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Combined morphological and molecular data unveils relationships of *Pseudobranchiomma* (Sabellidae, Annelida) and reveals higher diversity of this intriguing group of fan worms in Australia, including potentially introduced species

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Abstract

Pseudobranchiomma (Sabellidae, Annelida) is a small and heterogeneous group of fan worms found in shallow marine environments and is generally associated with hard substrates. The delineation and composition of this genus is problematic since it has been defined only by plesiomorphic characters that are widely distributed among other sabellids. In this study we have combined morphological and molecular (mitochondrial and nuclear DNA sequences) data to evaluate species diversity in Australia and assess the phylogenetic relationships of these and other related sabellids. Unlike morphological data alone, molecular data and combined datasets suggest monophyly of *Pseudobranchiomma*. In this study, a new species of *Pseudobranchiomma* is described and three others are considered as potential unintentional introductions to Australian waters, one of them reported for the first time for the continent. *Pseudobranchiomma pallida* **sp. n.** bears 4–6 serrations along the radiolar flanges, lacks radiolar eyes and has uncini with three transverse rows of teeth over the main fang. In the new species the colour pattern as well is characteristic and species specific.

Keywords

new species, sabellids, feather duster worms, dichotomous key, taxonomy, invasive species, translocations

Introduction

Pseudobranchiomma Jones, 1962 (Sabellidae, Annelida) is a heterogeneous worldwide-distributed genus of fan worms inhabiting shallow marine habitats. Their tubes are made of muddy sediment embedded into a mucous matrix usually attached to hard substrates. Some species of *Pseudobranchiomma* are considered fouling organisms, settling on artificial surfaces and in some cases are common in harbour environments (Russell and Hewitt 2000, Swami and Udhayakumar 2010, Tovar-Hernández and Dean 2014). At least six species have been described as reproducing asexually, by fission of posterior segments, also known as scissiparity (Nogueira and Knight-Jones 2002, Knight-Jones and Giangrande 2003, Tovar-Hernández and Dean 2014). This reproductive strategy is not infrequent among sabellids (e.g. Knight-Jones and Bowden 1984; Fitzhugh 2003; Nogueira and Knight-Jones 2002; Nogueira et al. 2004, Tovar-Hernández and Knight-Jones 2006, Tovar-Hernández et al. 2009a, 2011, Kolbalsova et al. 2013) and allows them to colonise or form aggregations of clones in a short period of time under favourable conditions.

Due to these attributes, some members of *Pseudobranchiomma* are susceptible to being translocated by attachment to ship hulls, and may settle in new locations, if environmental factors permit. Unintentional translocations have been assessed and are well documented in members of the related genus *Branchiomma* (e.g. Knight-Jones et al. 1991, Licciano et al. 2002; Zenetos et al. 2005, 2010; Çinar et al. 2006; Tovar-Hernández and Knight-Jones 2006; El Haddad et al. 2008, Çinar 2009; Román et al. 2009, Tovar-Hernández et al. 2009a,b, 2011; Tovar-Hernández and Dean 2010, Arias et al. 2012; Giangrande et al. 2012, Capa et al. 2013). There is some indication that potential introduction of some *Pseudobranchiomma* species has already occurred in northern Australia (Russell and Hewitt 2000). For this reason, correct identification and assessment of potential introduced species is of great importance.

There are 16 species currently circumscribed within the genus (Nogueira and Knight-Jones 2002, Knight-Jones and Giangrande 2003, Tovar-Hernández and Dean 2014). The most conspicuous morphological interspecific differences within *Pseudobranchiomma* are the absence or presence of serrated radiolar flanges (paired lappets along the radioles lateral margins that may be few in number or extend along the full radiolar length), absence or presence of paired compound radiolar eyes, shape of the ventral collar glandular shield (rectangular, M-shaped, trapezoidal or divided in two), absence or presence of pinnular appendages, number of thoracic segments (Knight-Jones and Giangrande 2003), together with a broad variety of colour-morphs (Nogueira and Knight-Jones 2002, Knight-Jones and Giangrande 2003, Tovar-Hernández and Dean 2014). The monophyly of the genus has not yet been assessed. Species have been grouped into three artificial groups based on the absence, presence and relative length of the serrated radiolar flanges (Knight-Jones and Giangrande 2003): Group A, with radiolar serrations evenly distributed along the entire length of the radioles, or at least for most of their length; Group B, with serrations restricted to the distal part of the radioles; and Group C with smooth radiolar flanges.

Prior to the present study, *Pseudobranchiomma* has been reported from Australia as *P. orientalis* (McIntosh 1885), and *P.* cf. *P. emersoni* Jones 1962, in Northern Territory ports by Russell and Hewitt (2000). Capa and Murray (2015) also reported two species from the Great Barrier Reef, Queensland.

Pseudobranchiomma belongs to a group of sabellids possessing segmental eyespots between the noto- and neuropodia, spine-like chaetae arranged in oblique rows in the inferior thoracic fascicles, and well-developed conical abdominal neuropodia with chaetae arranged in C-shaped fascicles, together with *Bispira* Krøyer, 1856, *Branchiomma* Kölliker, 1858, *Sabella* Linnaeus, 1767, *Sabellastarte* Savigny, 1818 and *Stylomma* Knight-Jones, 1997 (e.g. Fitzhugh 1989, Fitzhugh and Rouse 1999; Capa 2008). *Branchiomma* and *Pseudobranchiomma* have long been considered to be closely related taxa due to the presence of stylodes (Jones 1962; Fitzhugh 1989) but the radiolar structures present in members of both genera were later considered not to be homologous (Knight-Jones 1994, Nogueira and Knight-Jones 2002, Knight-Jones and Giangrande 2003, Nogueira et al. 2006). Recently, other evidence of this close relationship has emerged, including the absence of companion chaetae, presence of four rows of vacuolated cells supporting the radioles, and a multicellular supporting axis of the radiolar appendages of the dorsal lips (Capa 2008, Capa et al. 2011).

The aims of this study are (1) to assess monophyly of *Pseudobranchiomma* and relationships with other members of the clade - *Bispira*, *Branchiomma*, *Sabella*, *Sabellastarte* and *Stylomma* - integrating morphological data and available mitochondrial and nuclear sequences; (2) to test whether the artificial groups proposed by Knight-Jones and Giangrande (2003) have some evolutionary meaning; (3) to assess species diversity in Australian waters and describe new species; (4) to provide a dichotomous key to enable identification of *Pseudobranchiomma* species.

Methods

Specimens and features examined

Fourteen *Pseudobranchiomma* terminals, including at least two species of each of the groups proposed by Knight-Jones and Giangrande (2003), were included in a morphological matrix, in order to assess their evolutionary relationships and test if these groups have any evolutionary meaning (i.e. natural groups). Members of other related genera including *Branchiomma*, *Sabella*, *Sabellastarte* and *Stylomma* were also incorporated in the analyses to test monophyly of *Pseudobranchiomma*, using *Pseudopotamilla* Bush, 1905 as the outgroup. The matrix (Table 1) was constructed in Mesquite (Maddison and Maddison 2015) and was scored after direct examination and using original descriptions and illustrations. Characters, states and scoring methods have been based on previous studies (e.g. Fitzhugh 1989, Fitzhugh and Rouse 1999, Capa 2008, Capa et al. 2010) or developed for the present study (see Table 2). The codification scheme included the presence or absence of traits and unordered multistate characters. Taxa

Table 1. Matrix of morphological character states (‘–’, inapplicable; ‘?’, uncertain/unknown, V, variable).

Species	1				5					10					15					20					25					30			33
Pseudopotamilla cf. *P. reniformis*	0	0	0	-	0	0	1	1	1	1	0	1	0	1	0	1	0	0	2	0	0	1	0	1	0	0	1	1	1	1	0	1	?
Bispira manicata	0	1	1	0	1	0	1	1	3	0	-	0	1	0	1	0	1	2	2	1	1	1	0	1	1	1	0	0	1	0	0	0	1
Bispira porifera	0	1	0	-	0	0	1	0	-	1	0	0	1	1	1	0	1	0	2	1	1	1	0	1	1	1	0	0	1	0	0	0	?
Bispira serrata	0	1	1	1	0	0	1	1	3	1	0	0	1	1	1	0	1	0	2	1	1	0	0	1	1	1	0	0	0	0	0	1	?
Branchiomma sp. 1	0	0	0	-	1	1	0	1	3	0	-	0	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1
Branchiomma bairdi	0	0	0	-	1	1	0	1	3	0	-	0	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1
Sabella spallanzanii	1	1	0	-	1	0	0	0	-	0	-	0	1	0	1	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	0	0	1
Sabella pavonina	1	1	0	-	1	0	0	0	-	0	-	0	1	0	1	0	1	0	2	1	1	1	0	1	1	1	0	0	1	0	0	0	1
Sabellastarte australiensis	1	1	0	-	0	0	1	0	-	1	0	0	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	1
Sabellastarte sp.	1	1	0	-	0	0	1	0	-	1	0	0	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	1
Stylomma palmatum	0	1	1	0	0	0	1	1	2	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	0	0	0	?
Stylomma juani	0	1	1	1	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	0	0	0	?
P. emersoni	0	0	1	1	?	0	0	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	1	1
P. cf. *P. emersoni* (Australia)	0	0	1	1	1	0	0	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	1	?
P. minima	0	0	0	-	1	0	0	0	-	0	-	0	1	0	1	0	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	?	1
P. orientalis	0	1	1	1	1	0	?	0	-	0	-	0	1	0	1	0	1	0	2	1	1	0	1	0	1	1	0	0	0	0	0	1	?
P. cf. *P. orientalis* (Australia)	0	1	1	1	1	0	1	0	-	0	-	0	1	0	1	0	1	0	2	1	1	0	1	0	1	1	0	0	0	0	0	1	?
P. pallida sp. n.	0	0	1	1	0	0	0	0	-	0	-	0	1	0	1	0	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	?	?
P. paraemersoni	0	0	1	1	1	0	0	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	?	?
P. paulista	0	0	1	1	1	0	0	0	-	0	-	0	1	?	1	0	1	V	2	1	1	0	1	0	1	1	0	0	0	0	0	?	?
P. perkinsi	0	0	0	-	0	0	0	1	3	0	-	0	1	0	1	0	1	2	2	1	1	0	1	0	1	1	0	0	0	0	0	1	1
P. punctata	0	1	0	-	1	0	1	0	-	1	0	0	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0	?	1
P. serratibranchis	0	0	1	1	1	0	0	?	?	?	-	0	1	0	1	0	1	0	0	1	1	?	1	0	1	1	0	0	0	0	0	?	?
P. schizogenica	0	1	1	1	1	0	?	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	1	1
P. cf. *P. schizogenica* (Australia)	0	1	1	1	1	0	0	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	1	1
P. tarantoensis	0	0	0	-	1	0	1	0	-	0	-	0	1	0	1	0	1	0	1	1	1	1	1	0	1	1	0	0	0	0	0	1	0

Table 2. Morphological characters and states scored in the matrix (Table 1). These are based on previous cladistic analyses (e.g. Fitzhugh and Rouse 1999, Capa 2008, Capa et al. 2010), in addition to other features consider diagnostic for *Pseudobranchiomma* species.

1.	*Lobes*: (0) semicircular or involuted; (1) spiral.
2.	*Basal membrane*: (0) absent (or reduced, shorter than one thoracic segment); (1) present (longer than one thoracic segment).
3.	*Radiolar flanges*: (0) absent or reduced to ridges; (1) present.
4.	*Serrations of radiolar flanges*: (0) absent; (1) present.
5.	*Transverse pigment bands on radioles*: (0) absent; (1) present.
6.	*Stylodes*: (0) absent; (1) present.
7.	*Number of rows of vacuolated cells supporting radioles*: (0) four; (1) more than four.
8.	*Radiolar eyes*: (0) absent; (1) present.
9.	*Radiolar eyes arrangement*: (0) ocelli; (1) unpaired proximal compound eyes on radiole dorsal margin; (2) unpaired terminal compound eyes on inner peduncule; (3) paired compound eyes;
10.	*Dorsal basal flanges*: (0) absent; (1) present.
11.	*"Press-stud" structure present on dorsal basal flanges*: (0) absent; (1) present.
12.	*Ventral basal flanges*: (0) absent; (1) present.
13.	*Dorsal lip radiolar appendage vacuolated cells (skeleton)*: (0) absent; (1) present.
14.	*Dorsal pinnular appendages*: (0) absent; (1) present.
15.	*Position of ventral sacs*: (0) inside the radiolar crown; (1) outside the radiolar crown.
16.	*Dorsal margin of posterior peristomial ring collar*: (0) widely separated; (1) fused to the faecal groove.
17.	*Interramal eyespots*: (0) absent; (1) present.
18.	*Number of thoracic segments*: (0) 8; (1) generally less than 8; (2) generally more than 8.
19.	*Gap between thoracic tori and ventral shields*: (0) absent, all ventral shields in contact with tori; (1) gap between ventral shields and tori of anterior thoracic segments; (2) present, gap in all thoracic segments.
20.	*Thoracic chaetal fascicles (notopodia)*: (0) transverse rows; (1) longitudinal bundles.
21.	*Inferior thoracic notochaetae shape*: (0) paleate; (1) spine-like.
22.	*Rows of teeth on thoracic uncini*: (0) few (1–5); (1) numerous (>5).
23.	*Length of thoracic uncini handles*: (0) medium length (more than distance from breast to tip of main fang); (1) short (shorter than distance of breast to tip of main fang).
24.	Thoracic *companion chaetae*: (0) absent; (1) present.
25.	*Abdominal neurochaetal tori*: (0) transverse ridges; (1) conical lobes.
26.	*Abdominal neurochaetal fascicles*: (0) transverse row(s); (1) spiralled.
27.	*Superior row of abdominal neurochaetal fascicles*: (0) elongated narrowly hooded; (1) broadly hooded.
28.	*Inferior row of abdominal chaetae*: (0) spine-like; (1) broadly hooded.
29.	*Abdominal uncini number of rows*: (0) few (1–5); (1) numerous (>5).
30.	*Abdominal uncini breast*: (0) well developed, expanded; (1) narrow, swelling.
31.	*Length of abdominal uncini handles*: (0) short (shorter than distance of breast to tip of main fang); (1) medium (1–2 times distance of breast to tip of main fang).
32.	*Pygidial shape*: (0) rim; (1) bilobed.
33.	*Scissiparity*: (0) absent; (1) present.

lacking a feature were scored as inapplicable and indicated as a gap '-' and unknown as a question mark '?'.

More than 100 specimens deposited in Australian museum collections were examined and identified to species to assess the species diversity in Australian waters. These included specimens identified for the Darwin Ports Survey and mentioned in the report by Russell and Hewitt (2000) which had been deposited at the Museum and Art Gallery of the Northern Territory (NTM). Type material of herein newly described species was deposited in the Australian Museum (AM). After study of all specimens with stereo microscopy, some parapodia (typically from mid-thoracic as well as abdominal regions) were removed and mounted with glycerine on slides for studying thoracic and abdominal chaetae. Line drawings were made to scale with a drawing tube attached to a Zeiss MI compound microscope. Final drawings were created using Adobe Illustrator© software. Descriptions in the text of relative dimensions of chaetal features are based on the terminology used by Nogueira et al. (2006). Some specimens were stained with methyl green to reveal thoracic glandular patterns. Other specimens were dehydrated in ethanol, critical-point dried, covered with 20 nm of gold and examined under a Leo 435VP scanning electron microscope at the Australian Museum, using ET secondary electron detector. A detailed morphological comparison was performed between species considered as Group A of Knight-Jones and Giangrande (2003), in order to find out clear differences between species (Table 3).

Molecular data

Genomic DNA was extracted from sample tissue using standard protocols for the DNeasy Animal tissues protocol (manufactured by QIAGEN Pty Ltd). Sections of two mitochondrial genes cytochrome b (*cob*) and cytochrome oxidase I (*cox1*), and one nuclear gene ribosomal internal transcribed spacer 1 (ITS1), were then amplified using the primers Cytb 424F (RT-1) and cobr825 (Burnette et al. 2005) for cob, HCO2198 and LCO1490 (Folmer et al. 1994) for cox1and ITSF (Chen et al. 2002) and ITSR1 (Capa et al. 2011) for ITS1 (Table 4). Standard PCR conditions (carried out in 25ul volumes containing 2.5uL of QIAGEN 10x PCR buffer, 1.5mM MgCl2, 0.05mM of each dNTP, 10 pmol of each primer, 1 unit of QIAGEN Taq DNA polymerase, and 1–100ng of whole genomic DNA). A negative control (containing no DNA template) is included for each batch of amplifications to exclude the possibility that any results achieved are due to contaminant DNA. Amplifications were performed on a MastercyclerS Gradient (Eppendorf Inc). The PCR thermal cycling profile was 94°C for 2 min, followed by 35 cycles of 94°C for 20 sec, 52°C for 40 sec, 72°C for 1 min and a 5 min final extension at 72°C. Successful amplifications were then purified using the ExoSAP-IT PCR purification (USB Corporation) system, then bi-directionally sequenced, using the original PCR primers, at an external sequencing facility. Chromatographs were annotated with the program SEQUENCHER v. 5.1 (Gene Codes Corporation). ITS1 sequence chromatograms showed no evidence of double peaks, suggesting the presence of multiple copies.

DNA sequence alignments

Nucleotide sequences of *cob*, *cox1* and ITS1 were aligned with MAFFT v. 6.0 (Katoh 2013) using default parameters, in all cases auto-selected strategy was L-INS-i. Additionally, ITS1

Table 3. Comparison of species from Group A (according to Knight-Jones and Giangrande, 2003), possessing serrations along the radiolar flanges. Information retrieved from original descriptions except where indicated. ? = information not available.

