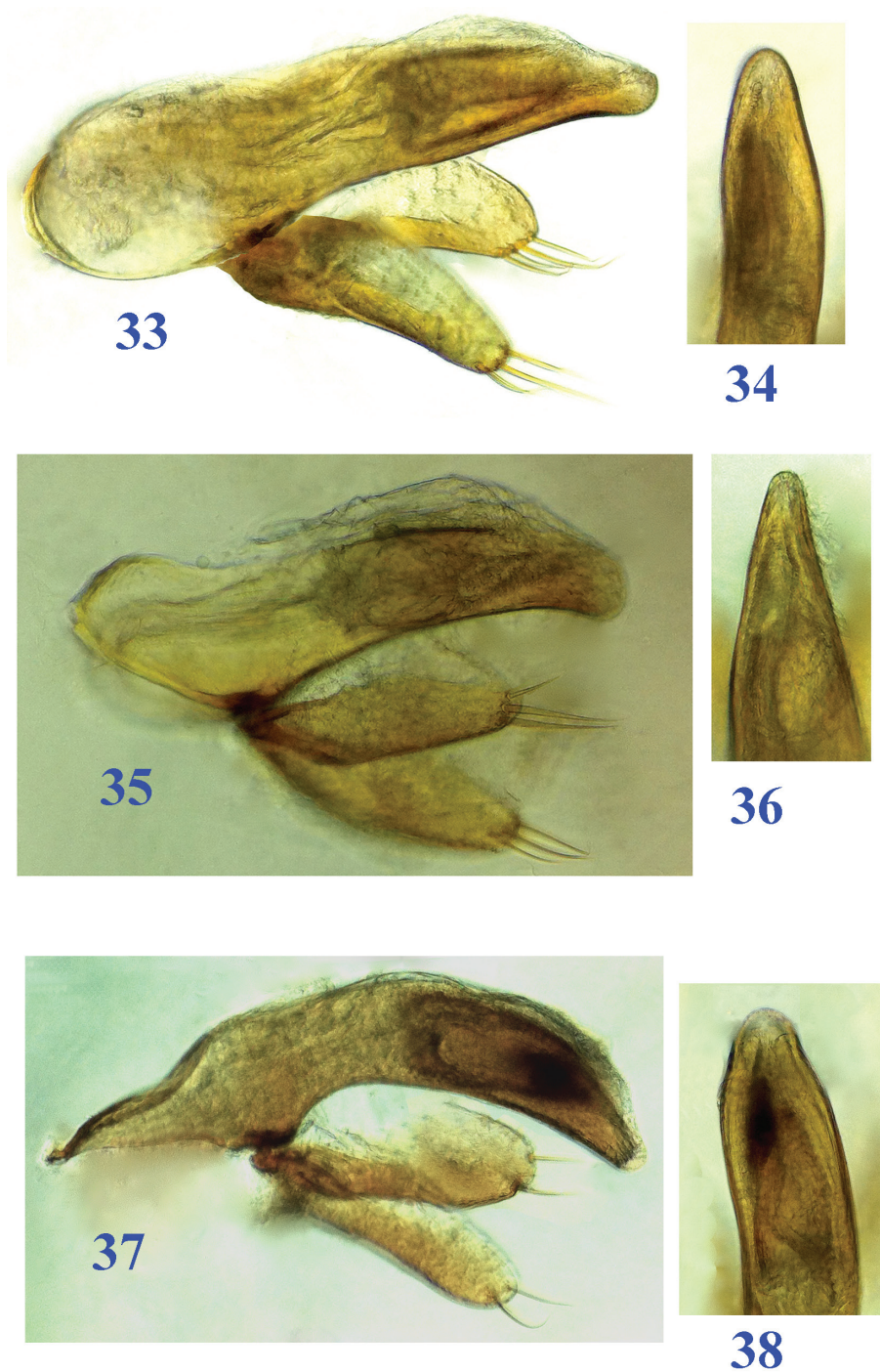


Figures 25–26. Abdominal ventrite VII of *Dongodytes* in male. **25** *D. (s. str.) lani* sp. n., paratype **26** *D. (Dongodytodes) jinzhushensis* sp. n., paratype.

Prothorax with propleura strongly tumid, widest at about 1/3 from base; base much wider than front, $PAW/PBW=0.7-0.8$ (mean 0.7); pronotum much narrower than prothorax, $PW/PTW=0.7-0.8$ (mean 0.8), and narrower than head, $PW/HW=0.8-1.0$ (mean 0.9), with two pairs of latero-marginal setae at a little before middle and a little before hind angles respectively, lateral sides distinctly sinuate in front of hind angles.



Figures 27–32. Basal parts of prothorax and elytra of subgenus *Dongodytes* (*s. str.*). **27** *D. (s. str.) baxian*, male, holotype **28** *D. (s. str.) elongatus* sp. n., male, holotype **29** *D. (s. str.) lani* sp. n., female, paratype **30** *D. (s. str.) troglodytes* sp. n., male, holotype **31** *D. (Dongodytodes) deharvengi* Tian, male, paratype **32** *D. (Dongodytodes) jinzhuenensis* sp. n., female, paratype.



Figures 33–38. Male genitalia of *Dongodytes* (*s. str.*) species (median lobe and parameres in lateral view, apical part of median lobe in dorsal view). **33–34** *D. (s. str.) elongatus* sp. n. **35–36** *D. (s. str.) lani* sp. n. **37–38** *D. (s. str.) troglodytes* sp. n.

Elytra moderately elongate ovate, twice as long as wide, $EL/EW=2.0-2.1$ (mean 2.0); widest at about $2/3$ from base; elytral base narrow, with sides almost straight; about twice as wide as prothorax, $EW/PTW=2.0-2.1$ (mean 2.0); striae well defined and punctate, only preapical dorsal pore present, at about $1/7$ from apex; chaetotaxy of marginal umbilicate pores similar in *D. deharvengi*, but 4th pore of humeral set is a little farther from 3rd.

Male genitalia (Figs 43–44): Median lobe of aedeagus very short, ventral margin gently arcuate, sagittal aileron distinct, basal orifice wide, apical part very short and bluntly rounded at apex; inner sac armed with a slender copulatory piece which covered with scale structures on surface, about $1/3$ as long as the median lobe; in dorsal view, apical lobe very wide, much broader than other species of *Dongodytodes*; parameres moderately developed, right and left ones each with three and four long setae at apex respectively.

Remarks. Differs from other congeners by its slender body, genae nearly parallel-sided at middle, sexsetose mentum, unique dorsal pore on 3rd elytral stria, and very short aedeagus.

Etymology. The name of this new species refers to its short aedeagus.

Material examined. Holotype: male, Guangxi: Du'an: Longwan: cave Nongqu Dong I, $23^{\circ}56.021'N$, $108^{\circ}10.962'E$, 459 m, 2013-VI-27, leg. Mingyi Tian, Wei Lin, Weixin Liu, Haomin Yin & Sunbin Huang, in SCAU; Paratypes: 2 males, 5 females, *ibid*; 1 male, Guangxi: Du'an: Chengjiang: Ganwan: cave Nongzhong Dong I, $23^{\circ}56.644'N$, $108^{\circ}10.072'E$, 469 m, 2013-VI-27, same collectors as above; 13 males, 7 females, Guangxi: Du'an: Chengjing: Wanmao: cave Diaomao Dong, $24^{\circ}01.723'N$, $108^{\circ}07.236'E$, 140 m, 2013-VI-23, same collectors as above, in SCAU, IOZ, MNHN and ZUBM, respectively.

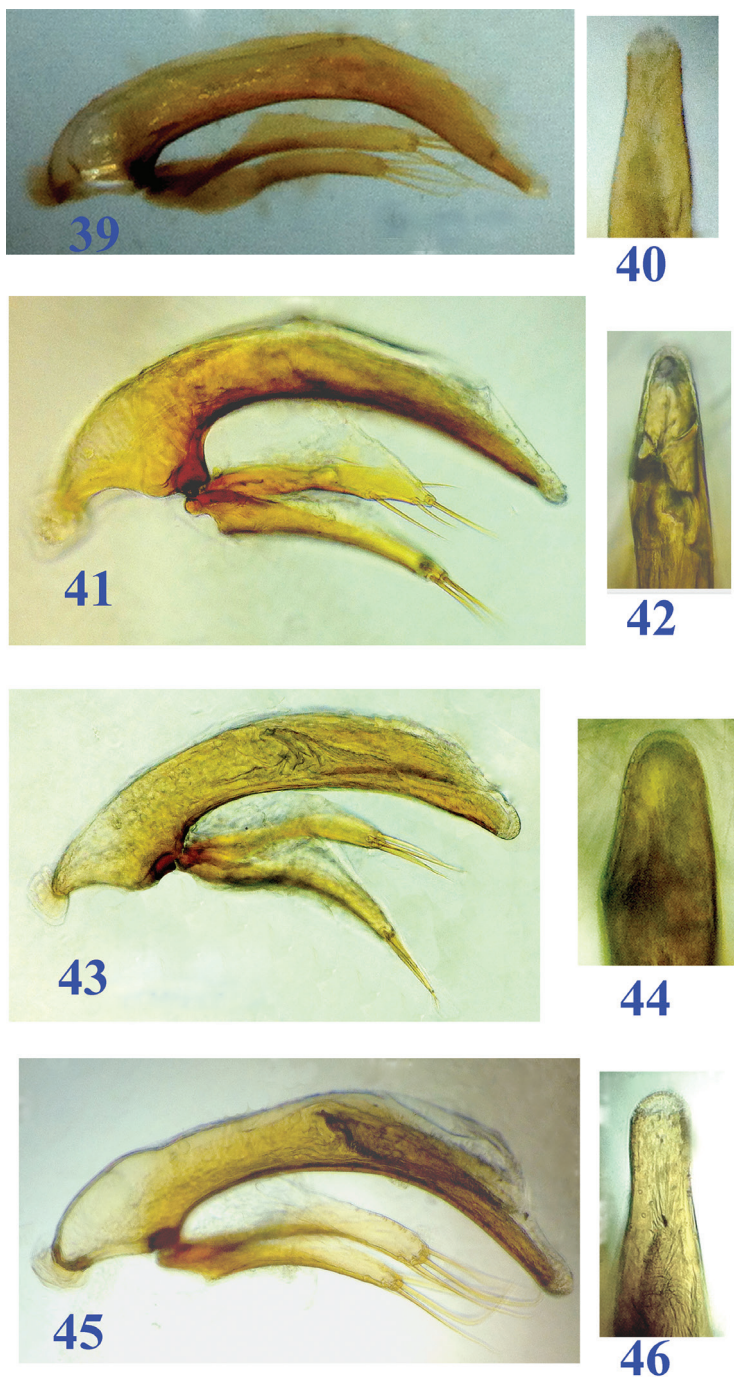
Distribution. Guangxi (Du'an). Known only from the type localities, cave Nongqu Dong in Longwan, and caves Diaomao Dong and Nongzhong Dong I in Chengjiang (Figs 1g, h, i and 73i).

The entrance of Nongqu Dong (Fig. 57) is localized on the bottom of a hill and close to a corn field surrounded by trees. It is about 300 m long, with a lot of water droppings, and a small stream inside. It is a beautiful cave, with magnificent stone pillars, stalactites and stalagmites.

The entrance of Nongzhong Dong I (Fig. 56) is in a sugarcane field. It is about 80 m long, composed of a main passage and several small galleries. At the end of the main passage there is an underground river which is about two kilometres long said by the local people.

Diaomao Dong I (Fig. 58) is localized at the foot of a hill near the village Nongzhong. Its length is about 100 m. The entrance is surrounded by bamboos. The cave is wet, with several small pools and a stream.

The trechine beetles were collected in several places of dark areas in the caves. Other animals living in the above caves are crickets, mosquitoes, staphylinids, millipedes, centipedes, isopods, harvestmen, spiders, snails and cave fishes.



Figures 39–46. Male genitalia of *Dongodytes* (*Dongodytodes*) species (median lobe and parameres in lateral view, apical part of median lobe in dorsal view). **39–40** *D. (Dongodytodes) jinzhuenis* sp. n. **41–42** *D. (Dongodytodes) inexpectatus* sp. n. **43–44** *D. (Dongodytodes) brevipenis* sp. n. **45–46** *D. (Dongodytodes) yaophilus* sp. n.

***Dongodytes (Dongodytodes) jinzhuensis* sp. n.**

<http://zoobank.org/CBEB2BCE-5B76-45F7-871B-B7FA2AC7EA0A>

Figs 1d, 7, 11, 21, 26, 32, 39–40, 61–65, 73g

Description. Length: 7.0–7.1 mm (mean 7.0 mm); width: 1.8–1.9 mm (mean 1.8 mm). Habitus as in Fig. 11.

Colour: Light dark brown, palps pale.

Macrosculpture: Head and pronotum smooth, elytra vaguely punctate, body moderately shiny and wholly pubescent.

Microsculpture: Densely and irregularly striate on head, pronotum and elytra.