TAXON	Distribution	Radiolar eyes	Radioles (pairs)	Radiolar serrations (pairs)	Radiolar lobes	Dorsal lips/ crown length	Crown pigment	Body pigment alive (preserved)	Interramal eyespots	Thoracic tori and ventral shields	Thoracic segments	Teeth thoracic uncini
P. emersoni Jones, 1962	Jamaica, Florida (USA), Cape Verde Islands?	no	14[†]	10	semicircular?	1/4	irregular	brownish with spots (same)	large[†]	gap[†]	4–6 (8[‡])	5 (5–6)[†]
P. cf. *P. emersoni*	Queensland, Australia	no	17	10	semicircular	1/6	irregular	pale with large anterior spots	small	gap	7	3
P. grandis (Baird, 1865)	New Zealand	yes[‡, §, ¶]	>10 (≤30)[¶]	? (>18)[¶]	semicircular	?	9 (4–9)[¶] irregular bands	pale with brown/ purple spots[¶] (dark brown)	small[¶]	Almost in contact[¶]	7 (8)[¶]	?
P. serratibranchis (Grube, 1878)	Philippines	yes[‡, §]	17	30	semicircular	?	7–8 bands	?	?	?	8	?
P. orientalis (McIntosh, 1885)	Hong Kong	no	26	13–16[†]	involuted	1/4[†]	23 bands	internal purple-brown spots on ventral lappets (colourless[#])	present only in abdomen	gap[#]	8[†,#]	6–7 (4–5)[†]
P. cf. *P. orientalis*	Queensland, and Northern Territory, Australia	no	10–30	10–20	involuted–1 whorl	1/6–1/3	10–20 bands	(pale with few anterior spots)	tiny	gap	7–8	5–7
P. paraemersoni Nogueira et al., 2006	São Paulo, Brazil	no	6	3–4	semicircular	1/4	3–4 bands	bright yellow with few spots (white)	large	gap	4–5	4–5
P. paulista Nogueira et al., 2006	São Paulo, Brazil	no	22–25	13–19	semicircular	1/6	10–19 bands	pale yellow with purple spots (white with spots)	small	gap	6–10	4–5
P. pallida sp. n.	Queensland, Australia	no	9	4–5	semicircular	1/6	No banding	colourless	large	gap	7	3

TAXON	Distribution	Radiolar eyes	Radioles (pairs)	Radiolar serrations (pairs)	Radiolar lobes	Dorsal lips/ crown length	Crown pigment	Body pigment alive (preserved)	Interramal eyespots	Thoracic tori and ventral shields	Thoracic segments	Teeth thoracic uncini
P. schizogenica Tovar-Hernández and Dean, 2014	Gulf of California, Mexico	no	6–9	6–11	semicircular	1/4	4 or more purple bands with orange and translucent bands between	bright yellow with few purple spots (pale yellow)	large	?	5	4
P. cf. *P. schizogenica*	North Australia and Hawaii	no	9	4–6	semicircular	1/3	4–6 bands and orange band in base	pale with spots	large	gap	4–7	3

According to: † Tovar-Hernández and Dean 2014; ‡ Knight-Jones and Giangrande 2003; § Nogueira et al. 2006; ¶ Geoff Read, pers. comm.; # Knight-Jones unpublished drawings and description of the type.

Table 4. Taxa and GenBank accession numbers for the genes sequenced for the present study. NSW, New South Wales; NT, Northern Territory, QLD; Queensland; SA, South Australia; WA, Western Australia.

Taxon	Voucher	cox1	cob	ITS1	Locality
Pseudopotamilla cf. *P. reniformis*	AM W.36444	KX894903	KX894900	KX894909	Darwin, NT, Australia
Branchiomma sp.	AM W.35580	–	KF429111	KX894915	Oahu, Hawaii, USA
Branchiomma bairdi	AM W.31822	KP254646	KF429105	KF459971	Fort Pierce, Florida, USA
Bispira serrata	AM W.36979	KX894907	–	KX894916	Lizard Island, QLD, Australia
Bispira manicata	AM W.36964	KX894904	KX894902	KX894910	Aquarium at Oceanword, NSW, Australia
Sabella spallanzanii	AM W.30505	KX894905	–	–	SA, Australia
Stylomma palmatum	AM W.36959	KX894908	KX894901	KX894914	Ningaloo Reef, WA, Australia
Sabellastarte australiensis	AM W.35608	–	KF429134	KF460007	Cape Banks, NSW, Australia
Sabellastarte sp.	AM W.36977	KX894906	–	KX894913	Port Phillip Bay, VIC, Australia
Pseudobranchiomma pallida sp. n.	AM W.36366	–	–	KX894911	Heron Island, QLD, Australia
P. cf. *P. schizogenica* (Australia)	AM W.36364	–	–	KX894912	Heron Island, QLD, Australia
P. cf. *P. schizogenica* (Hawaii)	AM W.35576	–	KF429108	KF459975	Oahu, Hawaii, USA

sequences was also aligned using the Q-INS-i algorithm that takes into account secondary structure. Poorly aligned positions from divergent regions of ITS1 were removed using GBLOCKS v. 0.91b with relaxed parameters (minimum number of sequences for a conserved position: 7, minimum number of sequences for a flanking position: 7, maximum number of contiguous non-conserved positions: 8, minimum length of a block: 5) to assess the impact of ambiguously aligned regions on the phylogenetic signal (Talavera and Castresana 2007). Matrices were concatenated in Mesquite (Maddison and Maddison 2015).

Phylogenetic analyses

Maximum parsimony (MP) heuristic searches used 10,000 replicates of random taxon addition and tree bisection-reconnection (TBR) branch swapping algorithm, saving 100 trees per replicate using TNT 1.1 (Goloboff et al. 2008a). All characters were given equal weight and multistate characters considered non-additive. Nodal support was estimated by 1,000 jackknife replicates using TBR, in TNT 1.1 (Goloboff et al. 2008a). New technology searches, such as ratchet, drift and tree fusing were implemented, isolated and in combination using TNT 1.1 (Goloboff et al. 2008a) performing 1,000 repetitions and hitting the most parsimonious trees 100 times. Tree metrics are abbreviated as follows: tree length (TL), consistency index excluding parsimony non-informative characters in the data matrix (CI), and retention index (RI). Support values are given on the trees. In order to reach a topology that better explains those characters with a better fit to the cladistic hypothesis, at the expense of the more homoplasious ones we have implemented implied weighting (Goloboff 1993, 1995, Goloboff et al. 2008a, b). With this method, a higher weight is given to those characters with less homoplasy, producing a much more resolved estimated consensus tree (Goloboff et al. 2008b). Results using a range of concavities (values for k) have been compared.

Maximum likelihood (ML) analyses were conducted using RAxML (Stamatakis et al. 2008). All analyses were performed for the morphological data (Tables 1 and 5) and each marker independently and in combination (molecular data and molecular + morphological data), and with and without the poorly aligned positions from divergent regions of ITS1, using GBLOCKS.

Results

Pseudobranchiomma monophyly and relationships

Maximum parsimony analyses of the complete morphological matrix (Table 1), including 26 terminals (14 terminals of *Pseudobranchiomma* and 12 species of other related sabellids) and 33 characters, all of which were parsimony-informative, yielded six most parsimonious trees (TL 69, CI 0.53, RI 0.75, Fig. 1A). *Branchiomma* was recovered nested within *Pseudobranchiomma* in all of these trees. Several polytomies within *Pseudobranchiomma* and between other related sabellids in the consensus tree, together with the low consistency index value, reflects the large amount of homoplasy in the dataset for resolving bifurcating branching pattern (Fig. 1A). Implied weighting with concavity of k = 3–6 recovered six most-parsimonious trees. Similar analyses with k values of 7–8 yielded three most parsimonious trees (Fig. 1B). In any of these topologies, monophyly of *Pseudobranchiomma* was assessed because *Branchiomma* was nested within the *Pseudobranchiomma* terminals. The few clades found within *Pseudobranchiomma* are not well supported. However, they do not concur with the groups proposed by Knight-Jones and Giangrande (2003), based on the presence and serration of the radiolar flanges, indicating these could be artificial.

The low success obtaining sequences out of tissue from members of *Pseudobranchiomma* (only three terminals belonging to two morphospecies), restricted the outcomes of the present study. Analyses of the combined molecular dataset yielded a phylogenetic hypothesis where *Pseudobranchiomma* was monophyletic and sister to *Sabella* + *Sabellastarte* (Fig. 1C). The same topology was recovered after the elimination of

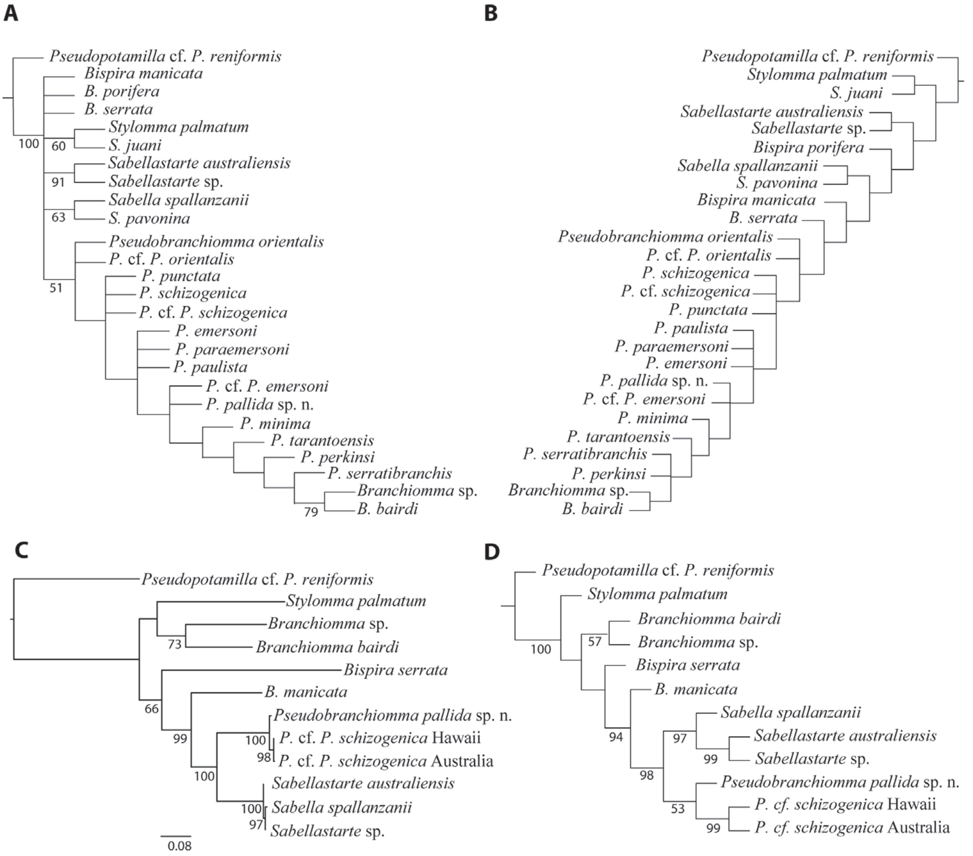

Figure 1. Phylogenetic hypothesis of *Pseudobranchiomma* and related taxa. **A** Strict consensus of six most-parsimonious trees after analyses of morphological data (33 characters) and 26 members of Sabellidae rooted with *Pseudopotamilla*. Jack-knife support values are given (>50) **B** Strict consensus of three most parsimonious tree after implementation of implied weighting (constant of concavity k = 7) **C** Tree after maximum likelihood analyses of mitochondrial and nuclear dataset. Bootstrap values on nodes if >50; scale: average of nucleotide substitutions per site **D** Single most-parsimonious tree after analyses of the combined morphological and molecular datasets (12 taxa and 2239 characters); Jack-knife support values are given (>50).

poorly aligned positions from divergent regions of ITS1 (not shown). Combination of morphological and molecular data (2239 characters, of which 783 were parsimony-informative, and 12 taxa) yielded a single most parsimonious tree (TL 2459, CI 0.76, RI 0.54; Fig. 1D) having the *Pseudobranchiomma* terminals in one clade, sister to *Sabella* + *Sabellastarte*. The two representatives of *Bispira* were not recovered as monophyletic (Fig. 1D) similar to the results obtained after analyses of morphological and molecular data alone (Fig. 1A–C). The combined dataset recovers *Branchiommma* and *Stylomma* branching off at the base of the ingroup (Fig. 1D).

Table 5. Morphological matrix for the specimens with DNA sequence data.

Species	1				5					10					15					20					25					30			33
Pseudopotamilla cf *reniformis*	0	0	0	-	0	0	1	1	1	1	0	1	0	1	0	1	0	0	2	0	0	1	0	1	0	0	1	1	1	1	0	1	?
Bispira manicata	0	1	1	0	1	0	1	1	3	0	-	0	1	0	1	0	1	2	2	1	1	1	0	1	1	1	0	0	1	0	0	0	1
Bispira serrata	0	1	1	1	0	0	1	1	3	1	0	0	1	1	1	0	1	0	2	1	1	0	0	1	1	1	0	0	0	0	0	1	?
Branchiomma sp.	0	0	0	-	1	1	0	1	3	0	-	0	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1
Branchiomma bairdi	0	0	0	-	1	1	0	1	3	0	-	0	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	1
Sabella spallanzanii	1	1	0	-	1	0	0	0	-	0	-	0	1	0	1	0	1	0	1	1	1	1	0	1	1	1	0	0	1	0	0	0	1
Sabellastarte sp.	1	1	0	-	0	0	1	0	-	1	0	0	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	1	0	1
Stylomma palmatum	0	1	1	0	0	0	1	1	2	1	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	0	0	0	?
P. pallida sp. n.	0	0	1	1	0	0	0	0	-	0	-	0	1	0	1	0	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	?	?
P. cf *P. schizogenica*(Australia)	0	1	1	1	1	0	0	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	1	1
P. cf *P. schizogenica* (Hawaii)	0	1	1	1	1	0	0	0	-	0	-	0	1	0	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	1	1

Taxonomy

Pseudobranchiomma Jones, 1962

Pseudobranchiomma Jones, 1962: 198–201, figs 115–124; Fitzhugh 1989: 73; Nogueira and Knight-Jones 2002: 1661–1670; Knight-Jones and Giangrande 2003: 95–103; Nogueira et al. 2006: 588.

Type species. *Pseudobranchiomma emersoni* Jones, 1962.

Diagnosis. Radioles with or without radiolar flanges, serrated or smooth. Some species with paired compound eyes along radioles. Four rows of vacuolated cells supporting the radioles; a multicellular supporting axis of the radiolar appendages of the dorsal lips. Ventral sacs located outside the radiolar crown. Dorsal margins of collar separated from the faecal groove by a wide gap and without "pockets". Segmental eyespots between the noto- and neuropodia. Spine-like chaetae arranged in oblique rows in the inferior thoracic fascicles. Thoracic companion chaetae absent. Well-developed conical abdominal neuropodia with chaetae arranged in C-shaped fascicles.

Remarks. There is no apparent morphological synapomorphy supporting *Pseudobranchiomma*. The monophyly of the genus *Pseudobranchiomma* has not been tested prior to this study. The group has been defined by a combination of homoplastic characters: presence of radiolar flanges (shared with *Stylomma* and some *Bispira* species but absent in *P. longa* (Kinberg, 1867)); ventral sacs located outside the radiolar crown (shared with *Bispira*, *Branchiomma* and *Sabella*); dorsal margins of the collar separated from the faecal groove by a wide gap and without "pockets" (shared by *Bispira*, *Stylomma* and some species of *Branchiomma*); and absence of thoracic companion chaetae (shared with *Branchiomma* and *Sabellastarte*) (e.g. Knight-Jones 1994, Nogueira and Knight-Jones 2002, Nogueira et al. 2006). It has been suggested that the colour pattern of the crown, consisting of transverse yellow and purple bands, could be another diagnostic feature for the genus (Nogueira et al. 2006), but this feature is also very common in *Sabellastarte* species (e.g. Capa et al. 2010). The monophyly of *Pseudobranchiomma* is herein also questioned. Morphological data analysis recovers the group as paraphyletic, and the scarcity of molecular data gathered for the present study does not allow us to properly assess monophyly.

Pseudobranchiomma cf. *P. emersoni* Jones, 1962

Figures 2, 3A–F

? *Pseudobranchiomma emersoni* Jones, 1962:198–201, figs 115–124; Knight-Jones 1994: fig. 4j; Knight-Jones and Giangrande 2003: fig. 1 c–f; Tovar-Hernández and Dean 2014: 936, table 1.

Material examined. Australia: Queensland: AM W.36365, (1 spec.), Heron Island, First Point, North Heron Reef, 23°25'48"S, 151°55'48"E, in coral rubble, 13 m, 12 Nov 2009.

Diagnosis. Ten pairs of short flat radiolar serrations evenly distributed along entire length of radioles. RRadiolar eyes absent. Small gap between anterior thoracic ventral shields and neuropodial tori. Thoracic and abdominal uncini with five transverse rows of teeth surmounting main fang. Radiolar crown with wide purple band at base, irregular transverse purple bands on radioles and flanges and yellow band on distal end of radioles. Body pale with distinct interramal eyespots and purple pigment spots on thorax and dorsally on abdomen.

Description of Australian specimen. Gravid female, incomplete; body measuring 20 mm long and 2 mm wide, with seven thoracic (Fig. 2D) segments. Crown 8 mm long, slightly involuted ventrally at base, with 17 radioles on each side, connected by an inconspicuous membrane, nearly 1/8th of length of radioles. Radioles with pinnules of constant length along radioles (Fig. 2B, C), shorter distally; tips of radioles as long as pinnules or shorter. Radiolar flanges present, with around 10 short, flattened, flap-like serrations along entire length of radioles (Fig. 2B, C). Radiolar eyes absent. Dorsal lips with tapered radiolar appendages, almost as long as three thoracic segments, with dorsal lamellae attached to base of adjacent radioles. Dorsal pinnular appendage absent. Four rows of vacuolated cells basally supporting radioles. Ventral lips and parallel lamellae present, with prominent ventral sacs directed outside of the radiolar crown (Fig. 2D–F). Collar with wide dorsal gap, margins fused to end of first chaetiger (Fig. 2F); lateral collar margins smooth, just covering junction of crown and thorax (Fig. 2E, F). Ventral lappets large, subtriangular, non-overlapping (Fig. 2D). Ventral shields conspicuous, first shield trapezoidal in shape, but appearing as an anterior Y-shaped and a posterior W-shaped segment when stained with methyl green; shields not in contact with or indented by ventral tori in all thoracic chaetigers (Fig. 2D). Interramal eyespots conspicuous. (Fig. 2D, E). First chaetiger with narrowly hooded chaetae. Rest of thoracic chaetigers with about six superior elongate narrowly hooded chaetae (Fig. 3C) and 16 shorter spine-like inferior chaetae arranged in two rows (Fig. 3D). Neuropodial uncini with approximately five rows of teeth above the main fang, well developed breast and short handle (Fig. 3A). Abdominal chaetigers with narrowly hooded superior chaetae and shorter spine-like chaetae (Fig. 3E) appearing broadly hooded depending on angle (Fig. 3F). Notopodial uncini similar to thoracic ones (Fig. 3B). Pygidium missing. Eggs are present in thorax and anterior abdominal segments.

Colour pattern. Body pale with distinct interramal eyespots of same size in thorax and abdomen (Fig. 2D, E) and purple pigment spots sparsely distributed on thorax (Fig. 2D–F) and dorsally on abdomen. Crown with wide purple band at base (Fig. 2A) and approximately 10 irregular, purple bands (some incomplete transversely) evident on outer side of radioles and flanges; only one yellow band present on distal end of radioles. Dorsal margins of collar (Fig. 2F) and ventral lappets (Fig. 2D) with scattered spots.

Remarks. *Pseudobranchiomma emersoni* Jones, 1962 is a species that was originally described from Jamaica, but has also been reported from the Cape Verde Islands (according to Knight-Jones 1994, p.197, although not verified since) and Florida, USA (Nogueira et al. 2006). It is characterised by a combination of features: up to ten pairs

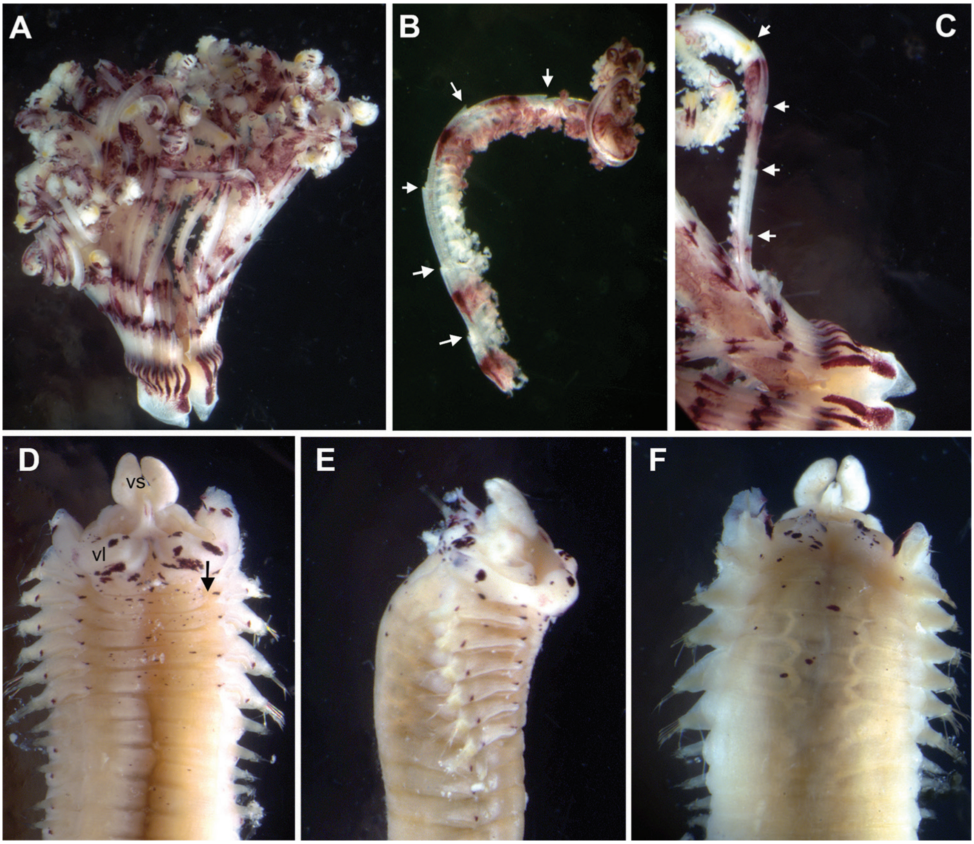

Figure 2. *Pseudobranchiomma* cf. *P. emersoni* AM W.36365; photographs of preserved specimen; **A** Radiolar crown, dorsal view **B** Detached radiole **C** Detail of base of crown and single radiole **D** Anterior segments, ventral view (crown detached) **E** Same, lateral view **F** Same, dorsal view. vl, ventral lappet; vs, ventral sacs; white arrows, serrations of radiolar lateral flanges; black arrow, gap between ventral shields and thoracic tori.

of short flat serrations along each radiole, 5–6 rows of teeth over the main fang in thoracic uncini, a branchial crown that has narrow irregular bands of purple colour (or "splotches"), with often a reduced number of thoracic segments (as few as four, indicating evidence of imperfect regeneration after asexual reproduction), large interramal eyespots, and a collar ventral shield that is trapezoidal in shape (according to Tovar-Hernández and Dean 2014). The Australian specimen, when stained with methyl green, displayed a similar staining pattern on the collar ventral shield as that described for *Pseudobranchiomma schizogenica* Tovar-Hernández and Dean, 2014, although the authors state that this feature differentiates *P. schizogenica* from *P. emersoni* and *P. orientalis* (Tovar-Hernández & Dean, 2014). Although these latter authors also describe the interramal spots of *P. emersoni* as "large", Knight-Jones and Giangrande's (2003) illustration of the type specimen indicates small spots, so there is some ambiguity regarding this feature, particularly as this can be a subjective assessment. The Australian

Figure 3. Line drawings of chaetae and uncini of *Pseudobranchiomma* species in Australia; **A**–**F** *Pseudobranchiomma* cf. *P. emersoni* **G**–**L** *Pseudobranchiomma* cf. *P. orientalis* **M–T** *Pseudobranchiomma pallida* sp. n. **U**–**Z, A1** *Pseudobranchiomma* cf. *P. schizogenica*; **A** Thoracic uncinus **B** Abdominal uncinus **C** Superior thoracic chaeta **D** Inferior thoracic chaeta **E, F** Inferior abdominal chaetae **G** Thoracic uncinus **H** Abdominal uncinus **I** Superior thoracic chaeta **J** Inferior thoracic chaeta **K, L** Inferior abdominal chaetae **M, N** Thoracic uncini **O** Abdominal uncinus **P, Q, R** Inferior thoracic chaetae **S** Superior abdominal chaeta **T** Inferior abdominal chaeta **U, V** Thoracic uncini **W** Abdominal uncinus **X, Y** Superior thoracic chaetae **Z, A1** Inferior thoracic chaetae. Scale bars: **A–F** = 2 µm; **G–L** = 4 µm; **M–T** = 2 µm; **U–Z, A1** = 2 µm.

specimen described above concurs in most respects with *P. emersoni*, particularly the flattened step-like form of the radiolar serrations, the irregular colour pattern of the branchial crown and the possession of large interramal eyespots, but because there are slight differences (e.g. 4–5 rows of teeth of the thoracic uncini; the similarity of staining pattern of the ventral shields with *P. schizogenica*), and the lack of multiple specimens, we prefer to reserve definite identification until there can be examination of more specimens from Australia, and comparison with the type specimens. The report of this species by Russell and Hewitt (2000) in the ports of Darwin, Northern Territory, is not confirmed, as material from this survey, deposited at the NTM, was examined, and specimens labelled as "*P. emersoni*", were found to be *P.* cf. *P. schizogenica*.

Distribution. Species known from Jamaica, Florida (USA), Cape Verde Islands, and now Heron Island, Queensland, Australia, where it inhabits coral rubble at shallow depths.

***Pseudobranchiomma* cf. *P. orientalis* (McIntosh, 1885)**

Figures 3G–L, 4, 5

? *Dasychone orientalis* McIntosh, 1885: 498—500, pl. LII, fig 5, Pl.XXXA, figs 19–21, pl. XXXIXA, fig 4.

? *Pseudobranchiomma orientalis*: Knight-Jones 1994: fig. 4k; Russell and Hewitt 2000: 69, 89; Tovar-Hernández and Dean 2014: 936, table 1.

Material examined. Australia: Queensland: AM W.10308 (1 on microscope slide), Calliope River, 23°49'S, 151°13'E, 8 Oct 1975; AM W.37752 (4 specs.), Calliope River, 23°51'S, 151°10'E, 1974; AM W.37204 (1 on 2 SEM pins), same site and date; AM W.32677 (1 spec.), Karumba, 17°29'S, 140°50'E, beam trawl, 1 m, Aug 2000; AM W.37749 (2 specs), Karumba port, Berth 2, 17°29'S, 140°50'E, scraping from pylon, 3m, Aug 2000; AM W.37751 (1 spec.), Karumba, 17°29'S, 140°50'E, benthic sled, 15m, Aug 2000; AM W.32678 (1 spec), Cairns, Wharf 8, 16°53'60"S, 145°48'E, scraping from wharf pile, 7 m, 20 Nov 2001; AM W.32679 (2 specs), Weipa, Lorim Point Wharf, 12°40'S, 141°57'E, scraping from wharf pile, 3 m, Oct 1999; AM W.37750 (1 spec.), Weipa, Lorim Point Wharf, 12°40'S 141°57'E, scraping from wharf pile, 7m, Oct 1999. **Northern Territory:** NTM W017392 (3 specs), Darwin Harbour, Iron Ore Wharf, 12°28'21"S, 130°50'34"E, scrapings from wharf pile, 5–10 m, 1998.

Diagnosis. Ten to 25 serrations evenly distributed along entire length of radiolar flanges, Radiolar eyes absent. Thoracic ventral shields and uncinal tori separated by a small gap. Thoracic and abdominal uncini with 5–7 transverse rows of teeth over main fang. Radiolar crown with broad purple basal band, and approximately 20 transverse purple pigment bands along radioles, interspersed with orange and thin white bands; body with few pigment spots and with small, indistinct interramal eyespots.

Description of Australian specimens. Specimens 5–24 mm long (with 12 mm long crown on longest specimen), 3 mm maximum width; 7–8 thoracic and 50 abdominal chaetigers. Crown strongly involuted ventrally (Figs 4A, 5A), almost forming circle, with 10–30 radioles on each side. Radiolar flanges with conspicuous serrations from end of basal membrane to tip (Figs 4C, D, 5B), 10–25 per radiole (Figs 4A, C, 5A). Radiolar eyes absent. Pinnules decreasing in size distally (Fig. 4B). Radioles supported basally by 6–10 rows of vacuolated cells. Basal membrane as long as one to two thoracic segments, 1/7th–1/8th length of radioles. Dorsal lips with long, thin and pointed radiolar appendage 1/3rd length of crown (Fig. 4A, E). Pinnular appendages absent. Ventral lips nearly half of length of dorsal lips, pointed in shape, attached to 5th or 6th ventral radiole, with large and conical ventral sacs, as long as two thoracic chaetigers, located outside crown (Fig. 4A, F). Collar with wide dorsal gap and dorsal margins reaching end of the first chaetiger; lateral margin of collar smooth, covering junction between crown and thorax with short ventrolateral notch present as oblique incision (Figs 4F, 5A). Ventral lappets large, sub-triangular and rounded tips directed laterally (Fig. 4A, F). First segment as long as remaining thoracic segments. Ventral shields conspicuous, with large intersegmental incisions; thoracic ventral shields similar in width, but some specimens with first two shields wider than subsequent ones. First shield trapezoidal in shape, but appearing as an anterior Y-shape and posterior W-shaped segment when stained with methyl green. Small gap between ventral shields and thoracic tori (Fig. 4A, G). Interramal eyespots small, inconspicuous (Fig. 4G, H). First thoracic notopodia with around 10 superior elongate narrowly hooded chaetae (Fig. 5C) and around 12 short, narrowly hooded chaetae arranged in two rows (Fig. 5C). Subsequent thoracic notopodia with superior elongate narrowly hooded chaetae (Figs 3I, 5D) and shorter spine-like inferior thoracic chaetae arranged in two rows (Figs 3J, 5D). Well-developed thoracic tori with uncini decreasing in size ventrally; uncini with five rows of small teeth over main fang, occupying about half its length, breast well developed, long neck and short handle (Figs 3G, 5E, F). Abdominal chaetigers with superior narrowly hooded chaetae (Fig. 3K) and inferior spine-like chaetae (Figs 3L, 5H). Abdominal uncini with several rows of teeth above main fang, breast well developed and short handle (Figs 3H, 5G). Pygidium bilobed. Tube thick with muddy particles attached. One specimen (AM W.32679) with eggs in mid abdominal chaetigers, others with eggs in thorax.

Colour pattern. Preserved specimens may have few pigment spots on body, with some pigment on end of the faecal groove and dark patches on bases of ventral lappets, internally. Crown with pigments units coinciding with serrations, about 20 thin transverse purple-brown bands on outer side of radioles and flanges, continuing in one or two pinnules, and orange and white bands in between, which may fade (Fig. 4A–F). Longitudinal purple-pigmented midline at bases of each radiole and at ventral and dorsal base of crown may be present (Fig. 4A). Dorsal lips sometimes pigmented; ventral sacs conspicuous due to their white colour (Fig. 4A, F).

Remarks. These Australian specimens are identified as *P.* cf. *P. orientalis*, a species originally described from Hong Kong. Knight-Jones reviewed, and illustrated the types (previously unpublished but shared with MC and reproduced here as Fig. 6) with characters not illustrated in the original description such as the details of the radiolar flanges serrations (Fig. 6A–C), details of the anterior and posterior parts of the body in different views, with special attention to the shape of thoracic ventral shields (fig. 6D–G),

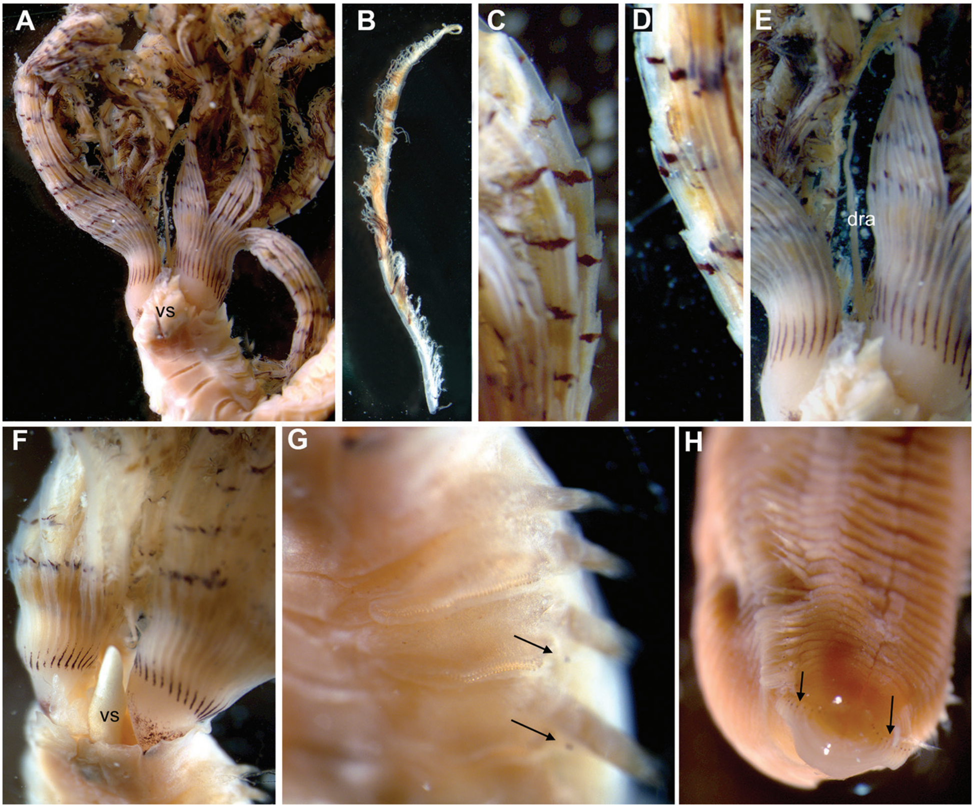

Figure 4. *Pseudobranchiomma* cf. *P. orientalis* AM W.32677, AM W.32679: Photographs. **A** Anterior end, ventral view **B** Detached radiole **C** Detail of lateral radiole, mid length **D** Detail of base lateral radiole **E** Detail of radiolar crown base with dorsal radiolar appendages **F** Detail of radiolar crown base with ventral sacs **G** Anterior thoracic parapodia **H** Posterior abdominal segments. dra, dorsal radiolar appendages; vs, ventral sac; black arrows, interramal eyespots.

and the shape of the parapodia in the thoracic and abdominal segments (Fig. 6H, I) that help confirm the identifications. The Australian specimens share most diagnostic features with the original description and drawings, as well as subsequently published supplementary information about the types (McIntosh 1885, Knight-Jones 1994, Tovar-Hernández and Dean 2014). These are: the number and shape of the serrations in the radiolar flanges (Figs 4C, D, 6A–C), presence of a small gap between the ventral shields and the adjacent thoracic tori (Figs 4G, 6E), and the presence of ventrolateral notches in the collar (Figs 4F, 6E, F) (McIntosh 1885, Knight-Jones 1994). There are some variations however from the reported descriptions, including the presence of interramal eyespots in the thorax, albeit small and inconspicuous, and the staining pattern of the first ventral shield which, as with *P.* cf. *P. emersoni*, yielded the same result as that reported by Tovar-Hernández and Dean (2014) for *P. schizogenica*, even though this was a feature used to differentiate the latter species from *P. orientalis* and *P. emersoni*. So,