Head (Fig. 21) very stout though elongate, distinctly longer than wide, HL/HW=2.6–2.8 (mean 2.7); widest at about middle from labrum, excluding mandibles as long as pronotum; head (including mandibles) plus prothorax as long as elytra; genae extremely dilated, making head much broader than any other species of the subgenus, about 2.7 times wider than collar-shaped neck, suddenly constricted before collar-shaped neck; nearly parallel-sided in median part; clypeus sexsetose; two pairs of supraorbital setae present, anterior setae distinctly longer than the posterior ones; a suborbital setae present, close to neck constriction; 2nd labial palpomere much longer than 3rd, bisetose on inner margin; ligula multi-setose apically; labial suture faintly traceable, mentum with two pairs of setae, at base and median parts respectively, a pair of mental pits present; mental tooth bluntly bifid at apex; submentum 10-setose; antennae short, extending at about apical 1/6 of elytra; 1st antennomere dilated, slightly longer than 2nd which is the shortest, 3rd the longest, twice as long as 2nd, gradually shortened from 4th towards 10th which is slightly shorter than 11th.

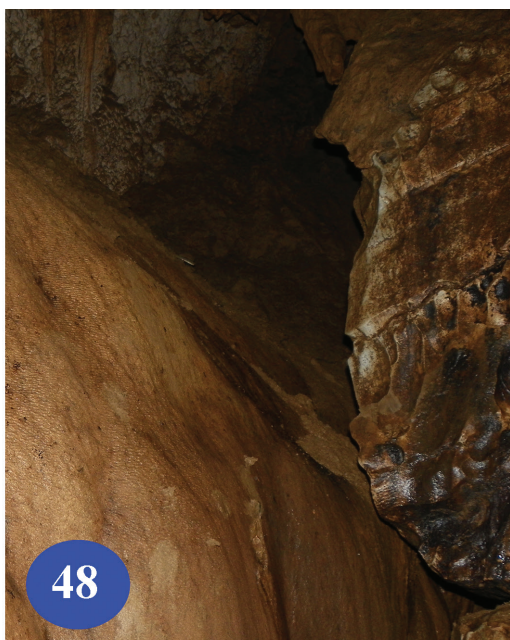
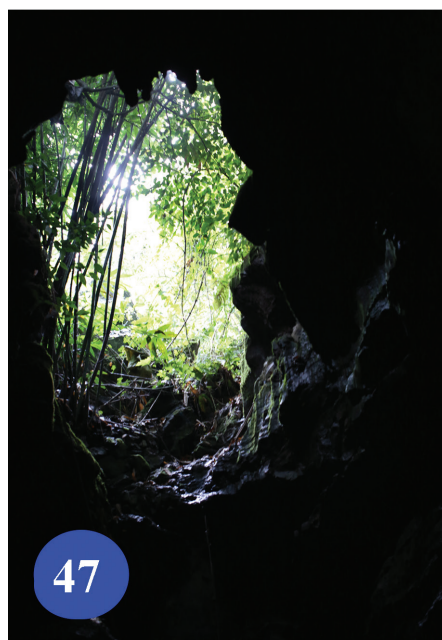
Prothorax much longer than wide though propleura distinctly tumid, widest at about 1/3 from base; front much narrower than base, PAW/PBW=0.8; pronotum narrower than head, PW/HW=0.8–0.9 (mean 0.9), and much narrower than prothorax, PW/PTW=0.8; lateral borders almost parallel-sided at apical and basal parts, gently and slightly expanded at about 1/3 from base, slightly sinuate before hind angles; front angles right, hind angles obtuse (Fig. 32); two pairs of latero-marginal setae present, at about 2/5 from base and a little before hind angles respectively.

Elytra moderately elongate (Fig. 7), much longer than wide, EL/EW=2.0; almost twice as wide as prothorax, EW/PTW=1.9–2.0 (mean 2.0); widest at about apical 2/5, lateral sides distinctly narrowed towards base (Fig. 32); striae well defined and punctate, two (middle and preapical) dorsal pores present on 3rd stria, at about 3/7 and apical 1/7 respectively; chaetotaxy of marginal umbilicate pores similar in *D. deharvengi*.

Male genitalia (Figs 39–40): Median lobe of aedeagus similar in *D. deharvengi*, but slightly shorter; copulatory piece indistinct in inner sac; in dorsal aspect the apical lobe broader apically, with sides slightly wider; right and left parameres each with four long setae apically.

Remarks. *Dongodytes (Dongodytodes) jinzhuensis* sp. n. differs from other congeners by its extremely dilated head and narrowly elytral sides near base.

Etymology. This new species is named after its type locality.



Figures 47–49. Lapo Dong I, type locality of *D. (s. str.) elongatus* sp. n. **47** entrance **48** wall of the cave, to show where the beetles were collected **49** bats on roof of the cave.

Material examined. Holotype: male, Guangxi: Du'an: Gaoling: cave Jinzhu Dong II, 24°06.514N, 108°04.695E, 218 m, 2013-V-03, leg. Mingyi Tian, Weixin Liu, Feifei Sun & Haomin Yin, in SCAU; Paratypes: 1 males, 7 females, *ibid*; 3 males, 1 female, cave Jinzhu Dong I, 24°06.547 N, 108°04.785 E, 190 m, same date and collectors; all are in SCAU except one male paratype in MNHN.

Distribution. China (Guangxi). Known only from caves Jinzhu Dong I and Jinzhu Dong II in Gaoling (Figs 1d and 73g).

The entrance of Jinzhu Dong I (Figs 61, 65) is very narrow and almost vertical. The passage is about half to three metres wide, eight to twelve metres high, and about 40 m long, ending with a pool in which cave fishes are living. The trechine beetles were collected in a section at about 10 to 25 m from the entrance.

Jinzhu Dong II (Figs 62, 64) is about 200 m far from Jinzhu Dong I. The entrance is much bigger, having easier access than Jinzhu Dong I. The structure of this cave is complicated, which is composed of several big halls and many passages. The length is still unknown. The beetles were collected in wet areas from 20 to 40 m far from the entrance (Fig. 63).

Other animals living in above caves are crickets, millipedes, scutigerae, isopods, snails and fishes.

***Dongodytes (Dongodytodes) inexpectatus* sp. n.**

<http://zoobank.org/0A3CF02B-50DA-4543-9FC9-0CE55A1ACAA6>

Figs 1e, 12, 22, 41–42, 66–69, 73h

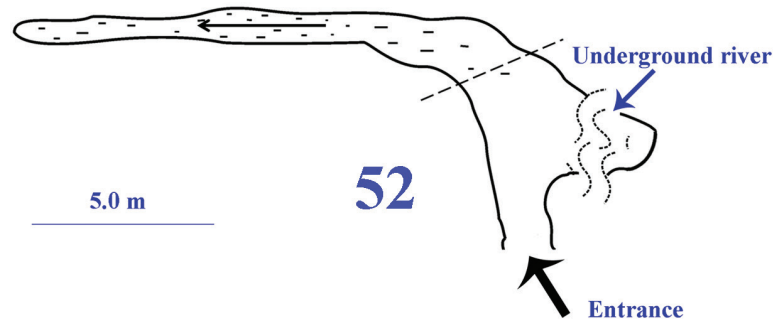
Description. Length: 6.2–7.0 (mean 6.6 mm); width: 1.6–2.0 mm (mean 1.83 mm). Habitus as in Fig. 12.

Colour: Light dark brown, palps pale.

Macrosculpture: Head and pronotum smooth, elytra vaguely punctate, body moderately shiny and wholly pubescent.

Microsculpture: Densely and more or less transversely striate on head and pronotum, faint on elytra.

Head rather elongate (Fig. 22), less stout than in *D. jinzhuensis* sp. n., distinctly longer than wide, HL/HW=2.7–2.9 (mean 2.8); widest at about middle from labrum, head excluding mandibles distinctly longer than pronotum (1.4–1.9 times, mean 1.6); head (including mandibles) plus prothorax as long as elytra; genae distinctly expanded posteriorly though less so than in *D. jinzhuensis* sp. n., collar-shaped neck distinct, head about 2.3 times wider than collar-shaped neck, suddenly constricted before collar-shaped neck; almost parallel-sided in median part; two pairs of supraorbital setae present, anterior ones slightly longer than the posterior which are distinctly longer than pubescent setae and easily recognized; clypeus 10-setose; a pair of suborbital setae present, close to neck constriction; labial suture well developed; mentum quadrisetose, setae at base and median parts respectively, basal pits distinct, mental tooth simple; submentum octosetose; ligula 12-setose apically; palps slender, 4th maxillary palpomere



Figures 50–52. Shuiyuan Dong in Longfu, type locality of *D. (s. str.) troglodytes* sp. n. **50** entrance (indicated by arrowhead) **51** passage of upper layer where the beetles were collected **52** a sketch of the cave.

slightly longer than 3rd, 2nd labial palpomere much longer than 3rd, bisetose on inner margin; antennae extending at about apical 1/6 of elytra, 1st antennomere distinctly longer than 2nd, which is the shortest, 3rd the longest, over twice as long as 2nd, gradually shortened from 4th until 10th, 11th as long as 8th and distinctly longer than 10th.

Prothorax much longer than wide though propleura distinctly tumid, widest at about 1/3 from base; pronotum narrower than head, PW/HW=0.9, and than prothorax, PW/PTW=0.7–0.8 (mean 0.8); front narrower than base, PAW/PBW=0.7–0.8 (mean 0.8); lateral borders almost parallel-sided in frontal half, then feebly expanded at about basal 1/3, distinctly sinuate before hind angles; front angles right, hind angles broadly obtuse; only basal pair of latero-marginal setae present, close to hind angles.

Elytra moderately elongate, much wider than prothorax, EW/PTW=1.5–2.0 (mean 1.8); much longer than wide, EL/EW=1.8–2.0 (mean 1.9); widest at about apical 1/3, lateral sides near base not well marked, and nearly straight; striae well marked, only preapical dorsal pore present, at about apical 1/6 of elytra; chaetotaxy similar in *D. deharvengi*.

Male genitalia (Figs 41–42): Median lobe of aedeagus much shorter than in *D. deharvengi*, widely and strongly arcuate, sagittal aileron moderately sized but very distinct, apex slender in profile; inner sac armed with a long and rather narrower copulatory piece about 2/5 as long as the median lobe; in dorsal view, apical lobe moderately in width, roundly truncate at apex, not parallel-sided at subapical part; right paramere thin at apex, with two long apical setae, left paramere stout, triangular, with four long setae at subapex and apex.

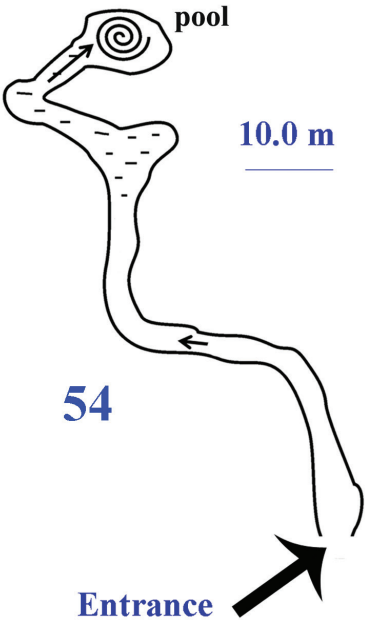
Etymology. The name of this new species indicates that it was really a surprise for us to collect the type material in a cave which is very close to caves Jinzhu Dong I and Jinzhu Dong II (about 2 km only), the type localities of *D. jinzhuensis* sp. n.

Remarks. *D. inexpectatus* sp. n. is similar to *D. brevipenis* sp. n., but it is easily distinguished from the latter by its stouter head and pronotum, and lateral sides of elytra distinctly sinuate against 1st and 2nd umbilicate pores (indistinctly sinuate in *D. brevipenis*). Compared to *D. jinzhuensis* sp. n., *D. inexpectatus* sp. n. is much slender and smaller, head much less expanded, clypeus 10-setose (sexsetose in *D. jinzhuensis*), and only posterior pair of latero-marginal setae present on pronotum (two pairs present in *D. jinzhuensis*).

Material examined. Holotype: male, Guangxi: Du'an: Gaoling: Nongchi: cave Nongguangshang Dong II, 24°05.4263N, 108°04.5726E, 175 m, 2013-XII-27, leg. Mingyi Tian, Weixin Liu, Haomin Yin & Xiaozhu Luo, in SCAU; Paratypes: 2 females, *ibid*, in SCAU.

Distribution. Guangxi (Du'an). Known only from the limestone cave called Nongguangshang Dong II in Gaoling (Figs 1e and 73h).

The entrance of Nongguangshang Dong II (Figs 66–69) is in a corn field. Along the artificial steps it is easy to enter. It is a small cave, with a pool at about 30 m from the entrance which is water source of the local people. On the right of the pool, there is a gallery partially covered by water. The length of Nongguangshang Dong II is unknown and we surveyed up to about 100 m. The beetles were discovered on the ground and the wall in a small area on the gallery's right side. Other cave animals found in the cave are crickets, spiders, isopods, shrimps, millipedes and snails.



Figures 53–55. Longhuan Dong, type locality of *D. (s. str.) lani* sp. n. **53** entrance of the cave **54** a sketch of the cave **55** picture to show where the type series were collected in the cave.