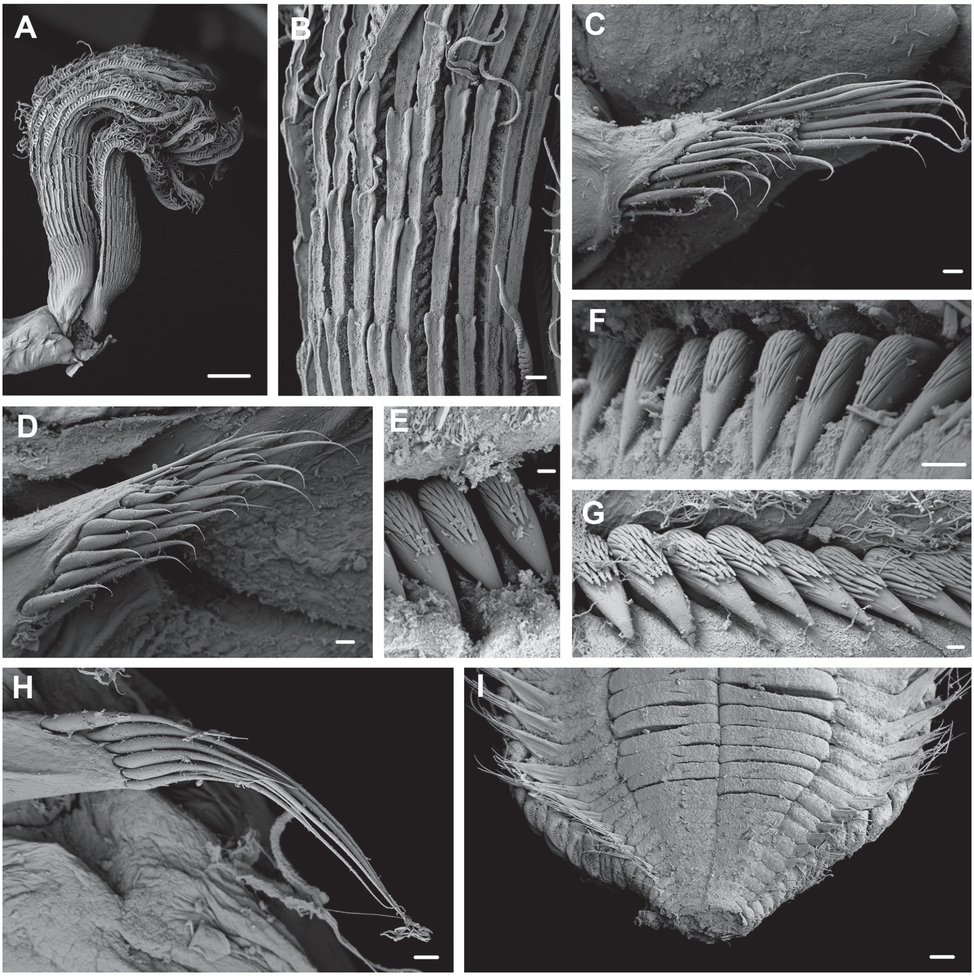

Figure 5. *Pseudobranchiomma* cf. *P. orientalis* AM W.37204: Scanning electron micrographs **A** Anterior end, lateroventral view **B** Detail of lateral flanges serrations **C** Notopodia, first thoracic segment **D** Notopodia, fifth thoracic segment **E** Uncini, second thoracic segment **F** Uncini, fifth thoracic segment **G** Posterior abdominal uncini **H** Neuropodia, mid abdominal segment **I** Posterior end, ventral view. Scale bars: **A** = 1 mm; **B, I** = 100 µm; **C, D, G, H** = 20 µm; **E** = 3 µm; **F** = 10 µm.

because of these differences we prefer to qualify a definite identification of these Australian specimens as *P. orientalis*. *Pseudobranchiomma orientalis* was reported in some ports in Northern Territory, Australia (Russell and Hewitt 2000), and after examination of these specimens, it is established that they are *P.* cf. *P. orientalis*, as described above. Should further sampling and molecular data confirm the status of *Pseudobranchiomma orientalis* in Australia, it is reasonable to suppose that it has been translocated from Asian waters, especially if its restricted range, in ports and harbours, is verified.

Distribution. Pacific Ocean (Hong Kong, Australia: Northern Territory and Queensland).

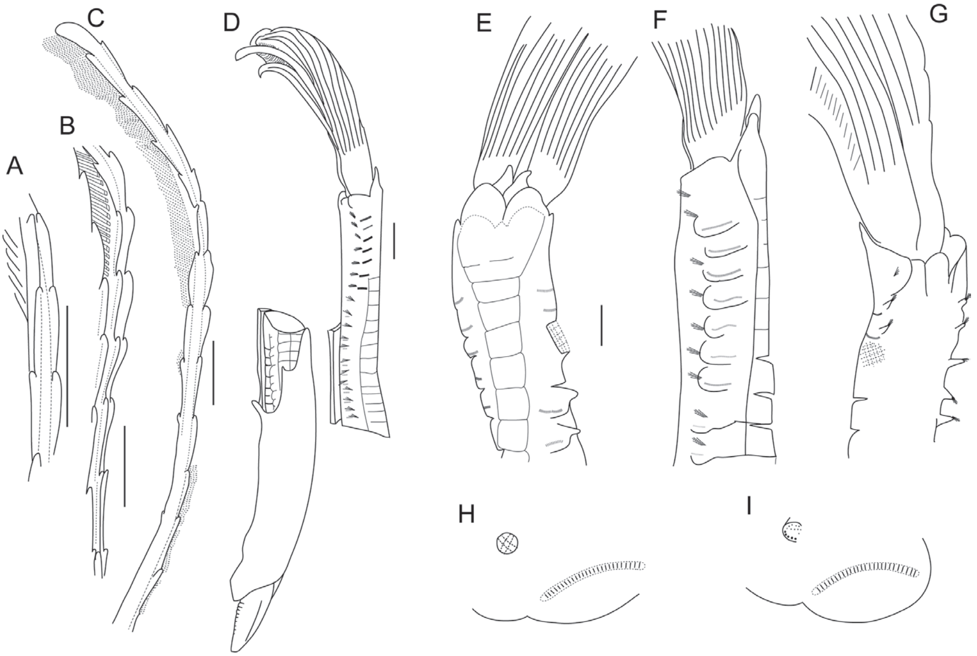

Figure 6. *Pseudobranchiomma orientalis* Type BMNH 85.12.1.393. Line drawings by Phyllis Knight-Jones. **A–C** Second dorsal radiole from different views **D** Holotype, divided in two, and partially covered by the tube, lateroventral view **E** Base of crown and anterior thoracic chaetigers, ventral view **F** Same, lateral view **G** Same, dorsal view **H** Thoracic parapodium **I** Abdominal parapodium. Scale bars: **A–C** = 1 mm; **D** = 2 mm; **E–G** = 1 mm; **H–I** = unknown.

Pseudobranchiomma pallida sp. n.

http://zoobank.org/91A0A21F-530D-48BE-AB44-5DF464BA2E73
Figures 3M–T, 7

Type material. Australia, Queensland. Holotype AM W.36366, Heron Island, First Point, North Heron Reef, 23°25'48"S, 151°55'48"E, coral rubble, 13 m, 12 Nov 2009.

Diagnosis. Approximately six pairs of low serrations evenly distributed along radiolar flanges. Radiolar eyes absent. Thoracic ventral shield separated from uncinal tori. Uncini with three transverse rows of teeth over main fang. Radiolar crown with broad purple band at base and distal third with wide yellow band, rest colourless white bands; body pale with distinct interramal eyespots.

Description. Specimen incomplete; body measuring 10 mm long (including crown) and 1 mm wide, with six thoracic and more than 18 abdominal segments (Fig. 7A, B). Crown 4 mm long, slightly involuted at base ventrally, with nine radioles on each side, connected by inconspicuous membrane extending 1/7th–1/8th of radiolar length, or length of one thoracic segment (Fig. 7D). Radiolar flanges present, with about six low serrations along entire length of radioles (Fig. 7C). Radiolar eyes absent (Fig. 7A–C). Radioles supported basally by four rows of vacuolated cells. Radiolar pin-

Figure 7. *Pseudobranchiomma pallida* sp. n. AM W.36366: Photographs. **A** Whole specimen, ventral view **B** Whole specimen, lateral view **C** Lateral radioles **D** Detail of base of radiolar crown and anterior segments **E** Anterior thoracic segments, ventrolateral view **F** Anterior end, dorsal view. vl, ventral lappet; vs, ventral sac; white arrows, serrations of radiolar lateral flanges; black arrow, gap between ventral shields and thoracic tori.

nules similar in length, shorter distally; tips of radioles as long as pinnules or shorter (Fig. 7C). Dorsal lips with tapered dorsal radiolar appendages, about as long as two thoracic segments, with dorsal lamella attached to base of adjacent radiole. Dorsal pinnular appendages absent. Ventral lips and parallel lamellae present with prominent ventral sacs directed outside of radiolar crown (Fig. 7A, B, D). Collar margins separated dorsally by wide gap, with dorsal margins fused to end of first chaetiger (Fig. 7F), lateral collar margins smooth, just reaching junction of crown and thorax (Fig. 7E).

Ventral lappets, sub-triangular and non-overlapping (Fig. 7D). Ventral shields of first two segments slightly shorter than other thoracic segments (Fig. 7E). First shield trapezoidal in shape, but appearing as anterior Y-shape and posterior W-shaped segment when stained with methyl green. Ventral shields not in contact with or indented by tori (Fig. 7E). Interramal eyespots conspicuous (Fig. 7D, E). First chaetiger with narrowly hooded chaetae arranged in two rows. Rest of thoracic chaetigers with about five superior narrowly hooded chaetae and 8–10 shorter inferior spine-like thoracic chaetae with hood similar width to shaft (Fig. 3R) appearing in some cases as broadly hooded (Fig. 3P, Q). Neuropodial uncini with three rows of teeth above main fang, well-developed breast and short handle (Fig. 3M, N). Abdominal chaetigers with narrowly hooded superior chaetae (Fig. 3S) and spine-like inferior chaetae (Fig. 3T). Notopodial uncini similar to thoracic ones (Fig. 3O). Pygidium missing.

Colour pattern. Body pale with distinct interramal eyespots (Fig. 7B, D, E) and pigment on dorsal margins of collar (Fig. 7F). Crown with broad purple band at base and distal third with wide yellow band, rest colourless (Fig. 7A–C). Ventral sacs and lappets colourless (Fig. 7D).

Remarks. *Pseudobranchiomma pallida* sp. n. is characterised by the remarkable colour pattern of the radiolar crown with a purple basal band and yellow radiolar tips, instead of the characteristic bands, as well as the absence of pigment spots on the body. This species belongs to the artificial Group A of Knight-Jones and Giangrande (2003), members of which possess serrations along the radiolar flanges (Table 3). The number of serrations (4–6) resembles that of *P. paraemersoni* and *P. schizogenica* (with 3–4 and 6–11 respectively), while other larger species bear nine or more (Table 1 of Tovar-Hernández and Dean 2014). The new species differs from *P. paraemersoni* and *P. schizogenica* in the morphology of the uncini, with three transverse rows of teeth over the main fang (4–5 and four rows respectively, for *P. paraemersoni* and *P. schizogenica*; Tovar-Hernández and Dean 2014).

Distribution. Australia (Queensland, Heron Island).

Etymology. This species is named after its colour pigmentation, pale compared with other *Pseudobranchiomma* species, and completely lacking pigment spots on the body.

Pseudobranchiomma cf. *P. schizogenica* Tovar-Hernández & Dean, 2014

Figures 3U–Z, A1, 8–10

Pseudobranchiomma schizogenica Tovar-Hernández & Dean, 2014: 936–945, figs 1–5.

Material examined. Australia: Queensland: AM W.36369 (1 spec.), Heron Island, Sykes Reef, 23°25'57"S, 152°02'02"E, coral rubble, 15 m, 13 Nov 2009; AM W.36368 (1 spec.), Heron Island, First Point, 23°25'56"S, 151°56'02"E, coral rubble, 13 m, 12 Nov 2009; AM W.36364 (1 spec.), Sykes Reef, 23°25'57"S, 152°02'02"E, coral rubble, 15 m, 13 Nov 2009; AM W.37753 (2 specs) same locality and date; AM W.32676 (1 spec.) Abbott Point, near Bowen, 19°53'S, 148°05'E, pylon scraping, 8 Jun 1998;

W.36978 (1 spec. used for sequencing), Lizard Island, MacGillivray Reef, deep reef slope, 14°39'25"S, 145°28'22"E, coral rubble, 30 m, 4 Sep 2010; AM W.41160 (1 spec.), Reef 14–141 south of South Direction Island, 14°42'31"S, 145°31'53"E, in coarse coral rubble, 15 m, 26 Aug 2010; AM W. AM W.43938 (>25 specs), south east of Lizard Island, reef on north west side of North Direction Island, 14°44'36"S, 145°30'20"E, from sand, 10 m, 15 Aug 2013; AM W. 47698 (1 spec.), Lizard Island group, reef on north eastern side of South Island, 14°42'13"S, 145°27'37"E, coral rubble, 5–12 m, 21 Aug 2013. **Northern Territory:** AM W.37754 (3 specs) Darwin, Lee Point, 12°20.0'S, 130°58.3'E, dead coral washings, 3 m, 11 Jun 1993; ex NTM W017392 (10 specs), Darwin Harbour, Iron Ore Wharf, 12°28'21"S, 130°50'34"E, scrapings from wharf pile, 5–10 m, 1998, originally identified as *Pseudobranchiomma orientalis*; NTM W017392 (part, 2 specs), Darwin Harbour, Iron Ore Wharf, 12°28'21"S, 130°50'34"E, scrapings from wharf pile, 7 m,16 Aug 1998, originally identified as *Pseudobranchiomma* cf. *P. emersoni*. **Western Australia:** AM W.37756 (13 specs) Ningaloo Reef, 22°45'19"S, 113°42'40"E, sponge and bryozoa, 15–17 m, 19 May 2009; AM W.37757 (3 specs), Ningaloo Reef, 22°45'19"S, 113°42'40"E, sandstone, 15–17 m, 19 Jun 2009; NTM W018246 (>50 specs) Ashmore Reef, inner lagoon, encrusting sponges, 15 m, 01 Jun 2002, originally identified as *Pseudobranchiomma orientalis*.

Comparative material. Hawaii: AM W.35576 (1 spec.), AM W.35577 (1 spec), AM W.35578 (1 spec.), AM W.37206, (1 spec. on SEM pin), AM W.37207 (1 spec. on SEM pin), all from Oahu, Coconut Island, 21°25'48"N, 157°57'43", epifauna growing on pier, 1 m, 4 Sep 2008.

Diagnosis. Three to six pairs of digitiform radiolar serrations evenly distributed along entire length of radioles. Radiolar eyes absent. Thoracic ventral shields and neuropodial tori separated by a gap. Thoracic and abdominal uncini with about four transverse rows of teeth surmounting main fang. Radiolar crown with transverse dark purple and orange bands at base and 4–6 irregular purple bands along radioles. Body pale, or with some purple patches; large interramal eyespots decreasing posteriorly.

Description of Australian specimens. Specimens range from 3–19 mm long, 0.2–1 mm wide, with 4–7 thoracic and numerous abdominal segments. One complete specimen from AM W.43938 measures 19 mm in length and 1 mm maximum width, including crown 4 mm long, with 6 thoracic and >80 abdominal chaetigers. Body thin and cylindrical. Crown length varies between 1.5 and 4 mm. Radiolar crown lobes semicircular at base, with about nine radioles on each side, connected by basal membrane equivalent to length of at least one thoracic chaetiger (Figs 8D, 9A, B) or 1/8th of radiolar length. Radioles with serrated radiolar flanges, 3–6 digitiform serrations along entire length of radioles (Figs 8C, 9A, G, 10C). Radiolar eyes absent. Pinnules of constant length along radioles, shorter distally; tips of radioles as long as pinnules or shorter. Radioles supported basally by four rows of vacuolated cells. Dorsal lips with tapered dorsal radiolar appendages, about as long as 3–4 thoracic segments (about one third of radiolar crown length), with dorsal lamella attached to base of adjacent radiole (Fig. 9B). Dorsal pinnular appendages absent (Fig. 9B). Ventral lips and parallel

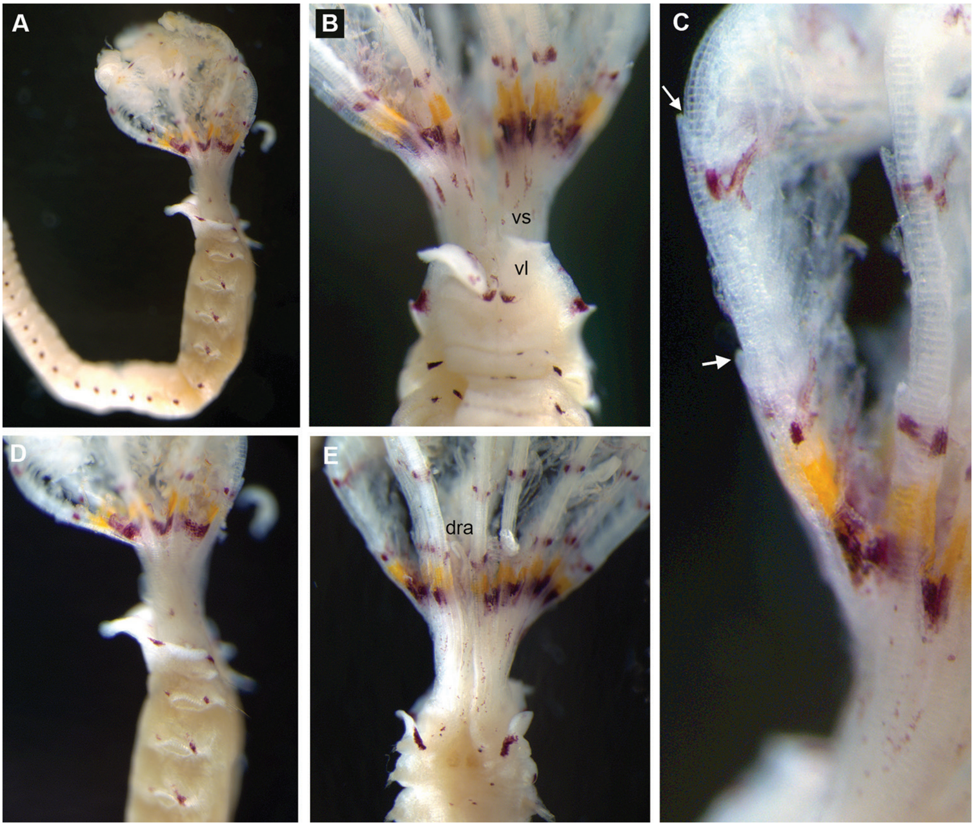

Figure 8. *Pseudobranchiomma* cf. *P. schizogenica*. AM W.36368, AM W.36369. Photographs. **A** Anterior end, lateral view **B** Detail of base of crown and anterior segments, ventral view **C** Detail of lateral radiole **D** Anterior thoracic segments, lateral view **E** Anterior thoracic segments, dorsal view **F** Anterior thoracic segments, dorsal view. dra, dorsal radiolar appendages; vl, ventral lappet; vs, ventral sac; white arrows, serrations of radiolar lateral flanges.