***Dongodytes (Dongodytodes) yaophilus* sp. n.**

<http://zoobank.org/6B5CB04C-AB89-4B4E-A81A-6345FD974265>

Figs 1a, 15, 24, 45–46, 70–73d

Description. Length: 7.7–7.9 mm (mean 7.76 mm); width: 1.8–1.9 mm (mean 1.83 mm). Habitus as in Figs 15 and 72.

Colour: Less depigmented than other species of *Dongodytodes*, yellowish to dark reddish brown, palps pale.

Macrosculpture: Head and pronotum smooth, elytra vaguely punctate, body moderately shiny and wholly pubescent except mesostenum which is glabrous.

Microsculpture: Engraved meshes densely striate, more transverse on head and pronotum, and irregularly on elytra.

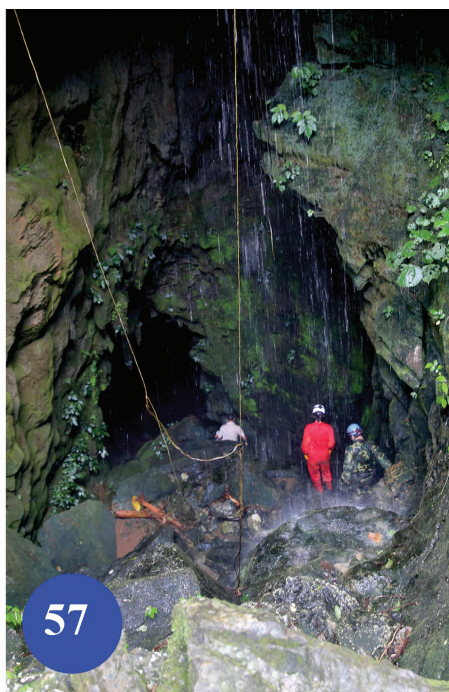
Head (Fig. 24) elongate, much longer than wide, HL/HW=3.0–3.1 (mean 3.1); widest at about middle including mandibles, excluding mandibles slightly longer than pronotum; genae moderately expanded posteriad, then suddenly constricted before the collar-shaped neck which is about 2/5 as wide as head; clypeus sexsetose; two pairs of supraorbital setae present, anterior ones far from each other and the posterior close to each other; a pair of suborbital setae present, mentum and submentum completely fused, mentum with two pairs of setae, at base and median part respectively, a pair of mental pits present; mental tooth bluntly bifid at apex; submentum 10-setose; 2nd labial palpomere bisetose on inner margin; ligula multi-setose apically; antennae comparatively long, extending at about apical 1/8 of elytra; 1st antennomere much more dilate than others, slightly longer than 2nd which is shortest, 2nd about half as long as 3rd which is the longest, then gradually shortened towards to 10th which is as long as 1st, and shorter than 11th.

Prothorax long, propleura less tumid than other species of the subgenus, PW/PTW=0.8–0.9 (mean 0.8); widest at about 2/7 from base, front distinctly narrower than base, PAW/PBW=0.7–0.8 (mean 0.7); pronotum slightly narrower than head, PW/HW=0.9; two pairs of latero-marginal setae present, at about 4/7 from base and a little before hind angles respectively, lateral sides distinctly sinuate just before hind angles; front angles right, hind angles obtuse.

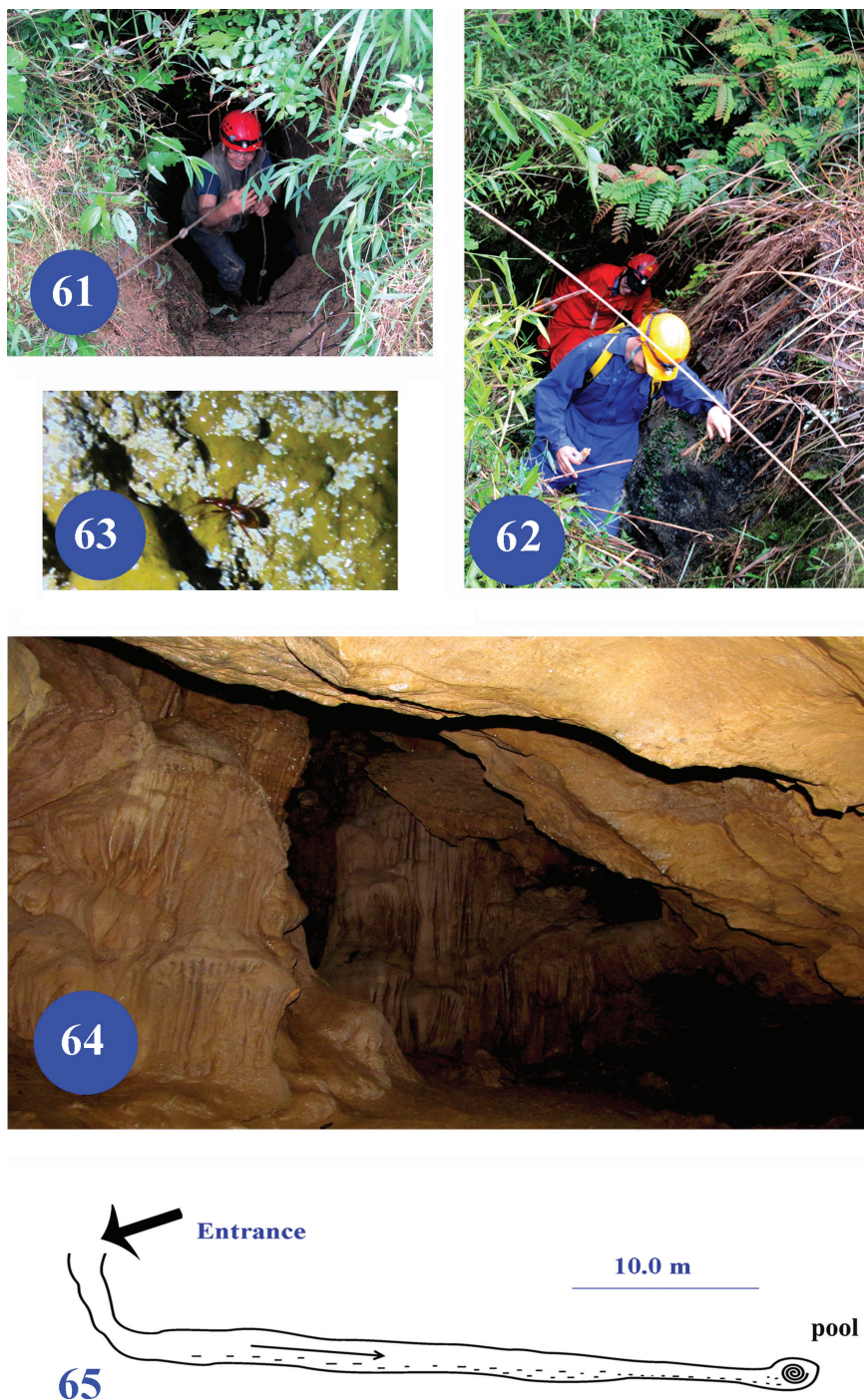
Elytra more elongate and a little more convex than other species of *Dongodytodes*, as long as head (including mandibles) and pronotum combined; almost twice as long as wide, EL/EW=2.1; much wider than prothorax, EW/PTW=1.7–2.1 (mean 1.9); base rather slender, lateral sides near base almost straight; widest at about apical 4/7 of elytra; striae punctate, more or less traceable, two (middle and preapical) dorsal pores present on 3rd stria, at about 3/5 and 1/6 respectively; chaetotaxy and other characters as in *D. deharvengi*.

Male genitalia (Figs 45–46): Median lobe of aedeagus long and slender, similar in *D. deharvengi*, but apical part more straight, and blunt at apex; inner sac armed with a large and long copulatory piece which covered with scale structures on surface, about 2/5 as long as the median lobe; in dorsal aspect the apical lobe broader and sides distinctly sinuate at subapical part; right and left parameres with three and four long setae at apex respectively.

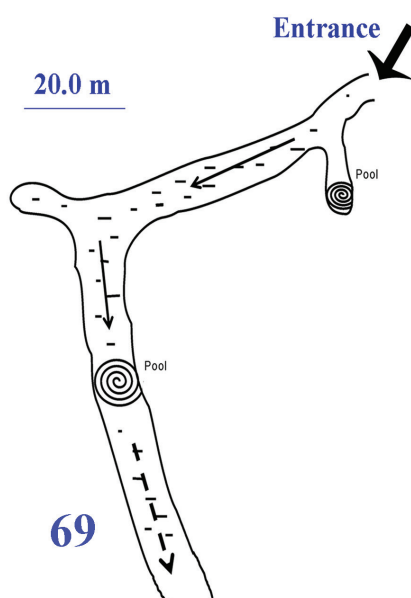
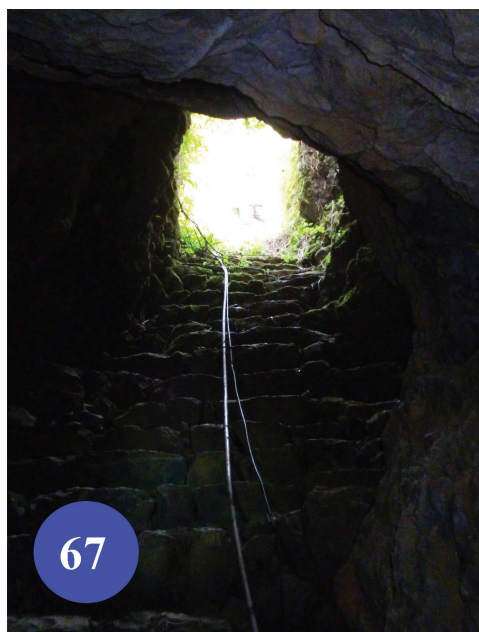
Remarks. By its long and large body, together with more elongate genae and longer antennae, *D. yaophilus* sp. n. is easily distinguished from other members of



Figures 56–60. Type locality caves of *D. (Dongodytodes) brevipenis* sp. n. **56** entrance of Nongzhong Dong I **57** entrance of Nongqu Dong I **58** entrance of Diaomao Dong **59–60** beetles running on walls in Diaomao Dong.



Figures 61–65. Jinzhu Dong I and II, type localities of *D. (Dongodytodes) jinzhuensis* sp. n. **61** entrance of Jinzhu Dong I **62** entrance of Jinzhu Dong II **63** wandering beetle on wall in Jinzhu Dong II **64** a room in Jinzhu Dong II, to show where the beetles were collected **65** a sketch of Jinzhu Dong I.



Figures 66–69. Nongguanshang Dong, type locality of *D. (Dongodytodes) inexpectatus* sp. n. **66–67** entrance of the cave **68** a pool at the end of the passage **69** a sketch of the cave.



Figures 70–72. Qiaoxu Dong, type locality of *D. (Dongodytodes) yaophilus* sp. n. **70–71** entrance of the cave **72** a wandering beetle on ground.

Dongodytodes. It is probably close to *D. deharvengi* because both of them have similar aedeagal structure and elytral chaetotaxal pattern.

Etymology. “Yao” is a short name for the minority Yao people who are living in the mostly karstic mountainous areas in several provinces or regions of southern China (Guangxi, Hunan, Guangdong and Guizhou). Both Dahua and Du’an are Yao Autonomous Counties. The name indicates that this new species lives in the same region as Yao people.



Figure 73. Distribution of the genus *Dongodytes*. **a** *D. (s. str.) giraffa* Uéno **b** *D. (s. str.) grandis* Uéno **c** *D. (s. str.) fowleri* Deuve **d** *D. (Dongodytodes) yaophilus* sp. n. **e** *D. (Dongodytodes) deharvengi* Tian **f** *D. (s. str.) troglodytes* sp. n. **g** *D. (Dongodytodes) jinzhushensis* sp. n. **h** *D. (Dongodytodes) inexpectatus* sp. n. **i** *D. (Dongodytodes) brevipenis* sp. n. **j** *D. (s. str.) baxian* Tian **k** *D. (s. str.) lani* sp. n. **l** *D. (s. str.) elongatus* sp. n. Star: species of *Dongodytes* (*s. str.*); square: species of *Dongodytodes*.

Material examined. Holotype: male, Guangxi: Dahua: Qibainong: cave Qiaoxu Dong, 24°04.370N, 107°40.140E, 535 m, 2013-VI-22, leg. Mingyi Tian, Wei Lin, Haomin Yin & Sunbin Huang; Paratypes: 3 females, *ibid*, all in SCAU.

Distribution. Guangxi (Dahua) (Figs 1a and 73d). Known only from the type locality, cave Qiaoxu Dong.

Qiaoxu Dong (Figs 70–71) is located at about 250 m from village Qiaoxu in the west, along the main road from Qibainong to Dahua. It is a large cave, 420 m long, 15 to 140 m wide and six to 30 m high, having three large halls. The largest hall is

about 336, 000 m² in area, one of the largest in Guangxi. It is a beautiful cave within Qibainong National Geopark in Dahua County. The beetles were collected in the areas of 70 to 100 m from the entrance. Other cave animals in Qiaoxu Dong are crickets, spiders, millipedes, isopods and snails.

Acknowledgements

First of all, we are so grateful to Ms. Bo Jiang (an official and expert on biodiversity conservation, Department of Environmental Protection, Guangxi Regional Government, Nanning) for her support and encouragement. We thank Prof. Jiahu Lan (Du'an Fishery Technique Popularization Station, Guangxi), a well-known cave fish specialist in China, and members of our team in SCAU, Weixin Liu, Feifei Sun, Wei Lin and Xiaozhu Luo, for their various assistances and great efforts during the surveys in Guangxi. In particular, we thank Dr. Thierry Deuve (MNHN, Paris), Dr. Arnaud Faille (Zoologische Staatssammlung, Munich) and two other anonymous reviewers for their discussions, corrections and suggestions which were helpful to improve the manuscript. This study is sponsored by Nanjing Institute of Environmental Sciences, Ministry of Environmental Protection, through a biodiversity conservation project in 2013 which was focused on cave biodiversity, and the Specialized Research Fund for the Doctoral Program of Higher Education of China (Grant no. 20134404110026) and National Natural Science Foundation of China (Grant no. 41271602).

References

- Deuve T (1993) Description de *Dongodytes fowleri* n. gen., sp. n., Coléoptère troglobie des karsts du Guangxi, Chine (Adephaga: Trechidae). Bulletin de la Société entomologique de France 98(3): 291–296.
- Deuve T (2002) Deux remarquables Trechinae anophtalmes des cavités souterraines du Guangxi nord-occidental, Chine (Coleoptera, Trechidae). Bulletin de la Société entomologique de France 107(5): 515–523.
- Deuve T, Tian MY, Ran JC (1999) Trois Caraboidea remarquables de la Réserve nationale de Maolan, dans le Guizhou méridional, Chine (Coleoptera, Carabidae et Trechidae). Revue française d'Entomologie (NS) 21(3): 131–138.
- Deuve T, Tian MY (2008) Deux nouveaux Trechidae cavernicoles de Chine (Coleoptera, Caraboidea). Revue française d'Entomologie (NS) 30(2): 55–60.
- Deuve T, Tian MY (2009) Un nouveau Trechini cavernicole aveugle au nord du fleuve Yangtze, dans le Hubei (Coleoptera, Caraboidea). Bulletin de la Société entomologique de France 114(2), 2009: 181–184.
- Deuve T, Tian MY (2011) Nouveaux Trechini et Tachyini des cavités souterraines de Chine méridionale (Coleoptera, Caraboidea). Nouvelle Revue d'Entomologie 27(2): 99–108.
- Faille A, Ribera I, Deharveng L, Bourdeau C, Garnery L, Quéinnec E, Deuve T (2010) A molecular phylogeny shows the single origin of the Pyrenean subterranean Trechini ground

- beetles (Coleoptera: Carabidae). *Molecular Phylogenetics and Evolution* 54: 97–106. doi: 10.1016/j.ympev.2009.10.008
- Faillle A, Casale A, Balke M, Ribera I (2013) A molecular phylogeny of Alpine subterranean Trechini (Coleoptera: Carabidae). *BMC Evolutionary Biology* 13(248): 1–16.
- Hu BQ, Wang DG, Su GS, Qin KX (2012) Systematic science in karstic land: a case of study in Du'an, Guangxi. Science Press, Beijing, 278 pp. [in Chinese]
- Lan JH, Gan X, Wu TJ, Yang J (2013) Cave fishes of Guangxi, China. Science Press, Beijing, 266 pp. [in Chinese, with English abstract]
- Lin W, Tian MY (2014) Supplemental notes on the genus *Libotrechus* Uéno, with description of a new species from Guangxi, southern China (Coleoptera: Carabidae: Trechinae). *The Coleopterists Bulletin* 68(3): 1–5. doi: 10.1649/072.068.0314
- Tian MY (2010) New records and new species of cave-dwelling trechine beetles from Mulun Nature Reserve, northern Guangxi, China (Insecta: Coleoptera: Carabidae: Trechinae). *Subterranean Biology* 7: 69–73.
- Tian MY (2011) A new subgenus and two new species of the troglobitic genus *Dongodytes* Deuve from Guangxi, China (Coleoptera, Carabidae). *Subterranean Biology* 8: 57–64. doi: 10.3897/subtbiol.8.1232
- Tian MY (2013) Occurrence of troglobitic clivinines in China (Insecta: Coleoptera: Carabidae). *Journal of Cave and Karst Studies* 75(2): 113–120. doi: 10.4311/2011LSC0226
- Tian MY (2014) New records and a new species of the cavernicolous genus *Guiodytes* Tian, 2013 from Guangxi, China (Coleoptera: Carabidae: Scaritinae). *Zootaxa* 3861(4): 355–362. doi: 10.11646/zootaxa.3861.4.5
- Tian MY, Clarke A (2012) A new eyeless species of cave-dwelling trechine beetle from north-eastern Guizhou Province, China (Insecta: Coleoptera: Carabidae: Trechinae). *Cave and Karst Science* 39(2): 66–71.
- Tian MY, Yin HM (2013) Two new cavernicolous genera and species of Trechinae from Hunan Province, China (Coleoptera: Carabidae). *Tropical Zoology* 26(4): 154–165. doi: 10.1080/03946975.2013.869097
- Uéno SI (1998a) Notes on *Dongodytes* (Coleoptera, Trechinae), with description of a new species. *Journal of Speleological Society of Japan* 23: 1–15.
- Uéno SI (1998b) Two new genera and species of anophthalmic trechine beetles (Coleoptera, Trechinae) from limestone caves of southeastern Guizhou, South China. *Elytra* 26(1): 37–50.
- Uéno SI (2005) A remarkably specialized new cave trechine (Coleoptera, Trechinae) from northern Guangxi, South China. *Elytra* 33(1): 333–339.
- Uéno SI (2007) Two new cave trechines (Coleoptera, Trechinae) from western Zhejiang, East China. *Journal of the Speleological Society of Japan* 32: 9–22.
- Uéno SI, Clark AK (2007) Discovery of a new Aphaenopoid trechine beetle (Coleoptera, Trechinae) in northeastern Jiangxi, East China. *Elytra* 35(1): 267–278.
- Uéno SI, Wang FX (1991) Discovery of a highly specialized cave trechine (Carabidae: Trechinae) in Southwest China. *Elytra* 19(1): 127–135.
- Vigna Taglianti A (1997) A new genus and species of troglobitic Trechinae (Coleoptera, Carabidae) from southern China. *International Journal of Speleology* 25: 33–41. doi: 10.5038/1827-806X.25.1.3

A new species of *Hemibrycon* (Characiformes, Characidae) from the upper San Juan River drainage, Pacific versant, Colombia

César Román-Valencia¹, Raquel I. Ruiz-C¹,
Donald C. Taphorn^{1,2}, Carlos A. García-Alzate^{1,3}

1 Universidad del Quindío, Laboratorio de Ictiología, A. A. 2639, Armenia, Colombia **2** 1822 N. Charles St., Belleville, IL, 62221 USA **3** Universidad del Atlántico, Programa de Biología, Barranquilla, Colombia

Corresponding author: César Román-Valencia (ceroman@uniquindio.edu.co)

Academic editor: C. Baldwin | Received 2 February 2014 | Accepted 17 October 2014 | Published 14 November 2014

<http://zoobank.org/E17D4CE8-68AA-4DB9-A6C4-B057012AFE0D>

Citation: Román-Valencia C, Ruiz-C RI, Taphorn DC, García-Alzate CA (2014) A new species of *Hemibrycon* (Characiformes, Characidae) from the upper San Juan River drainage, Pacific versant, Colombia. ZooKeys 454: 109–125. doi: 10.3897/zookeys.454.6954

Abstract

Hemibrycon sanjuanensis, new species, is described from the upper San Juan River drainage, Pacific versant, Colombia. It is distinguished from *H. boquiae*, *H. brevispini*, *H. cairoense*, *H. colombianus*, *H. mikrostiktos*, *H. metae*, *H. palomae*, *H. rafaelense* and *H. tridens* by the presence of a circular or oblong humeral spot that is located two scales posterior to the opercle (vs. 3–4 scales in *H. palomae*, *H. rafaelense*, *H. brevispini* and *H. cairoense*, and 0–1 scales, in *H. metae* and *H. boquiae*). It further differs from *H. colombianus* in having a round or oblong humeral spot (vs. rectangular). It differs from *H. beni*, *H. dariensis*, *H. divisorsensis*, *H. helleri*, *H. huamponicus*, *H. inambari*, *H. jabonero*, *H. jelskii*, *H. mikrostiktos*, *H. polyodon*, *H. quindos*, *H. raqueliae*, *H. santamartae*, *H. surinamensis*, *H. taeniurus*, *H. tridens*, and *H. yacopiae* in having melanophores on the posterior margins of the scales along the sides of body (vs. lacking melanophores on margins of scales along entire length of the sides of body). The new species differs from all congeners mentioned above in having, among other features, six teeth in the outer premaxillary row arranged in a straight line (vs. five or fewer teeth not arranged in straight line except *H. cairoense* with two to six teeth in the outer premaxillary row).

Resumen

Hemibrycon sanjuanensis, nueva especie, se describe de la cuenca alta del Río San Juan, vertiente Pacífico, Colombia. Este se distingue de *H. boquiae*, *H. brevispini*, *H. cairoense*, *H. colombianus*, *H. mikrostiktos*, *H. metae*, *H. palomae*, *H. rafaelense* y *H. tridens* por la presencia de una mancha humeral circular u ovalada que se localiza a dos escamas posterior al borde del opérculo (vs. 3–4 escamas en *H. palomae*, *H. rafaelense*, *H. brevispini* y *H. cairoense*, y cero o una escama desde el opérculo en *H. metae* y *H. boquiae*). Esta se distingue de *H. colombianus* en poseer una mancha humeral redondeada u ovalada (vs. rectangular). Esta se diferencia de *H. beni*, *H. dariensis*, *H. divisorensis*, *H. helleri*, *H. huamponicus*, *H. inambari*, *H. jabonero*, *H. jelskii*, *H. mikrostiktos*, *H. polyodon*, *H. quindos*, *H. raqueliae*, *H. santamartae*, *H. surinamensis*, *H. taeniurus*, *H. tridens*, y *H. yacopiae* en presentar melanóforos sobre el borde posterior de las escamas a lo largo de los lados del cuerpo (vs. ausencia de melanóforos sobre el borde posterior de las escamas de las escamas en los lados del cuerpo). La nueva especie se distingue de todos los congéneres, citados arriba, por presentar seis dientes en la fila externa del premaxilar ordenados en línea recta (vs. cinco o menos no ordenados en línea recta, excepto *H. cairoense* con dos a seis dientes en la fila externa del premaxilar).

Keywords

Biodiversity, taxonomy, tropical fish, new taxon

Palabras claves

Biodiversidad, taxonomía, pez tropical, nuevo taxón

Introduction

Today there are 36 species reported in the genus *Hemibrycon* (Eschmeyer and Fricke 2013). Of these, 21 species are distributed in Colombian watersheds, but only one species, *H. dariensis*, has been reported from the San Juan drainage on the Pacific coast. The present day distribution of *Hemibrycon* in Colombia suggests that this genus has its greatest diversity in Andean streams and high mountain habitats. But there are exceptions such as *H. dariensis*, which occurs in Pacific drainages, *H. santamartae* and *Hemibrycon* sp. n. found in northern Colombia, and *H. metae* from the upper Meta River drainage in the Orinoco River Basin (Bertaco and Malabarba 2010; Román-Valencia and Ruiz-C 2007; Román-Valencia et al. 2009a; Román-Valencia et al. 2013). The discovery of a new species of *Hemibrycon* from the upper San Juan River Basin, Pacific versant in Colombia, is a result of the authors' ongoing revision of *Hemibrycon* (Román-Valencia et al. 2010; 2013) and is further proof of undocumented biodiversity in the genus.

Material and methods

Fishes were captured using seines and were preserved in the field with 10% formalin and later stored in 70% ethanol. Measurements and counts follow Armbruster (2012) and Román-Valencia et al. (2010). Measurements were made with digital calipers to 0.01 mm precision and are expressed as percentages of standard length (SL) and head

length (HL). In reporting counts, values for the holotype are indicated with an asterisk (*). In the list of paratypes, the number of individuals is given immediately after the catalog number, which is followed by the range of SL in mm for that lot. Counts and measurements were taken on the left side of specimens when possible. A multivariate analysis was performed on the morphometric data with the PAST program, version 1.81 for Windows (Hammer et al. 2008), and a variable canonical analysis (CVA) was undertaken assuming allometric growth. All measurements were log transformed, correcting for size using Burnaby methods (Burnaby 1966) in the software PAST to adjust for or eliminate the influence of size and compensate for the allometric growth. In the CVA we included data for *H. dariensis* (n=71), which is allopatric with the new species in the San Juan River drainage and *H. cairoense* (n=46), which occurs in nearby watersheds. Morphological analysis based on bivariate or multivariate testing seeks to establish parameters (= morphological characters) for discriminating the closest species to the new taxon from other species present in the area of geographic distribution.