lamellae present, with prominent ventral sacs directed outside of the radiolar crown (Figs 9A, 10B). Collar with dorsal margins separated by wide gap (Figs 8E, 9B, 10D), margins fused to end of first chaetiger; laterally, collar margins smooth, only just reaching junction of crown and thorax (Figs 8E, 9A). Ventral lappets large, sub-triangular, non-overlapping (Figs 8A, B, 9A, 10B). Ventral shields conspicuous (Fig. 8B), first shield trapezoidal, but when stained with methyl green, appears separated into anterior Y-shaped half and posterior W-shaped half; second shield trapezoidal, following shields rectangular. All ventral shields not in contact with or indented by tori. Interramal eyespots conspicuous (Fig. 8A, D). First chaetiger with narrowly hooded chaetae arranged in two rows (Figs 9H, 10E); remaining thoracic chaetigers with about five superior elongate narrowly hooded chaetae and around nine shorter spine-like inferior chaetae (Figs 3X, Y, 9C, J, 10F) with hood as wide as shaft. Neuropodial uncini with about four rows of teeth above main fang (Figs 3U, V, 9D, F, 10G) well-developed

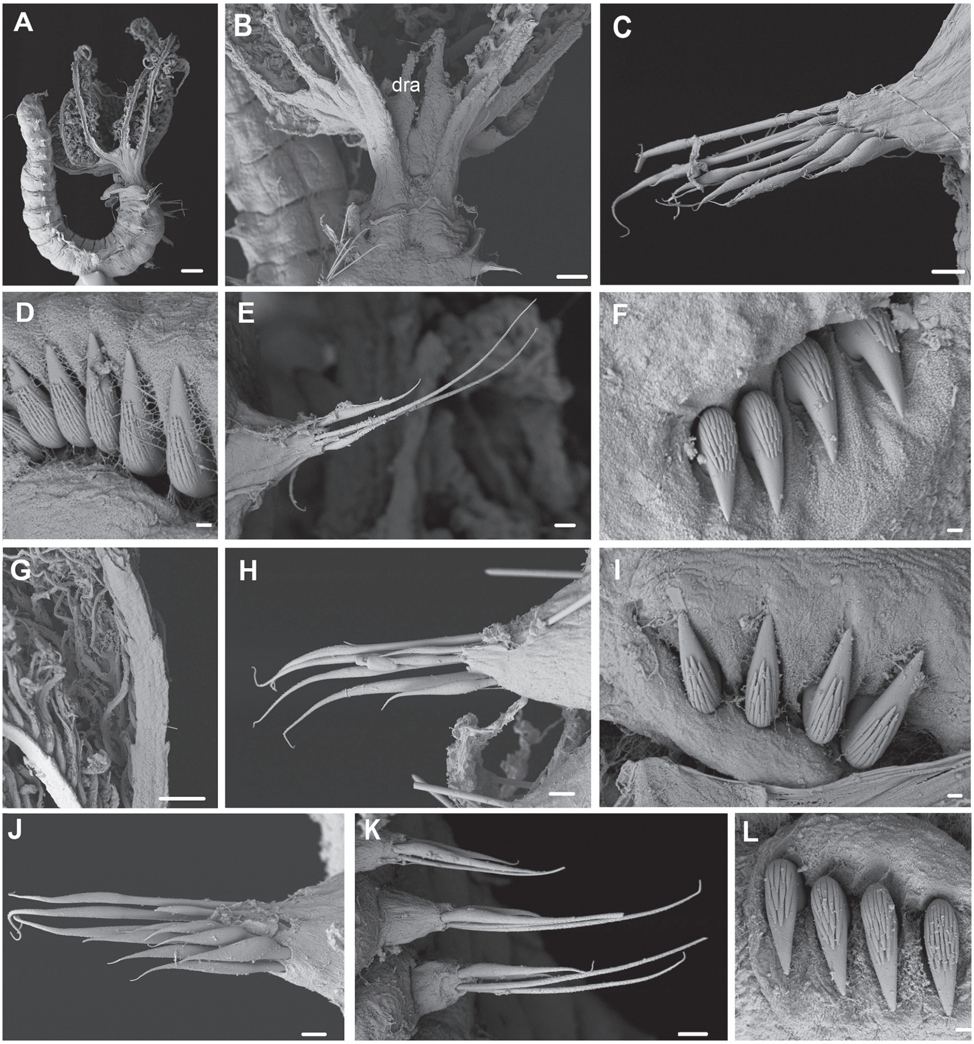

Figure 9. *Pseudobranchiomma* cf. *P. schizogenica*. Scanning electron micrographs. **A–F** specimen from Queensland AM W.37205 **G–L** specimen from Western Australia AM W.37203. **A** Whole specimen, lateral view **B** Base of crown, dorsal view with dorsal lips and radiolar appendages **C** Notopodia, second thoracic segment **D** Uncini, third thoracic segment **E** Posterior abdominal neurochaetae **F** Uncini, posterior abdominal segment **G** Detail of lateral radiole with serrations in flanges **H** Notopodia, first thoracic segment **I** Uncini, fifth thoracic segment **J** Notopodia fourth thoracic segment **K** Neuropodia, mid abdominal chaetigers **L** Posterior abdominal uncini. Scale bars: **A** = 200 µm; **B, G** = 100 µm; **C** = 20 µm; **D, F, I, L** = 2 µm; **E, H, J, K** = 10 µm.

breast and short handle with rounded knob on base (Fig. 3U, V). Abdominal chaetigers with narrowly hooded superior chaetae and spine-like inferior chaetae with hood about half width of shaft (Figs 3Z, A1, 9E, K, 10H). Notopodial uncini very similar to thoracic ones (3W, 9F, L, 10I). Pygidium bilobed.

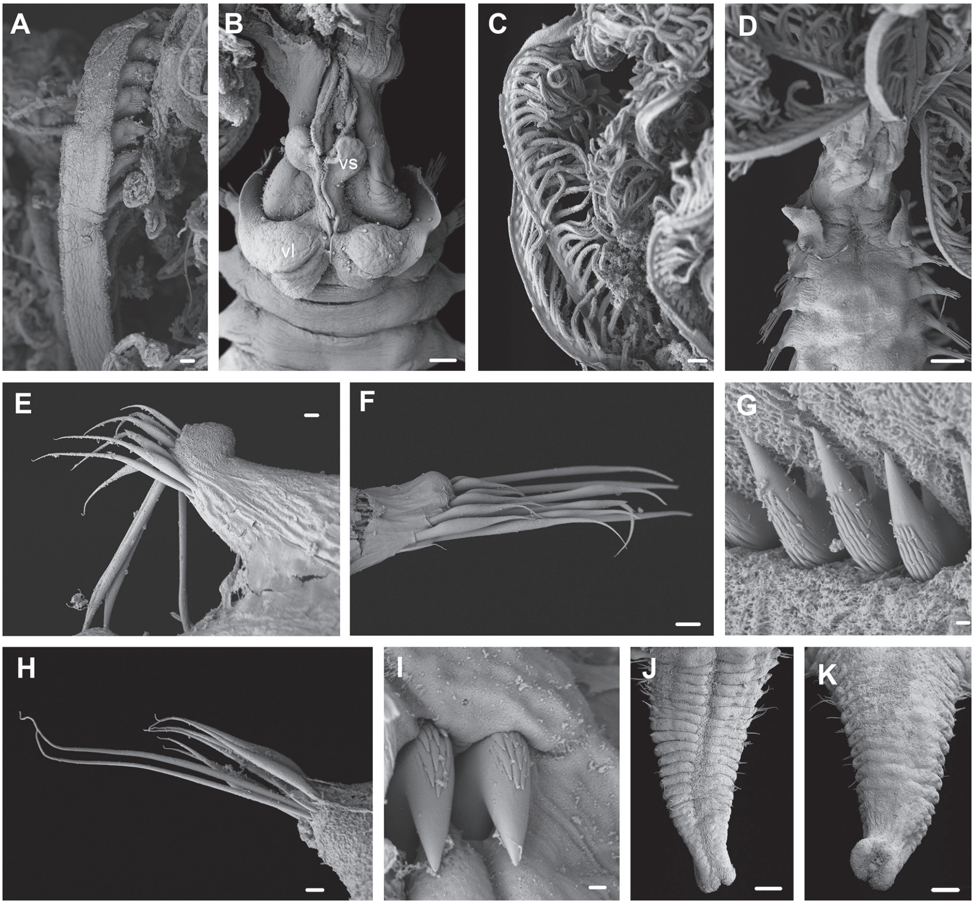

Figure 10. *Pseudobranchiomma* cf. *P. schizogenica* from Hawaii AM W.37206, AM W.37207: Scanning electron micrographs. **A** Detail of radiolar flanges serrations **B** Base of crown and anterior segments, ventral view **C** Lateral radioles **D** Anterior segments, dorsal view **E** Notopodia, first thoracic segment **F** Notopodia, second thoracic segment **G** Uncini, third thoracic segment **H** Neuropodia, posterior abdominal segment **I** Posterior abdominal uncini **J** Posterior end, ventral view (pygidium regenerating) **K** Posterior end, dorsal view. vl, ventral lappets; vs, ventral sac. Scale bars: **A** = 20 µm; **B, C, J, K** = 100 µm; **D** = 200 µm; **E, H** = 10 µm; **F** = 20 µm; **G, I** = 2 µm.

Colour pattern. Body pale with large interramal eyespots (Fig. 8A), decreasing in size gradually towards posterior; small dark purple pigment spots sparsely distributed (Fig. 8A, B, E) over entire body. Some specimens have purple patches on ventral shields as well as further along ventrum and dorsum. Crown with purple pigmentation in basal membrane (Fig. 8A–E), above which there is a pale band followed by dark purple and orange bands (Fig. 8A–E). Pairs of dark purple pigment spots on outer edge of radioles form 4–6 distinct bands along length of radioles (Fig. 8A–E), coinciding with number of serrations along radioles. On some radioles pigmentation extends to base of one or two pinnules. Dorsal margins of collar (Fig. 8E) and ventral lappets (Fig. 8B) have some purple pigmentation. Preserved specimens usually pale with few brown patches on collar and lappets, crowns with some bands of brown pigment, and may have brown longitudinal lines on base of crown. Conspicuous interramal eyespots are maintained after preservation.

Remarks. This species, originally described from the Gulf of California, is characterised by having radioles with short and digitiform serrations along the entire radiolar length, ventral shield of collar trapezoidal and divided into two halves, thoracic superior chaetae and abdominal chaetae with hoods narrower than shafts and thoracic inferior chaetae spine-like with hoods as wide as shafts (Tovar-Hernández and Dean 2014). The specimens found in several localities around the northern Australian coastline and in Hawaii match this diagnosis and additionally share the same colour pattern (four to six repeated pigment units, resembling transverse bands and a wider orange band on the base of radioles) and the number of teeth over the main fang (four). There are, however, some differences between these specimens and the original description of *P. schizogenica*, including one feature considered to be diagnostic of this species: the lateral margins of the collar, because they are oblique, do not always cover the anterior peristomial ring (Fig. 8E); there are also fewer flange serrations per radiole (up to six) in the Australian specimens, even the largest ones, compared with the Gulf of California specimens (6–11). The specimens also somewhat resemble *Pseudobranchiomma paraemersoni* Nogueira, Rossi and Lopez, 2006, from Brazil, a species that also shares a similar number of thoracic segments (between 5 and 7), large interramal eyespots, and the typical transverse bands of pigments in radiolar crown, but differs from *P.* cf. *P. schizogenica* by having fewer number of flange serrations per radiole (3–4) and inferior thoracic spine-like chaetae with hood twice as wide as shaft (hood only as wide as shaft in *P. schizogenica*). Similarly, *P. emersoni* shares some features with *P.* cf. *P. schizogenica*, but differs from it by the irregular branchial crown pigment pattern, the greater number of rows of teeth above main fang in thoracic uncini (5–6), greater number of radioles (14), and the non-differentiated first ventral shield.

Distribution. Southern Gulf of California (Mexico), northern Australia and Hawaii. This species is associated with coral rubble and epifauna attached to hard substrates in shallow depths (0–15 m).

Key to species of *Pseudobranchiomma*

The number of *Pseudobranchiomma* species considered as currently valid (17) follows Knight-Jones and Giangrande (2003) but includes subsequently described species. This key is based largely on descriptions in the literature, and most of them do not include intraspecific variation, so caution should be taken if specimens diverge from statements in the key. Old descriptions also lack enough relevant information to clearly separate species. Therefore, such points of weakness in the key are marked with an asterisk (*).

1 Radioles with distinct, paired, serrated flanges **2**
– Radioles with flanges reduced to low ridges (lacking distinct serrations)...... **9**
2 Serrations distinct along most (or all) length of radioles **3**
– Serrations only distinct on distal parts of radioles **7**

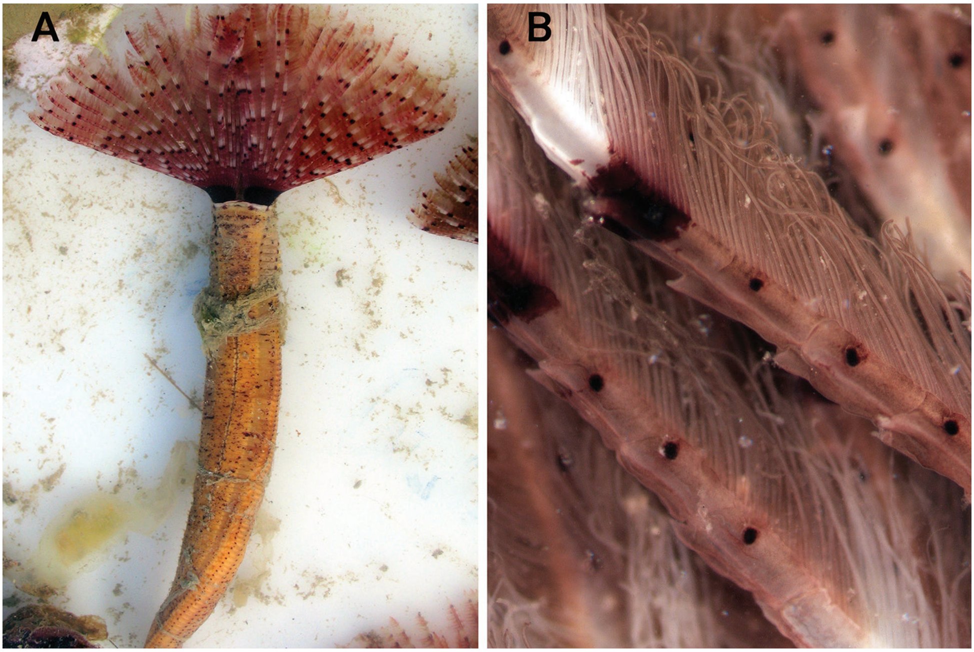

Figure 11. *Pseudobranchiomma grandis* from New Zealand. **A** Whole live animal **B** Section of radioles, showing paired radiolar eyes and serrations of lateral flanges. Photos by Rod Asher.