Osteological observations were made on cleared and stained specimens (C and S) prepared according to Taylor and Van Dyke (1985) and Song and Parenti (1995). Bone nomenclature follows Weitzman (1962), Vari (1995), and Ruiz-C and Román-Valencia (2006). Specimens are deposited in the Ichthyology Laboratory at the Universidad del Quindío, Armenia, Colombia (IUQ). Institutional acronyms for comparative material follow Sabaj-Pérez (2010). All collections were made in Colombia.

Taxonomy

Hemibrycon sanjuanensis sp. n.

<http://zoobank.org/5BF13995-FCD7-42FD-93E3-9B3F62A1BF80>

Table 1–2, Figures 1–4

Holotype. IUQ 3693, 53.5 mm SL, Colombia, Risaralda, Pueblo Rico, El Recreo, upper San Juan River, Aguas Claras River, Tatamá River tributary on Apia-Pueblo Rico road, 5°13'04.9"N, 76°01'50.1"W; 1519 m.a.s.l. (meters above sea level); **Paratypes:** IUQ 3039, 8, 47.0–58.4 mm SL, collected with holotype; IUQ 3040, 8, 39.3–81.2 mm SL, Risaralda, Pueblo Rico, La Selva, upper San Juan River Basin, La Selva Creek, tributary of Taiba River, 5°14'29.1"N, 76°04'42.1"W; 1359 m.a.s.l.; IUQ 3041, 2, 70.6–84.9 mm SL, Risaralda, Pueblo Rico, upper San Juan River Basin, creek 1 km from Pueblo Rico on road to Santa Cecilia, 5°14'06.1"N, 76°02'20.1"W; 1357 m.a.s.l.; IUQ 3042, 17, 21.3–70.9 mm SL, Risaralda, Pueblo Rico, upper San Juan River Basin, Agua Bonita Creek tributary of Tatamá River on road from Pueblo Rico to Santa Cecilia, 5°13'46"N, 76°02'05.1"W; 1530 m.a.s.l.; IUQ 3694, 2 C and S, 66.0–69.3 mm SL, Risaralda, Pueblo Rico, La Selva, upper San Juan River Basin, La Selva Creek, tributary of Rio Taiba, 5°14'29.1"N, 76°04'42.1"W; 1359 m.a.s.l.; IUQ 3695, 2 C and S, 55.0–66.7 mm SL, Risaralda, Pueblo Rico, upper San Juan River Basin, Agua Bonita Creek, tributary of Tatamá River on Pueblo Rico- Santa Cecilia road,



Figure 1. *Hemibrycon sanjuanensis* sp. n., holotype IUQ 3693. 53.5 mm SL, Colombia, Risaralda State, Pueblo Rico Municipality, El Recreo, upper San Juan River Basin, Aguas Claras River, tributary of the Tatamá River. Scale 1 cm.

5°13'46"N, 76°02'05.1"W; 1530 m.a.s.l.; IUQ 3697, 19, 57.5–82.2 mm SL, Risaralda, Pueblo Rico, El Indio on Pueblo Rico-Villa Claret road, 200 m upstream from bridge, upper San Juan River Basin, Tatamá River, 5°1'50.52"N, 76°0'9.36"W; 1407 m.a.s.l.

Diagnosis. *Hemibrycon sanjuanensis* sp. n. differs from *H. boquiae*, *H. brevispini*, *H. cairoense*, *H. colombianus*, *H. mikrostiktos*, *H. metae*, *H. palomae*, *H. rafaelense* and *H. tridens* by the presence of a circular or oblong humeral spot located two scales posterior to the opercle (vs. 3–4 scales in *H. palomae*, *H. rafaelense*, *H. brevispini* and *H. cairoense*, and 0–1 scales in *H. metae* and *H. boquiae*). It further differs from *H. colombianus* in having a round or oblong humeral spot (vs. rectangular). It differs from *H. beni*, *H. dariensis*, *H. divisorensis*, *H. helleri*, *H. huamponicus*, *H. inambari*, *H. jabonero*, *H. jelskii*, *H. mikrostiktos*, *H. polyodon*, *H. quindos*, *H. raqueliae*, *H. santamartae*, *H. surinamensis*, *H. taeniurus*, *H. tridens* and *H. yacopiae* in having melanophores present on the posterior margins of the scales all along the sides of body (vs. melanophores absent from margins of scales along entire length of sides of body). The new species further differs from all the species mentioned above in having a wide, concave pelvic bone (vs. narrow and straight); the middle part of the dorsal margin of the orbito-sphenoid bone flattened and not in contact with frontal (vs. dorsal margin straight and in contact with frontal); ventral tip of supracleithrum bifurcate (vs. not bifurcate); six teeth in the outer premaxillary row arranged in a straight line (vs. five or fewer teeth in outer premaxillary row and not arranged in straight line, except *H. cairoense* with two to six teeth in the outer premaxillary row).

Description. Body slender and elongate (mean maximum body depth about 26.1% SL). Area above orbits flat between anterior margin of orbits and supraoccipital spine. Dorsal profile of head and body oblique from supraoccipital to dorsal-fin origin and from last dorsal-fin ray to base of caudal fin. Ventral profile of body convex from snout to base of pelvic fin; straight from pelvic-fin origin to anal fin. Caudal peduncle laterally compressed. Head and snout short (21.2% SL and 25.0% HL respectively), jaws

equal, mouth terminal, lips soft and flexible, and outer row of premaxillary teeth; ventral border of upper jaw flat; posterior edge of maxilla reaching anterior edge of orbit. Premaxilla with two rows of teeth (Fig. 4). Six teeth of outer row tricuspid with central cusp largest, teeth arranged in straight line. Inner premaxillary row with four pentacusp teeth that diminish gradually in size. Maxilla long, posterior margin straight, with 5–11 uni- or tricuspid teeth, central cusp slightly longer than outer cusps in tricuspid teeth (Fig. 4). Dentary with three or four large tricuspid teeth with central cusp largest, followed by two to four smaller, uni- to tricuspid teeth (Fig. 4). Six infraorbitals present, the first thin and narrow, extending between the dorsal edge of maxilla and lateral ethmoid, with sensorial canal. Second infraorbital short and wide, not covering dorsal part of angulo-articular. Anterior part of second infraorbital overlaying anterior part of first infraorbital; its posterior margin extending below third infraorbital. Third infraorbital widest and longest, its ventral border in contact with sensorial canal of preopercle. Fourth, fifth and sixth infraorbitals short and wide, covering posterior margin of hyomandibular. Supraorbital absent. Eight to nine supraneurals present between head and anterior part of dorsal fin, without cartilage on upper and lower edges, and with medial sensorial canal. Scales cycloid, moderately large. Lateral line complete with 40–47 pored scales (44*, mean=42.5, n=40). Scale rows between dorsal-fin origin and lateral line 5–6 (5*, mean=5.9); scale rows between lateral line and pelvic-fin origin 4–6 (5*, mean=5, n=40); scale rows between lateral line and anal-fin origin 4–6 (5*, mean=4.8, n=40); predorsal scales 11–14, arranged in regular series 11–14 (12*, mean=12.4, n=40). Dorsal-fin rays iii, 7–8 (iii, 7*, n=40); first unbranched ray approximately one-half length of second ray, its tip not reaching first bifurcation of first branched ray. Anal-fin rays iii–iv, 24–30 (iii, 27*, n=40). Anal-fin origin posterior to vertical through base of last dorsal-fin ray. Pectoral-fin rays ii, 9–12 (11*, n=40). Pelvic-fin rays ii, 6 (6*, n=40). Pelvic-fin origin anterior to vertical through dorsal-fin origin. Caudal fin not covered with scales except at its base, forked with short pointed lobes. Total number of vertebra 39–41.

Secondary sexual dimorphism. Males have between 3–11 very short hooks present on all branched pelvic-fin rays, located on both branches of rays, but predominantly on internal and lateral branches; hooks present on one simple pelvic-fin ray. Males have row of very short hooks on first seven to fifteen branched anal-fin rays, each ray has from 3–5 hooks, which extend along the extreme distal branch of rays; no hooks on simple anal-fin rays.

Live colors. Dorsum of body and head silvery green; sides and ventrum silvery white from opercle to caudal peduncle. Caudal peduncle with dark midlateral stripe that extends on to middle caudal-fin rays and has a reddish spot on the ventral portion of the caudal-fin base. Humeral spot dark and rounded or oblong with some dispersed melanophores extending dorsally and ventrally. Pectoral and pelvic fins hyaline, but dorsal, anal and caudal fins with hues of reddish yellow and with dispersed melanophores on interradiar membranes.

Pigmentation in alcohol. Body dark brownish-yellow, melanophores more densely concentrated on dorsum and upper sides than on ventrum, most intense on head; with melanophores present on the posterior margins of the scales all along the

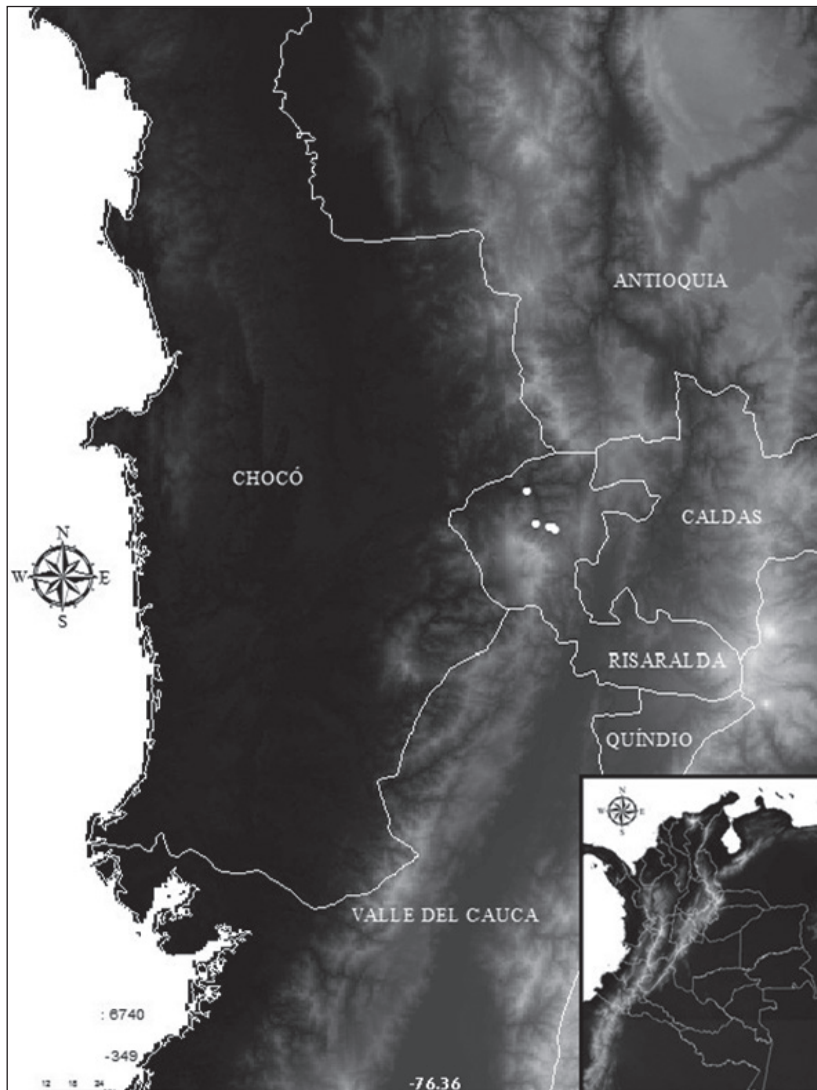


Figure 2. Distribution and location of *H. sanjuanensis* sp. n. in the Alto San Juan River, Risaralda state, Colombia.

sides of body. Trunk with dark, midlateral stripe from posterior margin of humeral spot to caudal peduncle, extending on to caudal fin. Humeral spot circular or oblong, located two scales posterior to the opercle, not reaching the first series of scales below the lateral-line canal. Ventral part of body light yellow. Dorsal fin with melanophores concentrated mostly on interradyal membranes and rays. Adipose fin hyaline. Dark melanophores present on middle caudal-fin rays, near caudal-fin base. Pectoral and pelvic fins hyaline; anal and caudal-fin lobes dusky and with melanophores concentrated on interradyal membranes to form band.

Table 1. Counts and measurements of *Hemibrycon sanjuanensis* sp. n. Standard and total lengths in mm, averages in parentheses.

	Holotype	Paratypes
Standard length	53.3	21.3–84.9 (60.0)
Total length	63	6.3–100.3 (71.1)
Percentages of SL		
Body depth	26.4	19.2–30.2 (26.1)
Snout-dorsal fin distance	50.7	23.3–53.5 (49.7)
Snout-pectoral fin distance	24	21.7–27.3 (23.0)
Snout-pelvic fin distance	41.5	41.4–47.5 (42.9)
Snout-anal fin distance	56.8	54.4–61.1 (56.6)
Dorsal fin-hypural distance	53.7	26.7–57.4 (51.5)
Dorsal-fin length	20.1	18.3–24.4 (20.4)
Pectoral-fin length	19.9	15.3–20.5 (18.5)
Pelvic-fin length	12.6	8.6–13.3 (11.7)
Caudal peduncle depth	11.8	5.3–12.3 (10.7)
Caudal peduncle length	12	5.6–13.6 (10.7)
Head length	21.7	18.9–26.2 (21.2)
Dorsal-anal fin distance	27.6	22.8–38.0 (27.9)
Dorsal-pectoral fin distance	37.7	34.2–43.5 (38.3)
Anal-fin length	15.8	11.0–17.5 (13.8)
Percentages of HL		
Snout length	25	16.0–29.0 (25.0)
Orbital diameter	37.3	29.5–44.2 (36.2)
Postorbital distance	34.2	29.1–44.9 (38.8)
Maxilla length	38.2	25.7–41.6 (33.7)
Interorbital distance	38.5	32.0–44.7 (36.8)
Mandible superior distance	30.8	25.7–37.4 (32.8)
Lateral-line scales	44	40–47
Scale row between dorsal-fin origin and lateral line	6	5–6
Scale rows between anal-fin origin and lateral line	5	4–6
Scale rows between pelvic-fin and lateral line	5	4–6
Predorsal median scales	12	11–14
Dorsal-fin rays	iii, 7	iii, 7–8
Anal-fin rays	iii, 27	iii-iv, 24–30
Pelvic-fin rays	ii, 6	ii, 6
Pectoral-fin rays	ii, 11	ii, 9–12
Maxillary teeth	5	7–10

Distribution and ecological notes. This species is so far known only from the upper San Juan River Basin, Tatamá River drainage, Pacific versant, Colombia (Fig. 2). *Hemibrycon sanjuanensis* sp. n. was captured in streams characterized by relatively rapid water running over rocky and sandy substrates with high transparency. The pH was near neutral, dissolved oxygen values were high, and conductivity and total solids were low (Table 2), typical of oligotrophic environments.

Table 2. Physicochemical variables in habitat of *Hemibrycon sanjuanensis* sp. n. San Juan River Basin, Colombia. Localities: 1. Aguas Claras River 2. La Selva Creek, 3. Agua bonita Creek. 4. Chupaderos Creek, 5. La Soledad Creek, 6. Itauri Creek, 7. Tatama River, m.a.s.l. = meters above sea level; Rd. Rocks and detritus; Rs. Rocks and Sand; width: of river at collecting site.

	Locality						
	1	2	3	4	5	6	7
m.a.s.l.	1519	1359	1530	1375	1219	446	1407
Water temperature (°C)	16.9	18.3	20.0	17.8	19.2	22.4	21.3
Air temperature (°C)	19.9	23.7	20.0	20.8	22.2	23.7	22.1
Dissolved oxygen (mg/l)	7.8	7.5	6.5	7.5	6.9	6.4	7.2
pH	7.51	7.47	6.3	7.6	7.57	7.67	7.57
Conductivity (us/cm)	0.49	0.446	0.001	0.698	-	1.443	0.72
Total solids (STD)	0	0	1	1	1	1	-
Width (m)	10	5–6	1–2	1–2	1–1.5	5–6	10.0–15.0
Depth (m)	1–2	0.5	0.5	0.3–0.5	0.5	0.5–1	0.5–3
Color	clear	clear	clear	clear	clear	clear	clear
Substrate	Rs	Rd, Rs	Rd, Rs	Rs	Rs	Rs	Rs

The new species is syntopic with *Bryconamericus emperador*, *Astroblepus* sp., *Pimelodella* sp. and *Characidium* sp. The analysis of stomach contents of four specimens revealed the presence of adults and larvae of two different species of Coleoptera: Hydrophilidae, *Promoresia* sp. and *Elmid* sp., Diptera: Simuliidae and Sarcophagidae, adult of Odonata Zygoptera, Dytiscidae, Trichoptera, Nematoda, Isopoda and fragments of unidentified arthropods. The presence of autochthonous and some allochthonous items suggest that this species is insectivorous with considerable plasticity in its diet.

Etymology. *Hemibrycon sanjuanensis* is named for the San Juan River Basin, where the type series was collected (Fig. 2).

Remarks. Canonical Variables Analysis (CVA) of *H. sanjuanensis* and species found in the San Juan and nearby rivers (including *H. dariensis* and *H. cairoense*), revealed significant differences among them, based on several characters, the most important of which are the length of the pelvic fin (variable M) and upper jaw length (related to variable W) (Fig. 3); the first canonical variable explained 84.3% of total variation, the second explained 15.6%. Linear regression analysis of the upper jaw length showed positive increment of these variables in *H. sanjuanensis* (vs. negative increment in the other species studied) and so separated it from the other species included in the analysis ($r=-0.15$, $P=0.02$).

Moreover, this new species is distinguished from *H. cairoense* (Román-Valencia and Arcila-Mesa 2009) by the number of unbranched dorsal-fin rays (iii vs. ii), by the number of scales rows between the dorsal-fin origin and the lateral line (5–6 vs. 6–7), between the anal-fin origin and the lateral line (5–6 vs. 6–7), and between the pelvic-fin insertion and the lateral line (4–6 vs. 6–7), by the presence of hooks on the males (only on the pelvic fin rays vs. on the anal, pelvic, pectoral and posterior portions of dorsal fin ray).

Discussion. *Hemibrycon sanjuanensis* has all of the synapomorphies observed in other *Hemibrycon* (Arcila-Mesa 2008, Mirande 2010). Although species of *Hemibrycon* have a similar color pattern throughout their geographic distribution, subtle differences in the concentration and distribution of black pigment in the humeral and caudal regions have been used to diagnose new species (Bertaco and Malabarba 2010; Román-Valencia et al. 2009a, b, c, 2013; Román-Valencia and Arcila-Mesa 2010).

Hemibrycon sanjuanensis has a reddish spot on the ventral portion of the caudal-fin base in life. This characteristic has also been observed in several other species of *Hemibrycon* (Bertaco et al. 2007; Román-Valencia et al. 2010) and has been suggested as a synapomorphy for the genus by Arcila-Mesa (2008) and Román-Valencia et al. (2013).

Two species, *H. dariensis* and *H. microformaa*, have been reported previously from the San Juan, Atrato and Leon River drainages (Román-Valencia and Ruiz-C 2007; Román-Valencia and Arcila-M. 2008). The new species is similar and probably related phylogenetically to *H. dariensis* but is distinguished from it by the following: the presence of a dark lateral stripe that continues on to the middle caudal-fin rays (vs. wide lateral band extending only to bases of middle caudal-fin rays); pectoral fins not reaching pelvic-fin origins (vs. pectoral fins reaching pelvic-fin origins); 39–41 total vertebrae (vs. 37–38); mean length of pelvic fins 11.7% SL, (vs. 15.2%). From *H. microformaa* (Román-Valencia and Ruiz-C 2007), the new species differs in attaining a larger adult size (greater than 31 mm SL vs. SL < 31 mm); in not having flat dorsal margins of the orbits and ventral profile of the snout (vs. flat); terminal mouth with upper jaw not surpassing lower (vs. mouth subterminal); greater total number of vertebrae 39–41 (vs. 33–34); and a greater number of branched anal-fin rays 24–30 (vs. 14–16).

Comparative material examined. *Hemibrycon beni*: UMSS 09585, 18, Bolivia, Amazonas/Madera/Beni/Bopo, Pekheñkhara River Imanblaya, 3 Jan. 1990; UMSS 0890, 50, Bolivia, Amazonas/Beni/Madera/Kaka, tributary of Taipiplaya-Taipiplaya Rivers, 3 Oct. 2008. *Hemibrycon boquiae*: All from Colombia, Quindío state, Salento municipality, Upper Cauca River, Quindío River: IUQ 301a, 3, (C and S), Boquia Creek, 4°38'35"N, 75°75'11"W, 1819 m.a.s.l.; IUQ 754,104, Boquia Creek (4°38'35"N, 75°75'11"W, 1819 m.a.s.l.; IUQ 871, 15, Boquia Creek, 4°38'35"N, 75°75'11"W, 1819 m.a.s.l. *Hemibrycon brevispini* paratypes: IUQ 883,6, Colombia, Quindío state, Calarcá municipality, Upper Cauca River, Quindío River, Venada Creek, tributary of Santo Domingo River, Quebrada Negra road, 4°26'52"N, 75°41'02"W, 1278 to 1304 m.a.s.l.; IUQ 1453,5 (C and S), Colombia, Quindío state, Calarcá municipality, Upper Cauca River, Quindío River, Quebrada Negra and Venada Creek, drainage of Santo Domingo River, 200 m along Quebrada Negra road after the bridge of the Santo Domingo River. *Hemibrycon cairoense* Paratypes: IUQ 537, 2 (C and S), Colombia, Risaralda state, El Cairo, Upper Cauca River, Los Ramirez Creek, tributary of La Italia Creek, road from Quinchia to El Cairo, 200 m beside the bridge; IUQ 537, 2 (C and S), Valle del Cauca state, El Cairo municipality, Upper Cauca River, Los Ramirez Creek, tributary of La Italia Creek, El Cairo, road from Quinchia to El Cairo, 200 m from bridge. *Hemibrycon colombianus*: IAvH 3130, 28, Colombia, Santander state, Magdalena River, Moniquira River, Suarez River, Sept 11

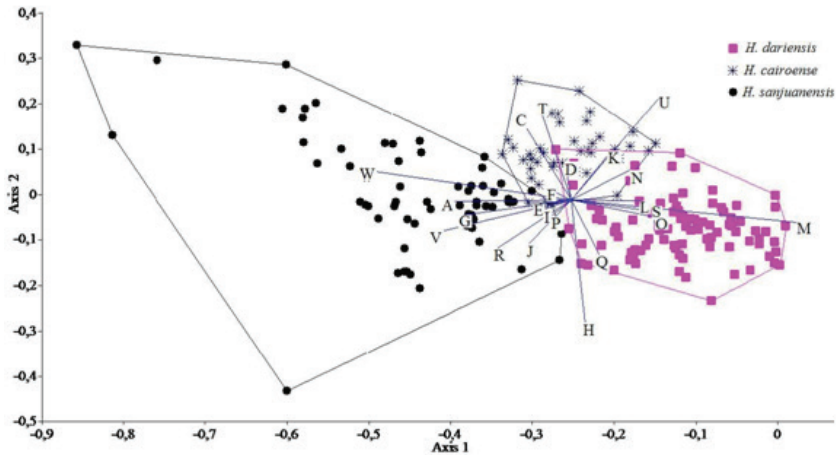


Figure 3. Representation of the Canonical Variables (CV canonical variable 1 is the X axis and canonical variable 2 is the Y axis) for *Hemibrycon sanjuanensis* sp. n., *H. cairoense* and *H. dariensis*.

and 13, 1995; IAvH 2942, 6, Colombia, Boyacá state, Suarez River and El Cobre Creek; IAvH 3132, 24, Colombia, Boyacá state, Moniquira and Suarez Rivers, El Cobre Creek; ICNMNH 755, 7, Colombia, Santander state, Capitanejo and Nevado Rivers. *Hemibrycon coxeyi* ANSP 70155 (Holotype), Ecuador, Hacienda Las Mascotas, mouth of the Pastaza River, Marañón River drainage. *Hemibrycon dariensis*: USNM 260697,1, Colombia, Choco state, Atrato River, Bernal Creek, tributary of Negua River, 17 Mar 1967; USNM 293218, 2, Panamá, of Kuna Yala, Madinga River between Pingandi River and Mandinga (Atlántico), 09°28'N, 70°06'W, 3 Mar 1985; USNM 293234, 1, Panamá, Darién, Pirre River about 1/2 km above El Real (Tuira River), Pacific, 19 Feb 1985; USNM 293245, 28, Panamá, Darién, Tuira River, Darién Province, Pucuro River about 3–4 km above the confluence of the Tuira River, Pacific, 17 Feb 1985; IUQ 523, 26, Colombia, Antioquia state, Uraba, Zungo River highway, León River system, 17 Dec 1990; IUQ 524, 2, Colombia, Antioquia, Uraba, Creek km 25 Mutatá-Chigorodo road, Dec 1990; IUQ 525, 26, Colombia, Antioquia, Uraba, Caribbean sea, León River drainage, Villarteaga River, Dec 1990. *Hemibrycon fasciatus* (paratypes): All from the state (Departamento) of Antioquia, middle Magdalena River Basin: IUQ 3065, 4; 32.4–71.5 mm SL, Santa Gertrudis Creek, tributary of Nare River, Concepción municipality 6°19'21.0"N, 75°09'38.6"W, 1820 m.a.s.l., 31 Jan 2010; IUQ 3156, 1, 52.7 mm SL, Santa Gertrudis Creek, tributary of Nare River, Concepción and Alejandría municipality, after the Peñol-Guatapé dam. *Hemibrycon guppyi*: BMNH 1906623, lectotype, 1. USNM 290406, 1, C and S. USNM 290406, 7. *Hemibrycon helleri*: (see Arcila-M., 2008). *Hemibrycon jelskii*: MUSM 36126, 7, Peru, Cusco state, Amazon River, La Convención, Echarate, Urubamba, Perotoni River, 28 May 2009; MUSM 35492, 13, Peru, Ucayali state, Amazonas, Atalaya, Sepaliva, Lazaro Creek tributary of Mishahua River, 28 May 2009. *Hemibrycon jabonero*: All from Venezuela: EBRG 7542, 10, Falcón state, Sierra San Luis, Mitare River on old road