3 Radioles with paired compound eyes present .... ***P. grandis* (Baird, 1865)** (New Zealand) (Fig. 11) or *reportedly present ***P. serratibranchis* (Grube, 1878)** (Philippines)

– Radioles without distinct radiolar eyes **4**

4 Radioles with over 10 pairs of serrations on lateral flanges **5**

– Radioles with maximum of 10 pairs of serration on lateral flanges **6**

5 Radioles with up to 25 serrations and coloured transverse bands; thorax generally with 8 thoracic chaetigers; thoracic uncini with 6–7 rows of teeth .... ***P. orientalis* (McIntosh, 1885)** (Hong Kong)

– Radioles with 13–19 serrations and 10–19 transverse pigmented bands; thorax with 6–10 thoracic chaetigers; 4–5 rows of teeth in thoracic uncini .... ***P. paulista* Nogueira et al., 2006** (Brazil)

6 Radiolar crown without pigmented transverse dark bands; radiolar lobes pigmented with purple and radioles white with yellow tips. Radioles with six serrations along their length; three rows of teeth above main fang of thoracic uncini .... ***P. pallida* sp. n.** (Australia)

– Radiolar crown with several pigmented transverse bands (regular or irregular) .. 7

7 Radioles with up to 10 serrations and 10 narrow irregular purple bands; thorax with 4–8 chaetigers; 5–6 rows of teeth above main fang of thoracic uncini....... .... ***P. emersoni* Jones, 1962** (Caribbean)

– Radioles with 3–4 serrations and transverse bands (purple and yellow; a few white); thorax with 4–5 thoracic chaetigers; 4–5 rows of teeth above main fang of thoracic uncini .... *P. paraemersoni* **Nogueira et al., 2006** (Brazil)

– Radioles with 6–11 serrations and 4–6 transverse bands (of purple-orange-white); four rows of teeth above main fang of thoracic uncini; lateral margins of collar oblique and covering anterior peristomial ring ....***P. schizogenica*** **Tovar-Hernández and Dean 2014** (Gulf of California)

8 Radiolar eyes reportedly* present ....***P. odhneri*** **(Fauvel, 1921)** (Madagascar) or* ***P. bocki*** **(Johansson, 1922)** (Japan)

– Radiolar eyes absent **8**

9 Radiolar crown with 12 dark pigment bands (and 7 wide yellow bands between) ....***P. tricolor*** **(Grube, 1881)** (Japan)

– Radiolar crown whitish, darker at base, lacking transverse pigmented bands; thorax with eight thoracic chaetigers; thoracic uncini with over five rows of teeth .... ***P. zebuensis*** **(McIntosh, 1885)** (Philippines)

10 Peristomial collar fused dorsally to sides of faecal groove.............................. ....***P. punctata*** **(Treadwell, 1905)** (Hawaii)

– Collar with free dorsal margins, widely separated from faecal groove **10**

11 Radioles with paired compound eyes **11**

– Radioles without distinct compound eyes (may have granular pigment patches).. **12**

12 Thorax broader than long (with up to 8 thoracic chaetigers); each side of crown in spiral of up to 5 whorls (mature specimens) .... ***P. longa*** **(Kinberg, 1867)** (South Africa)

– Thorax longer than broad (with up to 13 thoracic chaetigers); radiolar lobes never spiralled ......***P. perkinsi*** **Knight-Jones & Giangrande, 2003** (Florida)

13 Thorax with 4–6 segments; first thoracic chaetiger less than 1.5 times length of the following ones.........***P. minima*** **Nogueira & Knight-Jones, 2002** (Brazil)

– Thorax with 8 segments; first thoracic chaetiger 2–3 times length of the following ones...... ***P. tarantoensis*** **Knight-Jones & Giangrande, 2003** (Italy)

Discussion and conclusions

The genus *Pseudobranchiomma* was erected based on the short thorax (with less than the usual eight thoracic chaetigers), absence of compound radiolar eyes (unlike members of *Branchiomma* and some *Bispira*), and the presence of 'reduced stylodes' (Jones 1962), that are now considered to be serrations of the radiolar flanges (Knight-Jones and Giangrande 2003), features that have been recognised not to be unique to members of the genus and also not shared by all congeners (e.g. Fitzhugh 1989, Knight-Jones 1994, Fitzhugh and Rouse 1999, Nogueira and Knight-Jones 2002, Knight-Jones and Giangrande 2003, Nogueira et al. 2006, Capa 2008). It is therefore not surprising that monophyly of the genus has not been confirmed after our analyses of morphological data. The low number of sequences available for this study does not allow to assess its' monophyly either. However, and contrary to results obtained after analyses of morphological data, DNA sequences suggest that *Branchiomma* is not nested within *Pseudobranchiomma* or sister to it (Fitzhugh 1989, Capa 2008, Nogueira et al. 2010), and instead, *Sabellastarte* and *Sabella* are the closest related taxa. It is in fact difficult to discern between members of *Sabellastarte* (especially if small) and those *Pseudobranchiomma* without radiolar flanges and eyes. The only attribute to distinguish between members of these two genera in these cases, is the position of the ventral sacs, which are inside the radiolar crown in members of *Sabellastarte* and outside the crown in members of *Pseudobranchiomma* (e.g. Knight-Jones and Mackie 2003, Capa et al. 2010).

Relationships within the genus indicate that the groups proposed by Knight-Jones and Giangrande (2003) based on characteristics of the radiolar crown (presence of eyes, flanges and serrations), although still valuable for comparing similar-looking species do not seem to hold any phylogenetic information.

In this study, a new species, *Pseudobranchiomma pallida* sp. n., is herein described, and another species, *P.* cf. *P. schizogenica* is reported in Australia for the first time, an indication that the group is more diverse than previously considered. Nevertheless, this diversity could be due, in part, to unintentional translocations. Some specimens in this study could be assigned to three species, *P.* cf. *P. emersoni*, *P.* cf. *P. orientalis* and *P.* cf. *P. schizogenica*, originally described from distant and disjunct geographic areas (Jamaica, Southern Gulf of California and Hong Kong, respectively) but also reported from other worldwide localities (Knight-Jones 1994, Russell and Hewitt 2000, Swami and Udhayakumar 2010, Tovar-Hernández and Dean 2014). The hypothesis of these species being translocated requires testing. Due to the great morphological similarity displayed by individuals from such disjunct populations, the use of molecular markers could be an effective method to test whether they belong to the same species. Another issue to be resolved, if the translocations are indeed corroborated, would be the actual origin of the species. At this juncture, it is uncertain whether they have been introduced to Australia or were translocated from this continent. The fact that *P.* cf. *P. orientalis* is mainly reported from port environments in Australia may possibly be an indication of its introduction herein. *Pseudobranchiomma schizogenica* was originally collected in 2011 from marinas in Mexico as part of fouling communities (Tovar-Hernández and Dean 2014) and therefore it seems possible that it is also not its natural distribution range but the species has also been introduced there. In Australia, *P.* cf. *P. schizogenica* was collected from Darwin ports as early as 1998, possibly introduced, and may have spread to more pristine, non-port areas in Queensland and Western Australia. It has been found in Hawaii also, although not in a major port environment, but in the environs of a yachting port-of-call. Further analysis using molecular data of more specimens collected from around the world may eventually lead to some clarification of its true origin. Colonies of *Pseudobranchiomma schizogenica* (or *P.* cf. *P. schizogenica*) now appear to be abundant in fouling communities of marinas and ports, and may possibly be a potential pest species.

Acknowledgements

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A new species of the genus *Policordia* (Bivalvia, Verticordioidea, Lyonsiellidae) from off the coast of southern California

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Abstract

A new species, *Policordia hispida*, is described and compared with three similar species: *P. densicostata* (Locard, 1898); *P. pilula* (Pelseneer, 1911) and a yet un-described species, *Policordia* sp. (= *P. pilula* sensu Ivanova, 1977 not Pelseneer, 1911). This is a first record for the genus in the Californian province.

Keywords

Policordia hispida, Heterodonta, Anomalodesmata, Eastern Pacific, carnivorous bivalves, bathyal

Introduction

Like other lyonsiellids, the genus *Policordia* Dall, Bartsch & Rehder, 1938 (Bivalvia, Lyonsiellidae) comprises specialized carnivorous bivalves widely distributed in the world's oceans. Representatives of the genus live in a large range of depths, 138–9380 m (Allen and Turner 1974; Knudsen 1970) but most commonly occur in deep-sea ocean basins and trenches. *Policordia* is characterized by having a small thin fragile shell with an external sculpture consisting of very fine commarginal growth lines and radial threads. It lacks hinge teeth (Coan et al. 2000). It differs from other genera of the family Lyonsiellidae in that *Policordia* lacks any granules or spinules on the shell surface (Allen and Turner 1974; Poutiers and Bernard 1995). Anatomical modifications of the digestive and respiratory systems of *Policordia* are the result of adaptations for a carnivorous way of life. The digestive tract of *Policordia* includes a muscular stomach with an inner layer of scleroprotein used to crush prey. The stomach is connected to extensive digestive diverticula by one or two ducts. Members of *Policordia* have a large inhalant siphon surrounded by sensitive tentacles. Ctenidia are present but reduced, varying in their filament numbers and the degree of their muscularization among species (Allen and Turner 1974; Ivanova 1977).

Presently 25 species are assigned to the genus *Policordia* primarily on the basis of conchological features (Bouchet and Gofas 2013). However, data on anatomical characters show that diversity in the genus is much higher and *Policordia* may prove to be a paraphyletic group requiring thorough revision (Safonova 2007).

Recently specimens conchologically similar to the type species of the genus (*Policordia diomedea* Dall, Bartsch & Rehder, 1938) were collected from two separate sites off the coast of southern California. These are the first records of the genus from the Californian Marine Province (Coan et al. 2000). Here we describe it as a new species.

Methods

The new species is represented by preserved, live taken, specimens that were collected using a 0.1 m^2 chain-fired Van Veen Grab. Sediment samples were screened with a 1 mm sieve, fixed in a 10% solution of buffered formaldehyde and then transferred to 70% ethanol. Morphological measurements were made with calipers and an ocular micrometer (±0.1 mm). The length (L), height (H) and width (W) of the valves were recorded. Gross anatomy was observed using a dissecting microscope.

Additional material used. RV "Vityaz", Cruise 45, station 6103, 59.1167°N, 142.1°W; 1500 m, 1 specimen; 11 May 1969 (*Policordia* sp. = *P. pilula* of Ivanova, 1977 not Pelseneer, 1911, deposited in IORAS).

Institutional abbreviations:

LACM	Museum of Natural History of Los Angeles County
SBMNH	Santa Barbara Museum of Natural History
CSD-EMTS	City of San Diego Environmental Monitoring Technical Services Laboratory
OCSD	Orange County Sanitation District
IBS RAS	A.V. Zhirmunsky Institute of Marine Biology, Vladivostok, Russia
IO RAS	P. P. Shirshov Institute of Oceanology, Moscow, Russia.

Systematic account

Superfamily Verticordioidea Stoliczka, 1870

Family Lyonsiellidae Dall, 1895

Policordia Dall, Bartsch & Rehder, 1938

Type species. By original designation, *Policordia diomedea* Dall, Bartsch & Rehder, 1938.

Recent. Atlantic, Indian and Pacific Oceans.

Gender. Feminine.

Policordia hispida sp. n.

http://zoobank.org/95DD6BCE-3EB5-49B2-8C27-FCB685CDF25D

Type locality. USA, California, Orange County; 33.3688°N; 117.6899°W; 411 m (OCSD B13-9137; 30 July 2013).

Type material. ***Holotype:*** LACM 3322, valves separated, with soft parts in 70% ethanol, length 4.8 mm, height 4.3 mm, width 1.8 mm. ***Paratype:*** SBMNH 462739, USA, California, San Diego County; 32.7993°N; 117.4055°W; 449 m (CSD-EMTS 8338, 23 July 2014); valves separated, with soft parts in 70% ethanol, length 3.8 mm, height 3.4 mm, width 1.4 mm.

Diagnosis. Shell subquadrate, longer than high with broadly rounded posterodorsal margin; 30–32 radial periostracal lamellae present; umbones prominent. Each mantle margin with approximately 30 mantle glands lacking long cylindrical portion. Inhalant siphon with 18–19 papillated tentacles and 2 pairs of smooth tentacles. Exhalant siphon with 5 conical tentacles. Byssal thread present.

Description. ***Shell.*** The translucent fragile shell is subquadrate (Figs 1, 3) with the length greater than the height (Table 1); inequivalve, with the right valve overlapping the left. The beaks are prosogyrate, delimited from the posterior angle by compressions. The posterodorsal margin is straight and is directed obliquely downwards from umbo; the posteroventral margin is slightly rounded and forms extended and slightly compressed angle with the posterodorsal margin. The anteroventral margin is rounded on the left valve and nearly straight on the right valve. Shell with irregular fine commarginal growth checks, covered with a colorless periostracum, which in turn forms a series of regularly spaced, radial lamellae (30–32) extending from the umbo, of the total, 13–14 are secondary (incomplete). Adhering to some radial lamellae are bunches of fine fibers giving the shell a slightly hirsute appearance externally. Shell nearly completely covered with fragile thick-silt coating (not shown, removed prior to examination). Hinge margin thin, edentate, with relatively large lithodesma inserted posterior to umbo along posterodorsal margin. Lithodesma has small posterior sinus, about ¼ of length, right posterior branch less than the left (Fig. 1).

Anatomy. Mantle of the holotype has about 30 flask-shaped mantle glands located along the mantle edge. Mantle glands consist of short ducts formed by a few cells and

Table 1. Measurement of right valve (mm).

Measurement	L	H	W	H/L	W/L
Holotype (LACM 3322)	4.8	4.3	1.8	0.9	0.4
Paratype (SBMNH 462739)	3.8	3.4	1.4	0.9	0.4

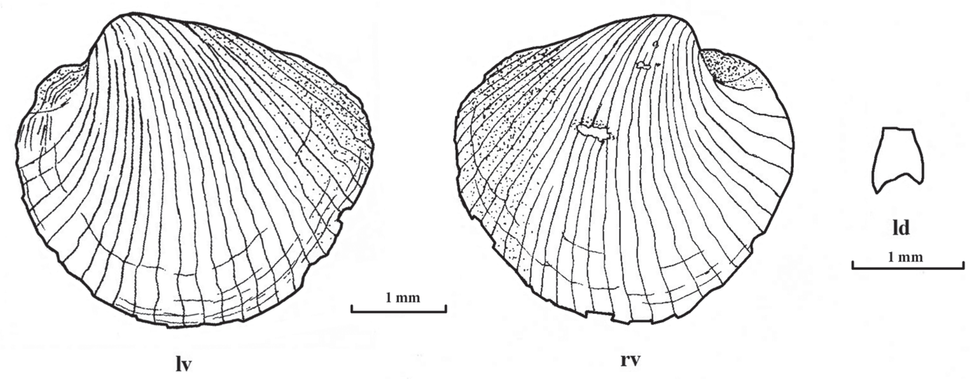

Figure 1. *Policordia hispida* sp. n. Shell of holotype, external view and lithodesma; **lv** left valve **rv** right valve **ld** lithodesma.

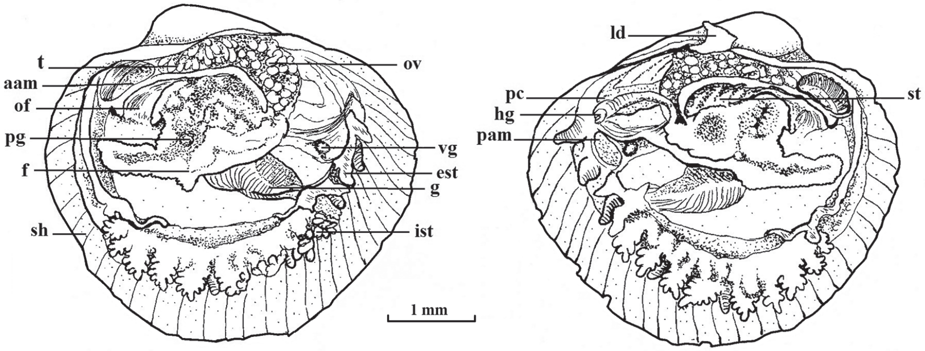

Figure 2. *Policordia hispida* sp. n. Body structure, medial section through the body (views from left and right respectively); **aam** anterior adductor muscle **est** exhalant siphon tentacles **f** foot **g** gills **hg** hindgut **ist** inhalant siphon tentacles **ld** lithodesma **of** oral funnel **ov** ovaries **pam** posterior adductor muscle **pc** pericardium **pg** pedal ganglion **sh** shell **st** stomach **t** testis **vg** visceral ganglion.

oval structure above them, similar to glands of *P. atlantica* (Allen and Turner 1974). There is one row of papillated tentacles surrounding the inhalant siphon, 10 tentacles on the right side and 9 on the left (Figs 2, 3). Each tentacle carries 6–8 short papillated extensions (Figs 2, 4). Additionally, slightly outside the row of papillated tentacles, there are two, left and right, pairs of simple conical tentacles (Fig. 4). The first pair (counting from anterior to posterior) is between the fifth and sixth papillated tentacles; the second pair is

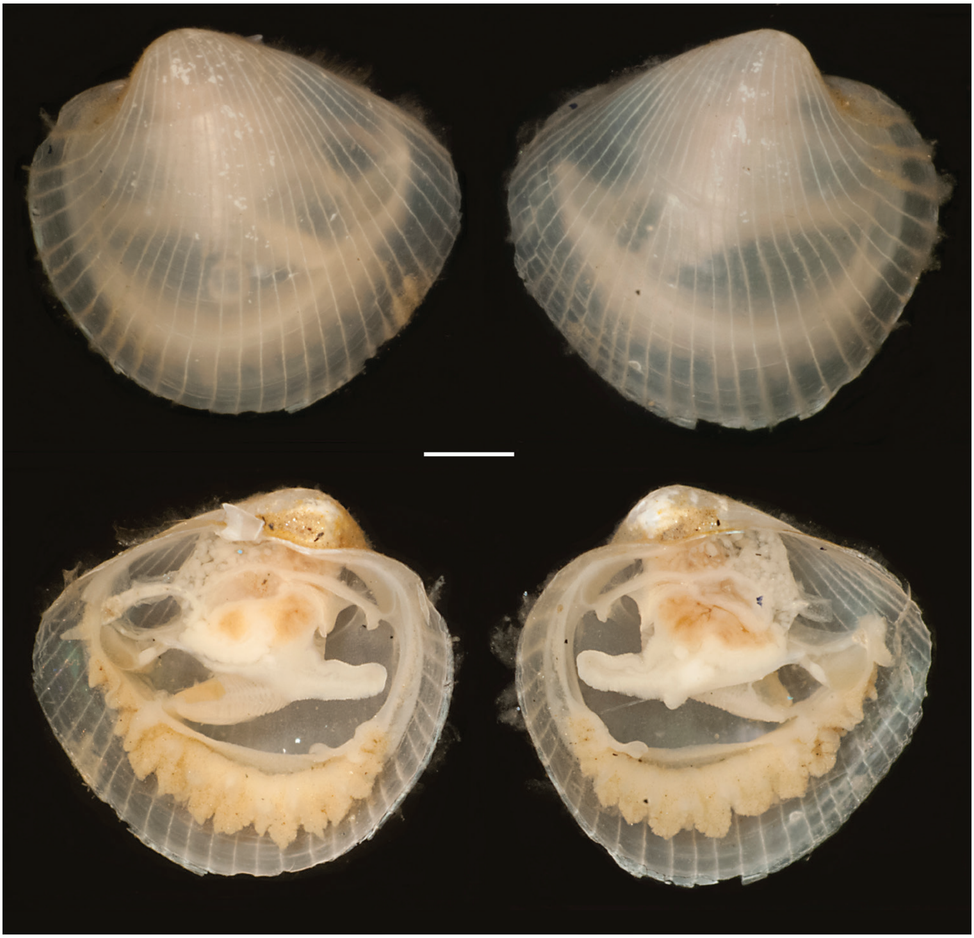

Figure 3. *Policordia hispida* sp. n. Holotype, wet specimens in 70% ethanol; left and right valve respectively; scale bar = 1 mm.

between the seventh and eighth papillated tentacles. The exhalant siphon is surrounded by a total of five conical tentacles, one located dorsally and two pairs laterally (Figs 2, 3).