between Cabure and San Luis, 28 Jun 1996; IUQ 553, 3, Carabobo state, Valencia Lake basin, El Ercigue river, north of San Joaquin, 4 May 1991; MBUCV 22854, 18, Carabobo state, Valencia Lake, 18 Jun 1968; MBUCV 12530, 4, Miranda state, Grande River 500 m after Santa Cruz River, Guatopo National Park, 1 Mar 1981; MBUCV 9736, 1, 66.4 mm SL, Monagas state, San Juan River, Los Morros Caripito, 28 Apr 1977; MBUCV 27652, 4, Carabobo state, Grande River, Guatopo National Park, 20 Dec 1980; MBUCV 12514, 5, Miranda state, Grande River, 500 m after Santa Cruz River, Guatopo Nacional Park, 3 Feb 1981; MBUCV 22809, 5, Carabobo state, Miquita River, 2 km south of GoaiGoaza, 2 Dec 1969; MCNG 42720, 17, Merida state, Chama River, Lake Maracaibo Basin, 14 Nov 2005; MCNG 33313, 1, Zulia state, Río Chama, 3 km from bridge at road, 14 Nov 2005; MCNG 27567, 1, Lara state, Caño Los Giles, 5 km. S.W. La Pastora, upper Tocuyo River, Caribbean Sea, 1 Jan 1992; MCNG 24838, 12, Zulia state Merida-Tachira, Maracaibo basin, Escalante River, 3 Mar 1991; MCNG 48498, 38; Portuguesa state, creek north of Ospino, road to Estación La Reinos, 3 Nov 1995; MCNG 188, 1, Zulia state, Negro River, Lake Maracaibo Basin, 14 Nov. 2005; MCNG 7475, 2, Merida state, road to Tovar, Uribante, 14 Nov 2005; MCNG 24821, 3, Merida state, creek ca. 3 km. East from Capazón, 1 Jul 1991; EBRG 4324, 23, Aragua state, Limón River, pool 350 m NW of Profauna building, El Limón, 21 Mar 1990; EBRG 9950, 2, Carabobo state, Salado River, Hacienda Urama II, 2 Jul 2004; EBRG 9349, 4, Cojedes state, road to Hato Piñero, Las Damitas Creek, under bridge, 21 Mar 1990; EBRG 4324, 33, Aragua state, Limón River, pool 350 m NW of Profauna, El Limón, 21 Mar 1990; EBRG 9953, 32, Carabobo state, Morón River, old highway to Morón Reservoir, 30 Jun 2004; EBRG 9951, 20, Carabobo state, Alpargaton River, above quarry, 13 Apr 2005; MCNG 54541, 25, Falcon state, El Hueque Creek, bridge on Churuguara-Coro road, 14 Nov 2005; MCNG 54589, 3, Yaracuy state, creek on Hacienda Guaquira, 14 Nov 2005; MCNG 54610, 20, state Yaracuy, Sarare Creek 1 km from Hacienda Corozal, 14 Nov 2005; MCNG 54566, 46, Carabobo state, El Samán on Alpargaton River, above sand quarry, 14 Nov 2005; MCNG 54602, 16, Yaracuy state, Hacienda Guaquira, upper Guaquira Creek at cement crossing, 14 Nov 2005; MCNG 49640, 5, Crucito River, Crucito Sector, 1 km from asphalt de road to Palma Sola, 16 Jan 2004; MCNG 16972, 8, Cocotal River (or Cocollar) at Campo Elias before San Antonio, at mouth with Guarapiche River, San Juan River system, 14 Nov 2005; MCNG 6475, 2, Apure state, mouth of creek tributary to Grande River, Tachira River drainage, 14 Nov 2005. *Hemibrycon metae*: IAvH 3122, 10, Colombia: Casanare state, Aguazul, Orinoco, Chichaca Creek, tributary of Cachiza River, 1 Mar 1994; IAvH 3125, 33, Colombia: Casanare state, Aguazul, Orinoco, Unete, Cravo Sur and Tua River drainage, 4 May 1996; IAvH 3129, 50, Colombia: Casanare state, Aguazul, Orinoco, Cuiagu Creek, Unete River drainage, 4 Mar 1994; all from Venezuela: MCNG 26774, 2, Barinas state, Santa Barbara River, 3 km NE, Santa Barbara, Apure River basin, 1 Jan 1992; MCNG 26774, 26, Barinas state, Santa Barbara River, 3 km NE Santa Barbara, Apure River basin, 1 Jul 1992; MCNG 7916, 1, Barinas state, Apure, Pedraza District, Ticoporo Creek at bridge on road from Acequia River, 7 Dec 1982; MCNG

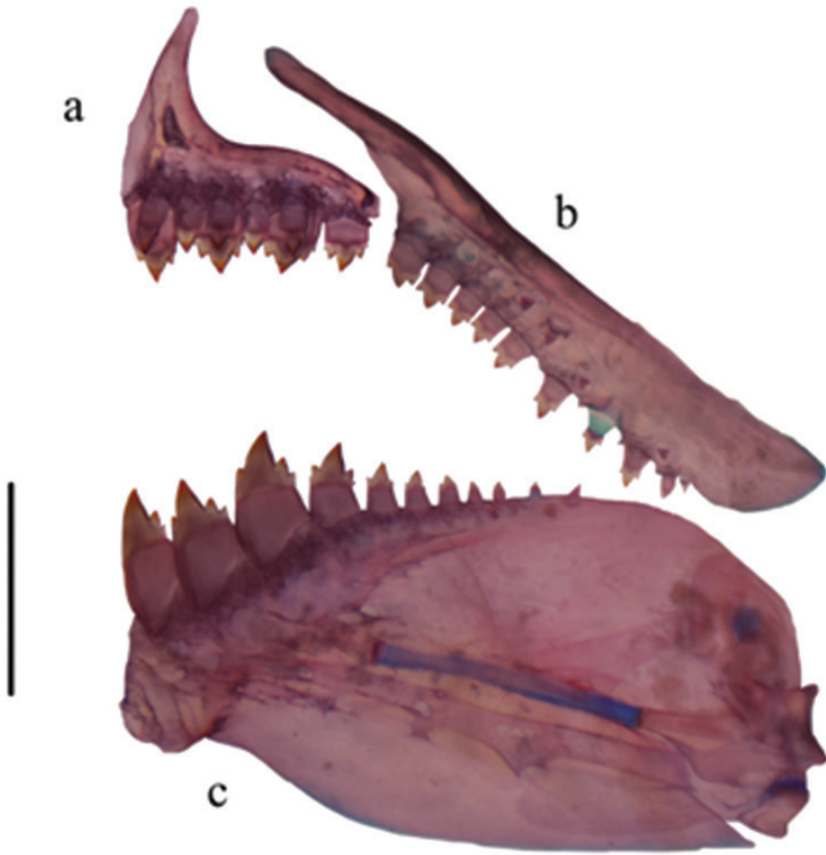


Figure 4. Upper and lower jaws of *Hemibrycon sanjuanensis* sp. n. IUQ 3695, 55.5 mm SL, A Premaxilla B Maxilla C Lower jaw. Scale bar = 1 mm.

50011, 1, Ventuari River, Tencua Falls, 58 km. E of San Juan de Manapiare, 5°2.86'N, 65°36.95'W, 21 Apr 2004; MCNG 41903, 2, Barinas state, upper La Yuca River, 3 Nov 1998; MCNG 32396, 30, creek NE of San Antonio, Highway 5, Curito River, 3 Feb 1993. *Hemibrycon surinamensis*: (see Arcila-Mesa 2008). *Hemibrycon tridens*: (see Arcila-Mesa 2008). *Hemibrycon micromorfaa* IUQ 512 (1 Paratype), (C and S), Colombia, Atrato River Basin, Chintado River, 100 m bridge on Yuto-Certegui; IUQ 1204, 1, paratype, (C and S), Atrato River Basin, Chintado River, 100 m bridge on the Yuto-Certegui. *H. mikrostiktos* (see Bertaco and Malabarba 2010). *Hemibrycon orcesi* ANSP 75904 (paratype), 2, Ecuador, Santiago-Zamora, headwaters of Macuma River, tributary of Morona River, 550–650 m.a.s.l. MEPN 001542, 2, paratype, Ecuador, Pastaza, Macuma River, Apr 1953; MEPN 001538, 17, Ecuador, Morona-Santiago, Tayusa River, tributary of lower Upano River, at bridge on Méndez-Sucua road, 4 May 1991. MEPN 001539, 66, Ecuador, Morona-Santiago, Tayusa River, tributary of Upano River at bridge on Méndez-Súcua road, 4 May 1991; MEPN 001540, 10, Ecuador, Pastaza, downstream from Sarayaco, Aug 1956. MEPN 001541, 5, Ecuador,

Pastaza, Pastaza River, AquaRAP, 22 Jul 1999. MEPN001543, 2, Ecuador, Pastaza, Bobonaza-Canelos River, Pastaza River Basin, Apr 1953. MEPN 13591–6, 39, Ecuador, Morona-Santiago, Tayusa River tributary Upano River 4, May 1991. *H. pautensis*: MEPN 001550, 10, Ecuador, Carchi, El Voladero lagoons in El Angel Biological Reserve, 0°40'N, 77°52'W, 3680 m.a.s.l., 20 Jul 2001. *Hemibrycon palomae* (paratypes), all from Colombia, Cauca-Magdalena River Basin, Quindío, Quimbaya, El Ocaso natural reserve, Roble River drainage, La Paloma creek: IUQ 2300,6, 46.4–65.4 mm SL, 15 May 2008. *Hemibrycon polyodon* IUQ 1142, 2, (C and S), Ecuador, Antonio-Guadalupe Creek, 12 Mar 1979. *Hemibrycon quindos* paratypes: IUQ 487, 28, Colombia, Quindío state, Salento municipality, Llano Grande, Upper Cauca, Quindío River, Tinaja Creek 300 m from Llano Grande - Boquia road 4°36'57"N, 75°36'36"W, 1712m.a.s.l., 29 Jan. 2002; IUQ 488, 2 (C and S), Colombia, Quindío state, Salento municipality, Upper Cauca, Quindío River, Tinaja Creek, 300 m from Llano Grande - Boquia road, 4°36'57"N, 75°36'36"W, 1712 m.a.s.l., 29 Jan. 2002; IUQ 489, 15, Colombia, Quindío state, Salento municipality, Upper Cauca, Quindío River, Tinaja creek, 300 m from Llano Grande - Boquia road, 4°36'57"N, 75°36'36"W, 1712 m.a.s.l., 11 Jul. 1996; MTD F 27621–27622, 2, Colombia, Quindío, Salento, Llano Grande, Upper Cauca, Quindío River Basin, Tinaja creek, 300m from Llano Grande -Boquia road, 4°36'57"N, 75°36'36"W, 1712 m.a.s.l., 29 Jan. 2002. *Hemibrycon rafaelse*: (Paratypes) IUQ 509, 27, Colombia, Risaralda state, Apia municipality, Upper Cauca River, San Rafael Creek in mouth of Apia River, at 100 of Santuario-Apia Road, 5°04'54"N, 75°56'36"W, 1253 m.a.s.l., 8 Jul 2003; MCNG 54101, 5, Colombia, Risaralda state, Apia municipality, Upper Cauca River, San Rafael Creek at mouth of Apia River, 100 m from Santuario-Apia Road, 5°04'54"N, 75°56'36"W, 1253 m.a.s.l., 8 Jul 2003; MTD F 27623–27624, 2, Colombia, Risaralda state, Apia municipality, Upper Cauca River, San Rafael Creek at mouth of Apia River, 100 m from Santuario-Apia Road, 5°04'54"N, 75°56'36"W, 1253 m.a.s.l., 8 Jul 2003. *Hemibrycon raqueliae* Paratypes: IUQ 496, 2, Colombia, Caldas state, Samaná municipality, Middle Magdalena River, La Miel River, Tasajo creek, 5°23'55"N, 74°59'05"W, 1482m.a.s.l., 3 Jan 2003; IUQ 497, 99, Colombia, Caldas state, Samaná municipality, La Vención, Middle Magdalena, La Miel River Basin, Santa Rita Creek, 4 Jan. 2003; MCNG 54102, 5, Colombia, Caldas state, Samaná municipality, La Vención, Middle Magdalena River, La Miel River, Santa Rita creek, 4 Jan. 2003; IUQ 498, 2 (C and S), Colombia, Caldas state, Samaná municipality, La Vención, Middle Magdalena River, La Miel River, Santa Rita creek, 4 Jan 2003; ICNMHN 3281, 5, Colombia, Caldas state, at Norcasia-Samaná road, Middle Magdalena River, La Miel River, El Aquila creek, 8 Dec. 1992; MHNUC 019, 1, Colombia, Caldas, state Manzanares municipality, Middle Magdalena River, Manzanares River, 5°03'06"N, 75°35'05"W, 7 Dec. 1997; MTD F 27625– 27626, 2, Colombia, Caldas state, Samaná municipality, La Vención, Middle Magdalena River, La Miel River, Santa Rita Creek, 4 Jan. 2003. *Hemibrycon taeniurus* All from Venezuela: EBRG 4541, 32 Sucre state, Paria Peninsula National Park, Los Mangos sector, Yoco River; EBRG4544, 47, Sucre state, Paria Peninsula National Park, Los Mangos sector, La Toma River. EBRG 4546, 39, Sucre