The foot has a heel; byssus present (Figs 2, 3).

Gills comparably wide, elongated, longer than base of foot. They consist of inner and outer demibranchs (Fig. 5); attached by outer demibranch margin laterally to mantle wall and posteriorly to junction between siphons. Outer demibranch without inter-filamentary junctions, inner demibranch with a single inter-filamentary connection.

Mouth is wide, funnel-liked, followed by a rigid oesophagus. Stomach covered with digestive diverticula; hindgut passes through pericardium (Fig. 2).

The holotype is a hermaphrodite with both testes covering anterior upper quarter of digestive diverticula and the ovaries located posteriorly (Figs 2, 3).

Variation. The shell of the paratype is slightly smaller in absolute dimensions but retains the same ratios of width to length and height to length (Table 1). Like the holotype, the translucent fragile shell is subquadrate; inequivalved with the right valve

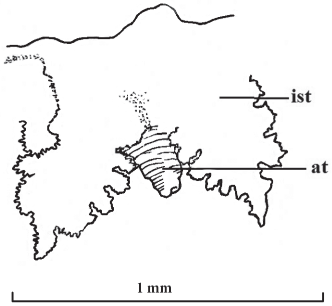

Figure 4. *Policordia hispida* sp. n. The fifth and sixth papillated tentacles of the inhalant siphon with a simple conical tentacle between them; **ist** inhalant siphon tentacles **at** conical tentacle.

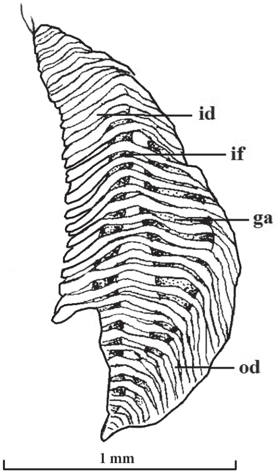

Figure 5. *Policordia hispida* sp. n. Left gill, ventral view; **ga** gill axis **id** inner demibranch **if** interfilamentar partition **od** outer demibranch.

overlapping the left. In keeping with its smaller size (Allen and Turner 1974), the shell surface has both fewer radial periostracal lamellae (27–29) and secondary lamellae (8–10). The hinge margin is thin and edentate, with a lithodesma that matches the holotype in size and proportions. No silt covering observed.

The mantle of the paratype, as with that of the holotype, has flask-shaped mantle glands. The inhalant siphon is surrounded by 17 papillated tentacles. As in the holotype, there are two left and right pairs of conical tentacles located slightly outside of the row of papillated tentacles. The first pair is located between the second and third papillated tentacles; the second pair is between fifth and sixth (counting from anterior to posterior). The exhalant siphon is surrounded by a total of five conical tentacles; one dorsal and two pairs of laterals. As in the holotype, the foot has a single byssal thread attached.

Etymology. The new species name is derived from the Latin adjective hispida due to the somewhat 'shaggy' appearance of the shell.

Distribution. Known only from the type material: Eastern Pacific, southern California, 411–449 m.

Habitat. Type specimens found in silt and fine sand.

Discussion

The new species was assigned to the genus *Policordia* on the basis of conchological features. The shell surface is smooth, wihtout granules and hinge teeth are absent (Dall et al. 1938; Allen and Turner 1974). Anatomical details of the type species of the genus, *Policordia diomedea*, are not known. Conchologically, the new species differs from the *P. diomedea* in that the length is greater than the height and the posterodorsal margin is straighter and longer. *P. diomedea* is taller; more rounded with a shorter posterodorsal margin (Dall et al. 1938).

Policordia hispida sp. n. most closely resembles *P. densicostata* (Locard, 1898); *P. pilula* (Pelseneer, 1911) and an undescribed species, *Policordia* sp. (= *P. pilula* sensu Ivanova, 1977 not Pelseneer, 1911) (L. Safonova pers. obs. 2016).

Policordia densicostata, an Atlantic species whose anatomical features were described by Allen and Turner (1974), has a taller shell with more prominent umbones. *Policordia densicostata* lacks simple conical inhalant tentacles of *P. hispida* sp. n. Unlike *P. densicostata*, the new species lacks long cylindrical portion of the mantle glands (Table 2).

Policordia pilula has a more vertically extended shell with a more rounded posterodorsal margin (Prashad 1932). The general anatomical characters of this species were described by Pelseneer (1911), but he did not provide any details about the siphon and siphonal tentacles (Table 2).

Specimens identified as *P. pilula* by Ivanova (1977) from the Gulf of Alaska differ from the original description by Pelseneer (1911) and the subsequent description by Prashad (1932). It is an undescribed species (L. Safonova, pers. obs. 2016). The shell shape of *P. hispida* sp. n. is very similar to *P. pilula* sensu Ivanova (1977), but differs in the number of radial ribs and mantle glands, the smaller number of tentacles of the inhalant siphon and the presence of a byssus (Table 2).

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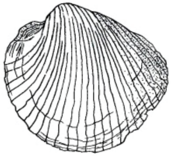
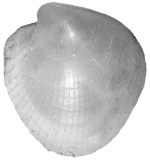
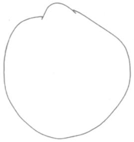
Table 2. Some characters of selected species of *Policordia* including geographical distributions.

	***P. hispida* sp. n.**[†]	***P. densicostata* (Locard, 1898)**[‡]	***P. pilula* (Pelseneer, 1911)**[§]	***Policordia* sp. (un–described)**[ǀ]
				
Length (mm)	4.8	18	5.8	7.0
Length:Height	L > H	L < H	L < H	L = H
Inhalant siphon tentacles	18–19, thick, flattened, with 6–8 papillated extensions; 4 outer, smaller, simple conical tentacles	22, all merged at base, each with 3–7 papillated lobes	Unknown	23, thick, flattened, with 7 extensions; 4 outer, smaller, simple conical tentacles
Exhalant siphon tentacles	Conical, 1 dorsal, 4 lateral (left and right pairs)	Conical, blunt with dense covering of papillae, 1 dorsal, 4 lateral (left and right pairs)	Unknown	Conical, 1 dorsal, 4 lateral (left and right pairs)
Byssus	Present	Present	Unknown	Absent
Mantle glands	~ 30; flask shaped without long cylindrical portion	~ 30; flask shaped with long cylindrical portion	Unknown	36–34 flask shaped without long cylindrical portion
Shell sculpture	30–32 radial periostracal lamellae (holotype)	30–37 radiating lines of slightly raised ridges	~ 30 radial hair like lines	~ 30 radial lines
Distribution	Eastern Pacific, Southern Californian Bight; 411–449 m	Atlantic; 1007–2503 m[¶]	West Pacific; 1301 m	Northeastern Pacific, Gulf of Alaska; 1230–2980 m

[†] Cited herein

[‡] Locard 1898; Allen and Turner 1974; Image: Oliver et al. 2010

[§] Pelseneer 1911; Prashad 1932; Soot-Ryen 1966; Image: Prashad 1932, fig.24

[ǀ] *P. pilula* of Ivanova 1977 not Pelseneer 1911; Image: Ivanova 1977, fig. 18a

[¶] Allen and Morgan 1981; Salas 1996

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Descriptions of two new genera of the spider family Caponiidae (Arachnida, Araneae) and an update of *Tisentnops* and *Taintnops* from Brazil and Chile

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Abstract

New members of the spider family Caponiidae from Brazil and Chile are presented. Three new species in previously known genera are described: *Taintnops paposo* **sp. n.** from Chile, and the Brazilian *Tisentnops mineiro* **sp. n.** and *Tisentnops onix* **sp. n.**, both belonging to a genus known only from its damaged type. Additionally, two new non–nopine Brazilian genera are proposed: *Nasutonops* **gen. n.** including three new species: *N. chapeu* **sp. n.**, *N. sincora* **sp. n.** and *N. xaxado* **sp. n.**; and *Carajas* **gen. n.**, known only from the type species *C. paraua* **sp. n.** Both new genera have entire, rather than sub-segmented tarsi. Therefore, they are not included in the caponiid subfamily Nopinae. *Nasutonops* **gen. n.** is characterized by the presence of a projected clypeal horn, unique among caponiids. Additionally, the first blind caponiids are described: *Tisentnops mineiro* **sp. n.** from the state of Minas Gerais and *Carajas paraua* **sp. n.** from the state of Pará. Both of these species are found only in caves and completely lack eyes.

Keywords

Taxonomy, new species, haplogynae, new genus, Neotropical region

Introduction

The family Caponiidae is currently represented by 15 genera and 98 species (World Spider Catalog 2016). The family was divided into two subfamilies by Petrunkevitch (1939): Nopinae includes genera with sub-segmented tarsi and Caponinae includes genera with entire tarsi. However, based on current data, only Nopinae could be monophyletic (Platnick 1995; Platnick and Lise 2007), whereas those genera with entire tarsi (non-nopine) may form a basal and paraphyletic group (Platnick 1994a; Kranz-Baltensperger et al. 2009). Although some of these genera seem to be more closely related each other than with the Nopinae (Platnick and Jäger 2008).

Currently nine non-nopine genera are known: *Caponia* Simon, *Diploglena* Purcell, *Iraponia* Kranz-Baltensperger, Platnick & Dupérré and *Laoponia* Platnick & Jäger from Africa and Asia, and *Calponia* Platnick, *Caponina* Simon, *Notnops* Platnick, *Taintnops* Platnick and *Tisentnops* Platnick from the New World. Recently, the first genera from Asia were described (Platnick and Jäger 2008; Kranz-Baltensperger et al. 2009), and the African genus *Diploglena* was revised (Haddad 2015). However, *Caponia*, the first described Caponiidae genus, has not been studied since the works of Purcell (1904) and Lessert (1936) in the early twentieth century. Other than *Caponina*, the non–nopine New World genera are monotypic, and *Tisentnops* is known only from an extremely damaged type species, precluding a detailed morphological description (Platnick 1994b).

During several field trips to collect haplogynae spiders in Brazil and Chile, three new species of the genera *Taintnops* and *Tisentnops* were found (the Chilean *Taintnops paposo* sp. n. and the Brazilian *Tisentnops mineiro* sp. n. and *Tisentnops onix* sp. n.). The new species allowed us to gather detailed morphological information, expand the distributional range, and provide information about the natural history of these two genera. Additionally, we found two new non–nopine Brazilian genera: *Nasutonops* gen. n. and *Carajas* gen. n.; the first with three new species *N. chapeu* sp. n., *N. sincora* sp. n., *N. xaxado* sp. n., and the second known from only one species *C. paraua* sp. n. All these new genera and species are also described in this paper.

Some of the new species are remarkable among caponiids. We describe the first known blind caponiids: *T. mineiro* sp. n. and *C. paraua* sp. n.; both species are known only from caves and completely lack eyes. Another unique characteristic occurs in the new genus *Nasutonops*, which has a hard, distally projected clypeal horn, similar to the goblin spider genus *Unicorn* Platnick & Brescovit (see Platnick and Brescovit 1995: figs 1–2). No other caponiids are known to have such a dramatic carapace modification.

Material and methods

Morphological observations and illustrations were made using a Leica MZ12 stereomicroscope with a camera lucida. Photographs were taken with a Leica DFC 500 digital camera mounted on a Leica MZ 16A stereomicroscope. Extended focal range images were composed with Leica Application Suite version 2.5.0. The female internal genitalia were dissected following Levi (1965), and soft tissues were digested after immersion in clove oil for visualization of internal structures. SEM images were taken under high vacuum in a FEI Quanta 250 Scanning Electron Microscope from the Laboratório de Biologia Celular do Instituto Butantan and in a LEO 1450VP from the Laboratório de Microscopia Eletrônica do Museu Paraense Emílio Goeldi (MPEG). All figures were edited using Adobe Photoshop CS5 ver. 12.0. Descriptions and measurements follow Platnick (1994b). Measurements are in millimeters (mm) and were made using an ocular micrometer.

The specimens examined are deposited in the following collections (Abbreviation and curator in parentheses): American Museum of Natural History, New York (AMNH, N.I. Platnick); Instituto Butantan, São Paulo (IBSP, A.D. Brescovit); Coleção de Invertebrados Subterrâneos da Universidade Federal de Lavras, Lavras (ISLA, R.L. Ferreira), Museu Paraense Emílio Goeldi, Belém (MPEG, A.B. Bonaldo).

Taxonomy

Tisentnops Platnick, 1994

Tisentnops Platnick, 1994b: 9 (Type species by original designation *Caponina leopoldi* Zapfe).

Note. Platnick (1994b: 9) reported that the holotype of *Tisentnops leopoldi* (Zapfe) was in the Museo de Historia Natural de Santiago de Chile, and this specimen, probably a female, was extremely deteriorated. The type was examined by the first author during a recent trip to Chile. Now, with specimens of *T. mineiro* sp. n. and *T. onix* sp. n., an emendation is presented to the generic description. The eyes previously used in Platnick (1994b) as diagnostic characters are no longer applicable because some species in this genus lack eyes (Figs 1A, 5E).

Diagnosis. Members of the genus can be easily separated from all other caponiid genera by the distally widened palpal endites, as in *Diploglena*, but uniquely modified with a series of setae with elongated sockets in the sub-marginal and anterior margin(Fig. 2C–E). These elongated sockets may also be present in anterior legs (Fig. 1C, J).

Description. Described by Platnick (1994b), but new data are included here. Caponiids of moderate-size (Figs 1A; 17A, C–D), eyeless (Figs 1A; 17A), or with two small eyes, near the anterior border of the carapace (Fig. 5E). Carapace broadly oval, anteriorly narrowed to less than half its maximum width, pars cephalica rounded, ocular tubercle not projecting forward; pars thoracica relatively flat, gradually sloping toward laterally and posteriorly, without submarginal elevations opposite the coxal bases or submarginal depressions opposite the coxal interspaces (Fig. 5C); cuticle smooth; clypeus unremarkable (Fig. 5E); thoracic groove obsolete (Figs 1A, 5D). Cheliceral paturon with long, relatively strong bristles; short fang with unmodified base (Fig. 2B);

median lamina long with short tooth-shaped tip and a white membranous lobe opposite the tip of the cheliceral fang (Fig. 2A–B); lateral surface with short stridulatory ridges, pick on prolateral side of palpal femur, next to base of male palp (Fig. 4A, F) and inconspicuous on the female pedipalp (Fig. 2K). Endites convergent, distally widened and extending far beyond the posterior margin of the labium (Fig. 2E, G), not touching at tip, covered by setae with elongated sockets which form a row along the anterior margin (Figs 1B, I; 2C–E; 5G), serrula absent. Labium almost pentagonal, much longer than wide, fused to sternum (Figs 1B, I; 5G), slightly invaginated at base, covered with a few scattered setae, distal area acuminate (Fig. 2E–F); labrum short, narrow, with few setae. Sternum longer than wide, covered with scattered large setae, without radial furrows between coxae, not fused to carapace (Fig. 1I); cephalothoracic membranes without epimeric sclerites, but short triangular sclerites extend from sternum between coxae I and II, II and III, and III and IV; shorter triangles extend to coxae II-IV. Leg formula 4123; legs without spines, legs I and II with setae with elongated sockets (Fig. 1C, J); metatarsi and tarsi entire, without sub-segmentation or membranous processes; tarsi with three claws; paired claws with approximately ten teeth on legs I-II, distal teeth largest (Fig. 3D); legs III-IV with paired claws very long, with two small basal teeth, distal teeth largest (Fig. 3E); unpaired claw shorter than paired ones on all legs, without teeth (Fig. 3D–F). Tibiae, metatarsi, and tarsi with long trichobothria in a single row (Figs 3A, 5H), bases with semicircular rim bearing low ridges (Fig. 3C); tarsal organ exposed, with very short longitudinal ridge in proximal end, covered by semicircular long ridges (Fig. 3B); female palpal tarsus moderately elongate, prolateral surface densely covered with setae, retrolateral surface covered by few setae (Fig. 2H, K). Abdomen with only slightly sclerotized epigastric area, with two pairs of respiratory spiracles; posterior spiracles connected by rebordered groove extending farther back at middle than at sides (Fig. 1H). Six spinnerets (Fig. 5I) in typical caponiid arrangement (Platnick et al. 1991: 56, Sánchez-Ruiz et al. 2010: 96, 140). Male palpal patella and tibia short, unmodified; cymbium ovoid, circular alveolus, prolateral surface densely covered with strong setae; bulb stout and globose; cylindrical embolus, slightly curved with enlarged tip, directed retrolaterally (Figs 1D–G; 4A–C, F–H). External female genitalia without scutum, weakly sclerotized (Figs 1H; 5F). Internal female genitalia with an elongate anteromedian membranous receptaculum accompanied by wide, transverse and anteriorly directed sclerotized bars that are coated with a transparent hyaline membrane, and by a V-shaped dorsal fold internally on the posterior plate (Figs 3G–L, 4D).

Distribution. Known from Chile and southeastern Brazil.

Tisentnops mineiro **sp. n.**

http://zoobank.org/B7485A08-D81A-4EB7-B350-7B1DD7F07304
Figures 1, 2, 3, 4A–E, 17A

Types. Male holotype from Gruta da Serra da Moeda (20°19'58"S, 44°03'10"W), Moeda, Minas Gerais, Brazil, X.2005, R.L. Ferreira, deposited in IBSP 191293; female paratype from Gruta MP-10 (20°15'58"S, 43°53'16"W), Itabirito, Minas Gerais, Brazil, IX.2007, R.L. Ferreira, deposited in IBSP 191294.

Etymology. The specific name is the designation for the native people from the state of Minas Gerais, Brazil, where this species was found.