state, Paria Peninsula National Park, Los Mangos sector, Bautista River; EBRG 4547, 17, Sucre state, Paria Peninsula National Park, Los Mangos sector, Las Cabreras Creek; EBRG 4550, 3, Sucre state, Paria Peninsula National Park, Los Mangos sector, Solis Creek; EBRG 4553, 2, Sucre state, PN Península de Paria, Las Melenas Sector, Río El Chispero (upper sector). EBRG 4556, 12, Venezuela, Sucre state, Paria Peninsula National Park, Los Mangos sector, Río Yoco. EBRG 4558, 7, Sucre state, Paria Peninsula National Park, Los Mangos sector, Río El Hoyo; EBRG 4560, 5; Sucre state, Paria Peninsula National Park, Los Mangos sector, Creek Las Cabreras; EBRG 4566, 12, Sucre state, Paria Peninsula National Park, Los Mangos sector, Río Guarama; EBRG 4569, 3, Sucre state, Paria Peninsula National Park, Los Mangos sector, Creek Solis. EBRG 4570, 2, Sucre state, Paria Peninsula National Park, Los Mangos sector, Creek Las Cabreras; EBRG 4571, 7, Sucre state, Paria Peninsula National Park, Los Mangos sector, Bautista River; EBRG 4581, 9, Sucre state, Paria Peninsula National Park, Los Mangos sector, Río Salado; EBRG 4584, 5, Sucre state, PN Península de Paria Las Melenas Sector, El Chispero River. EBRG 4605, 1, Sucre state, PN Península de Paria Las Melenas Sector San Antonio River about 200 m upstream from San Antonio; EBRG 4627, 2, Sucre state, PN Península de Paria Las Melenas Sector, Maraval River about 500 m upstream from Maraval. EBRG 8488, 45; Monagas state, El Guamo Dam, in cove east of MARN campsite. EBRG 8599, 1, Anzoategui state, Amana River, river crossing on Mundo Nuevo Road. EBRG 8708, 5, Monagas state, El Guamo dam below the spillway, 10°05'25"N, 63°39'20"W; EBRG 8712, 1, Monagas state, El Guamo dam beside spillway, 10°05'46"N, 39°30',02"W; EBRG 8714, 12, Monagas state, Negro River tributary from Guarapiche River, 10°09'23"N, 63°41'27"W; EBRG 8915, 1, Venezuela, Sucre state, Colorado River at bridge near transfer tunnel of treatment plant, 10°10'39"N, 64°18'02"W; EBRG 8916, 2, Sucre state, Turimiquire Dam at tunnel outlet, 10°10'38"N, 64°17'59"W; EBRG 8925, 7, Sucre state, Colorado River, tributary of Neveri River, 10°10'42"N, 64°18'06"W; EBRG 8970, 18, Sucre state, Turimiquire Mountain Range, Santa Cruz River at Santa Cruz, 10°20'43"N, 63°34'33"W, 33 m.a.s.l. ; MHNLS 8046, 2, Monagas state, Punceres River, 15 km from Quiriquire, 63°53'30"N, 63°9'W; MHNLS 8070, 119, Monagas state, Aragua River (Los Beceros Creek) at bridge, Maturín-Quiriquire road, 10 km from Aragua de Maturín, 63°25'W, 63°55'N, 100 m.a.s.l., 13 Feb 1991; MHNLS 8091, 72, Monagas state, Aragua River (Los Beceros Creek at bridge), Maturín-Quiriquire road, 10 km from Aragua de Maturín, 63°25'W, 63°55'N, 100 m.a.s.l., 13 Feb 1991; MHNLS 8157, 52, Venezuela, Sucre state, Río Parare, 5 km from Río Grande, Quiriquire-Cariaco road, 63°17'W, 10°19'N, 15 Feb 1991; MHNLS 8888, 191, Monagas, Aragua River (Los Beceros Creek at bridge), Maturín-Quiriquire road, 10 km Aragua from Maturín, 63°25'W, 63°55'N; 100 m.a.s.l., 3 Feb 1991; MHNLS 8891, 6, Monagas state, Aragua River (Los Beceros Creek at bridge), Maturín-Quiriquire road, 10 km. from Aragua de Maturín, 63°25'W, 63°55'N, 100 m.a.s.l., 3 Feb 1991; MBUCV 5036, 76, Sucre state, La Toma, Carúpano, 18 Jun 1967. *Hemibrycon santamartae* (Paratypes) all from Colombia in Cesar state, Rancheria River drainage: IUQ 924, 1, Atanquez municipality, Sierra Nevada de Santa Marta, Candela

River, approx. 11°15'N, 74°05'W; IUQ 929, 3, Magdalena River, Sierra Nevada de Santa Marta, Honduras Creek on road to Mutaiahi, approx., 11°15'N, 74°10'W; IUQ 1443,1 CandS), Atanquez municipality, Sierra Nevada de Santa Marta, Candela River, approx. 11°00'N, 72°46'W; ICNMMNH 10834,18, La Guajira, Distracción municipality, Chorreras, bridge at Cercado, road from Distracción to Caracolí, approx. 11°15'N, 74°05'W; ICNMMNH 10839, 19, Colombia, La Guajira, Marocaso municipality, approx. 11°15'N, 74°05'W. ICNMMNH 10881, 24, La Guajira, Marocaso municipality, Marocaso River, approx. 11°15'N, 74°05'W. *Hemibrycon virolinica* (Paratypes): ICNMMNH 6736, 12, Colombia, Santander, Charalá, Virolín, Luisito-Virolín Rivers, La Cristala Creek, 6°06'24"N, 73°11'55"W, 1759 m.a.s.l., 29 Nov. 1978; IUQ 521, 9, Colombia, Santander, Charalá, Virolin River, Cañaverales River on the Virolin-Sogamoso road, 6°05'40"N, 73°11'58"W, 1744 m.a.s.l., 4 Feb. 2004; MCNG 54103,2, Colombia, Santander, Charalá, Virolín Creek, Cañaverales River on the Virolin-Sogamoso road, 6°05'40"N, 73°11'58"W, 1744 m.a.s.l., 4 Feb. 2004; IUQ 522, 4, Colombia, Santander, Charala, Virolín Creek on the Virolin-Sogamoso road, 6°06'02"N, 73°11'35"W, 1790 m.a.s.l., 4 Feb. 2004. *Hemibrycon tridens* (see Bertaco and Malabarba 2010). *Hemibrycon yacopiae* (Paratype): IUQ 515, 4, Colombia, Cundinamarca, Yacopi, Hatoco-Moral, Hatoco River, Aldana River system, Middle Magdalena River Basin, 5°31'22"N, 74°19'30"W, 761 m.a.s.l., 26 Aug. 2003; IUQ 516, (8); Colombia, Cundinamarca, Yacopi, La Mina Creek at Yacopi-La Mina road, Magdalena River Basin, 5°25'51"N, 74°19'59"W, 1094 m.a.s.l., 27 Aug. 2003; MCNG 54104, 2, Colombia, Cundinamarca, Yacopi, La Mina Creek at Yacopi-La Mina road, Magdalena River Basin, 5°25'51"N, 74°19'59"W, 1094 m.a.s.l., 27 Aug. 2003; MTD F 26627, 1, Colombia, Cundinamarca, Yacopi, La Mina Creek at Yacopi-La Mina road, Middle Magdalena River Basin, 5°25'51"N, 74°19'59"W, 1094 m.a.s.l., 27 Aug. 2003.

Acknowledgments

We are grateful for the support of the University of Quindío (UQ), Vicerrectoria of Investigations for grants 304, 357, 464 to C.R-V. and R.I.R-C. and Facultad de Ciencias Basicas and Tecnologías U.Q. for financial support for Research Project 594 and funding for a visiting researcher to IUQ (DCT) in June–July 2013 and 2014. Cristian Román-P (IUQ and UV) identified stomach contents and elaborated figure 2. We thank the editor of ZooKeys and one anonymous referee for their comments and corrections which helped to improve this paper.

References

- Arcila-Mesa DK (2008) Análisis filogenético y biogeográfico de las especies del género *Hemibrycon* (Characiformes, Characidae). Trabajo de grado B. Sc. Programa de Biología, Universidad del Quindío, Armenia, Colombia.

- Armbruster JW (2012) Standardized measurements, landmarks, and meristic counts for cypriniform fishes. *Zootaxa* 3586: 8–16
- Bertaco VA, Malabarba LR, Hidalgo M, Ortega H (2007) A new species of *Hemibrycon* (Teleostei: Characiformes: Characidae) from the rio Ucayali drainage, Sierra del Divisor, Peru. *Neotropical Ichthyology* 5: 251–257. doi: 10.1590/S1679-62252010000400005
- Bertaco VA, Malabarba LR (2010) A review of the Cis-Andean species of *Hemibrycon* Gunther (Teleostei: Characiformes: Characidae: Stevardiinae), with description of two new species. *Neotropical Ichthyology* 8: 737–770.
- Burnaby TP (1966) Growth invariant discriminant functions and generalized distances. *Biometrics* 22: 96–110. doi: 10.2307/2528217
- Eschmeyer WN, Fricke R (Eds) (2013) Catalog of Fishes electronic version (March 2014). <http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>
- Hammer Ø, Harper DA, Ryan PD (2008) PAST – Paleontological Statistics, ver. 1.81: 1–88.
- Mirande JM (2010) Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology* 8: 385–568. doi: 10.1590/S1679-62252010000300001
- Román-Valencia C, Ruiz-C RI (2007) Una nueva especie de pez del género *Hemibrycon* (Characiformes: Characidae) del Alto Río Atrato, Noroccidente de Colombia. *Caldasia* 29: 121–131.
- Román-Valencia C, Arcila-Mesa DK (2008) *Hemibrycon rafaelense* n.sp. (Characiformes, Characidae), a new species from the upper Cauca River, with keys to Colombian species. *Animal Biodiversity and Conservation* 31: 67–75.
- Román-Valencia C, Arcila-Mesa DK (2009) Two new species of *Hemibrycon* (Characiformes: Characidae) from the Magdalena river, Colombia. *Animal Biodiversity and Conservation* 32: 77–87.
- Román-Valencia C, Arcila-Mesa DK (2010) Five new species *Hemibrycon* (Characiformes: Characidae) from the Magdalena River Basin, Colombia. *International Journal Tropical Biology* 58: 339–356.
- Román-Valencia C, Ruiz-CE RI, García-Alzate CA, Taphorn DC (2009a) *Hemibrycon santamartae* a new species from the Ranchería River of eastern Caribbean Colombia (Characiformes: Characidae). *Revista de Investigaciones Universidad del Quindío* 19: 144–150.
- Román-Valencia C, Arcila-Mesa DK, García MD (2009b) Diversidad fenotípica en peces del género *Hemibrycon* (Characiformes: Characidae) del sistema del río Magdalena-Cauca, Colombia. *Brenesia* 71–72: 27–40.
- Román-Valencia C, Vanegas-Ríos JA, García MD (2009c) Análisis comparado de las especies del género *Bryconamericus* (Teleostei: Characidae) en la cuenca de los ríos Cauca-Magdalena y Ranchería, Colombia. *Revista Mexicana de Biodiversidad* 80: 465–482.
- Román-Valencia C, García-Alzate C, Ruiz-C RI, Taphorn DC (2010) New species of *Hemibrycon* (Teleostei, Characiformes, Characidae) from the Roble River, Alto Cauca, Colombia, with a key to species known from the Magdalena – Cauca River Basin. *Vertebrate Zoology* 60: 99–105.
- Román-Valencia C, Ruiz-C RI, Taphorn DC, Mancera-Rodríguez NJ, García-Alzate C (2013) Three new species of *Hemibrycon* (Characiformes: Characidae) from the Magdalena River Basin, Colombia. *International Journal Tropical Biology* 61: 1365–1387.

- Ruiz-C RI, Román-Valencia C (2006) Osteología de *Astyanax aurocaudatus* Eigenmann, 1913 (Pisces: Characidae), con notas sobre la validez de *Carlastyanax* Géry, 1972. *Animal Biodiversity and Conservation* 29: 49–64.
- Sabaj Pérez MH (Ed.) (2010) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an on line reference. Version 2.0 (8 November 2010). Electronically accessible at <http://www.asih.org/>, American Society of Ichthyologists and Herpetologists, Washington, D.C.
- Song JL, Parenti R (1995) Clearing and staining whole fish specimens for simultaneous demonstration of bone, cartilage and nerves. *Copeia* 1995: 114–118. doi: 10.2307/1446805
- Taylor WR, van Dyke GC (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium* 9: 107–119.
- Vari R (1995) The Neotropical fish family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): supra and intrafamilial phylogenetic relationships, with a revisionary study. *Smithsonian Contribution to Zoology* 564: 1–96.
- Weitzman SH (1962) The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* 8: 1–77.