Diagnosis. *Tisentnops mineiro* sp. n. is easily separated from other species of the genus by the absence of eyes (Figs 1A, 17A).

Description. Male (holotype). Total length 3.6. Carapace 1.6 long, 1.2 wide. Coloration: cephalothorax orange reddish. Palps yellow. Legs yellow, except coxae I-II orange-reddish. Abdomen uniformly yellow-white. Eyes absent of setae with elongated bases forming a row on the anterior margin of the endites, infrequent on the sub-marginal part (Fig. 1B). Leg measurements: I: femur 1.3/ patella 0.6/ tibia 1.1/ metatarsus 0.6/ tarsus 0.6/ total 3.7; II: 1.1/ 0.6/ 1.0/ 0.5/ 0.4/ 3.6; III: 0.9/ 0.4/ 0.6/ 0.6/ 0.4/ 2.9; IV: 1.1/ 0.6/ 1.1/ 0.8/ 0.7/ 4.3. Sockets bases of setae elongate on leg I forming an asymmetric row on the ventral margin of the femur and the tibia (Figs 1C, J). Palpal cymbium twice the length of the bulb, embolus short and curved, half the length of the bulb (Figs 1D–F; 4A–C).

Female (paratype). Total length 3.8. Carapace 1.7 long, 1.2 wide. Coloration: cephalothorax and legs orange, except legs III-IV yellow and external border of endites brown. Abdomen grayish. Palpal endites as in male, but with fewer sub-marginal modified sochets (Fig. 1I). Leg measurements: I: femur 1.1/ patella 0.5/ tibia 0.9/ metatarsus 0.5/ tarsus 0.4/ total 3.4; II: 1.0/ 0.5/ 0.7/ 0.5/ 0.4/ 3.1; III: 0.8/ 0.4/ 0.5/ 0.6/ 0.5/ 2.8; IV: 1.2/ 0.5/ 0.9/ 0.8/ 0.5/ 3.9. Internal female genitalia with a triangular anterior margin of the hyaline membrane that covers transverse sclerotized bars, an elongate membranous anteromedian receptaculum with a wide base, and a transverse, enlarged, V-shaped dorsal fold (Figs 3G–L, 4D–E).

Other material examined. BRAZIL, **Minas Gerais**: Conceição do Mato Dentro, Cave CSS-05 (18°55'02"S, 43°25'41"W), 1♀, 12–26/VIII/2013, L. Madeira (IBSP 191297, MEV); Cave CSS-06 (18°55'02"S, 43°25'42"W), 1♀ 2 imm., 15/XII/2010-14/I/2011, L. Tunes (IBSP 191299); Cave CSS-06 (18°55'02"S, 43°25'42"W), 1 imm., 15/XII/2010-14/I/2011, C.R.A. Souza (IBSP 191300); Cave CSS-06 (18°55'02"S, 43°25'42"W), 1♀, 03-13/V/2011, K. Pinheiro (IBSP 191301, MEV); Cave SERP-118 (19°05'55"S, 43°20'34"W), 2♀, 03/XII/2013, L.G.S. Soares (IBSP 191304); Santa Bárbara, Cave SG-07 (20°02'59"S, 43°41'05"W), 1 imm., 26-30/IX/2011, K. Pinheiro (IBSP 191312); Cave SG-10 (20°03'18"S, 43°41'09"W), 2♀, 26-30/IX/2011, K. Pinheiro (IBSP 191313); Cave AP-47 (20°01'40"S, 43°40'53"W), 1♀, 31/IV-05/V-2012, G.P. Perroni (IBSP 191314), Cave AP-38 (20°01'51"S, 43°40'45"W); 1♀, 31/IV-05/V-2012, G.P. Perroni (IBSP 191317); Nova Lima, Serra da Piedade, Cave SC-11 (19°57'03"S, 43°53'28"W), 2♀ 4 imm., 18/VII- 21/XI/2014, M. P.A. Oliveira (IBSP 191296, IBSP 191298); Cave SC-07 (19°57'39"S, 43°53'28"W), 1 imm., 18/XI/2014, M.P.A. Oliveira (IBSP 191302); Cave SC-05 (19°57'05"S, 43°53'28"W), 1 imm., 21/VII/2014, M.P.A. Oliveira col. (IBSP 191303); Rio Acima, Cave VG-27 (20°06'59"S, 43°53'54"W), 1♀, 02-10/VIII/2011, I. Cizauskas et al. (IBSP 191318); Cave VG-28 (20°06'58"S, 43°53'55"W), 1 imm.,

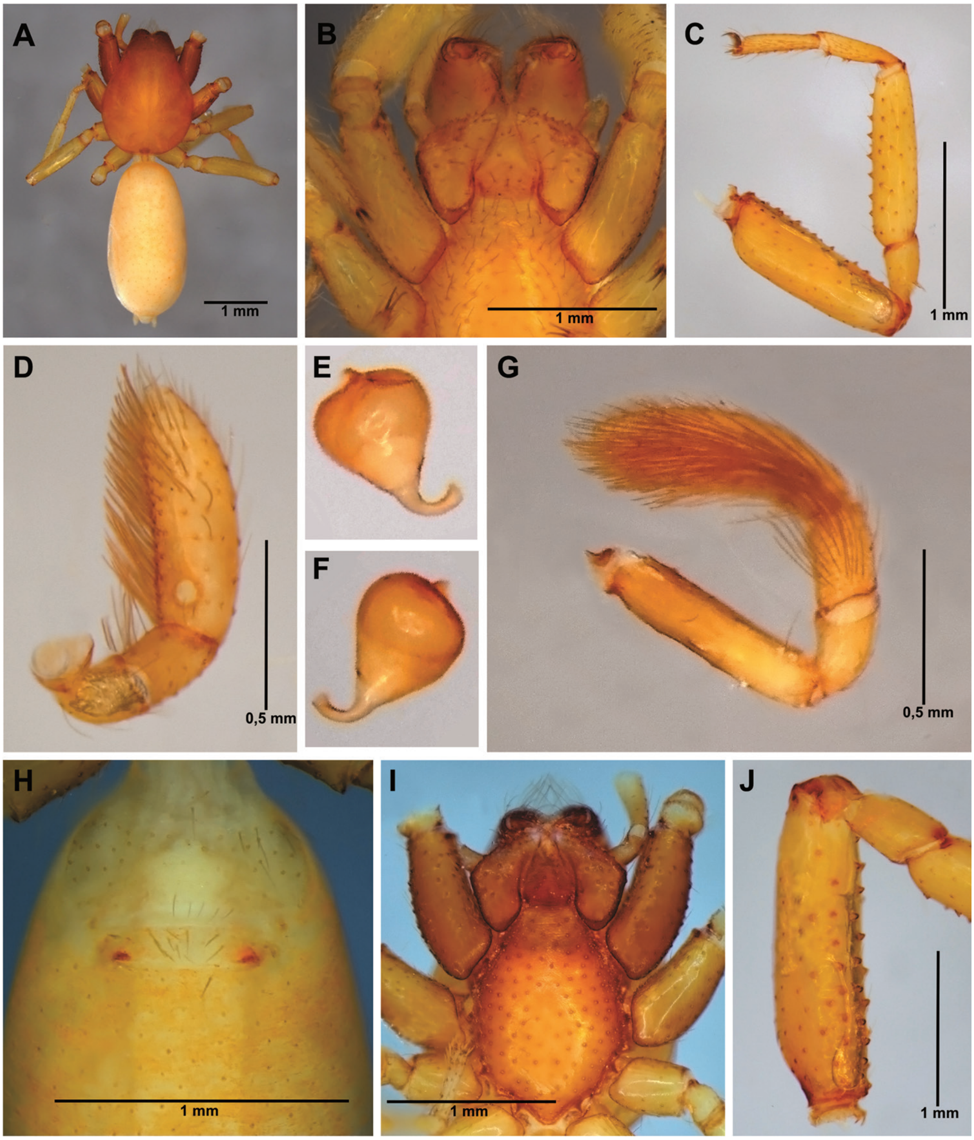

Figure 1. *Tisentnops mineiro* sp. n., male holotype (**A–G, J**), female paratype, IBSP 191294 (**H–I**). **A** habitus, dorsal view **B** mouthparts, ventral view **C** leg I, prolateral view **D** left male palp, ventral view, showing alveolus (bulb removed) **E** male bulb, prolateral view **F** same, retrolateral view **G** left male palp, prolateral view (bulb removed) **H** female external genitalia, ventral view **I** carapace, ventral view **J** male femur I, retrolateral view.

02-10/VIII/2011, I. Cizauskas et al. (IBSP 191319); Caeté, Gruta do Triangulo (19°49'03"S, 43°40'51"W), 2♀ 1 imm., 25/III/2012, M.E. Bichuette & J.E. Gallão (IBSP 191322-191323); Cave AVG-30 (19°49'21"S, 43°41'50"W), 1♀, 18/V/2013 (IBSP 191324); Cave AVG-47 (19°49'22"S, 43°41'44"W), 3♀ 6 imm., 19/XII/2012-

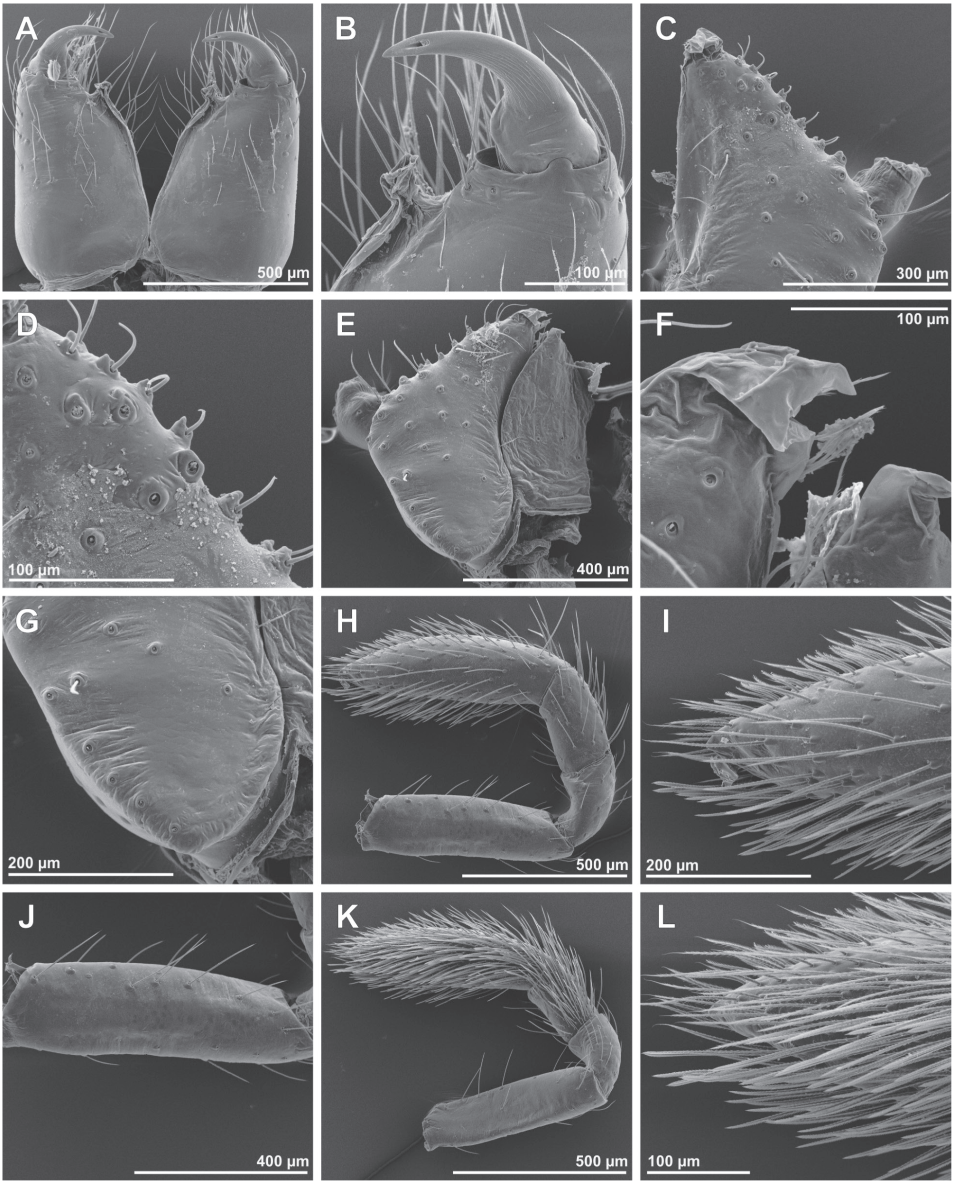

Figure 2. SEM images of *Tisentnops mineiro* sp. n., female (IBSP 191297) (**A**–**L**). **A**–**B** chelicerae, ventral view **C** left endite, ventral view **D** detail on left endite, ventral view **E** right endite and labium, ventral view **F** detail apical on right endite, ventral view **G** base of right endite, ventral view **H** left pedipalp, retrolateral view **I** tip detail of left pedipalp, retrolateral view **J** femur of left pedipalp, retrolateral view **K** right pedipalp, prolateral view **L** tip detail of right pedipalp, prolateral view.

17/V/2013 (IBSP 191325-191326); Cave AVG-66 (19°49'28"S, 43°41'34"W), 1♂, 08/IV/2014 (IBSP 191305), all collected by M. P.A. Oliveira; Itabirito, Gruta MP-10 (20°15'58"S, 43°53'16"W), 1 imm., 30/III/2012, Equipe Carste col. (IBSP 191295);

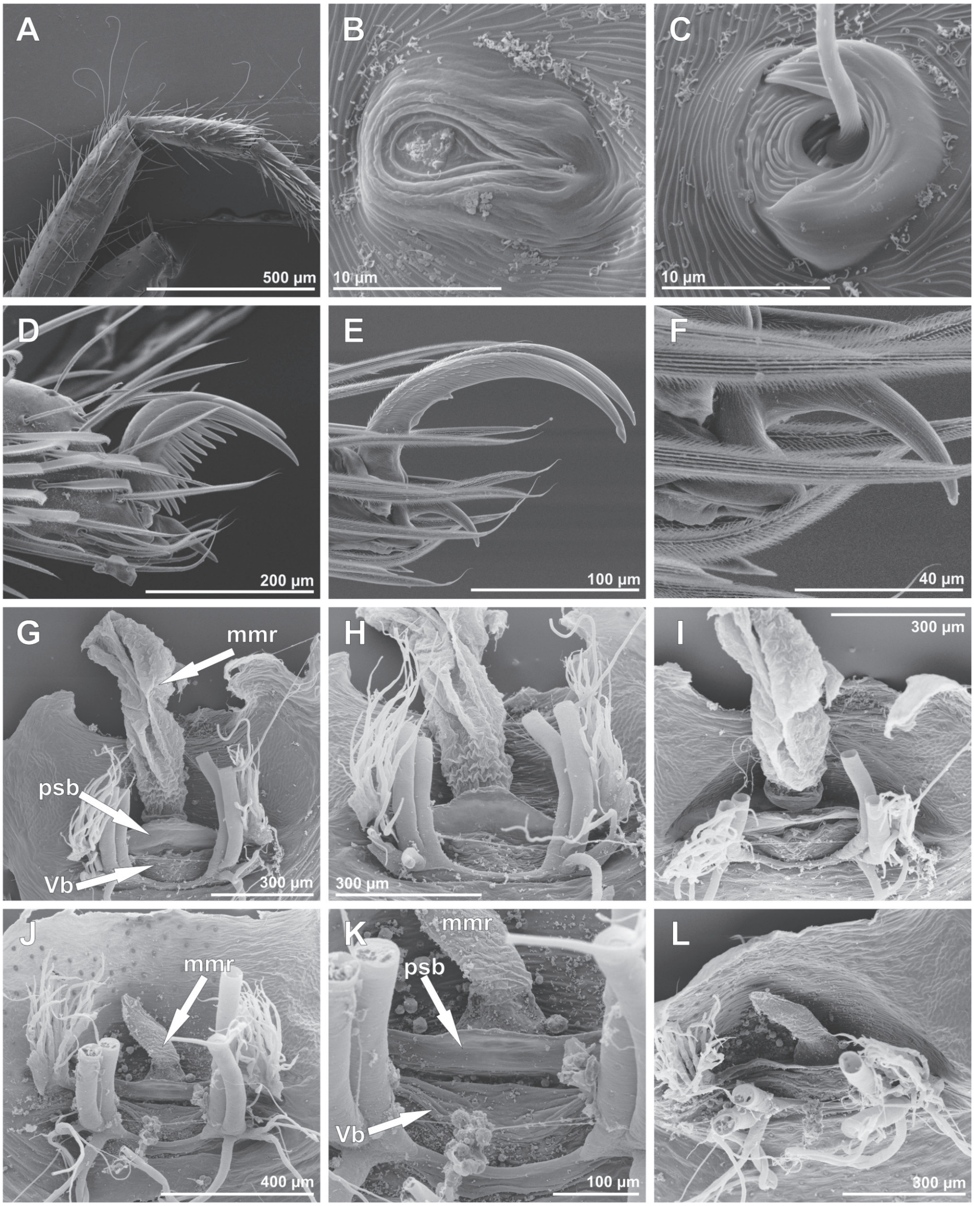

Figure 3. SEM images of *Tisentnops mineiro* sp. n., female (IBSP 191301) (**A**–**I**), female (IBSP 191297) (**J–L**). **A** right tibia, metatarsus and tarsus I, prolateral view **B** tarsal organ on leg I, dorsal view **C** tricobothrial base on leg I, dorsal view **D** claws on left tarsus I, prolateral view **E** claws on left tarsus IV, prolateral view **F** same, detail unpaired claw, prolateral view **G** female internal genitalia, dorsal view **H** same, posterior view **I** same anterior view **J** same, dorsal view **K** same, detail of receptaculum, dorsal view **L** same, anterior view (mmr = membranous anteromedian receptaculum; psb = pair of sclerotized bars; Vb = V-shaped bar).

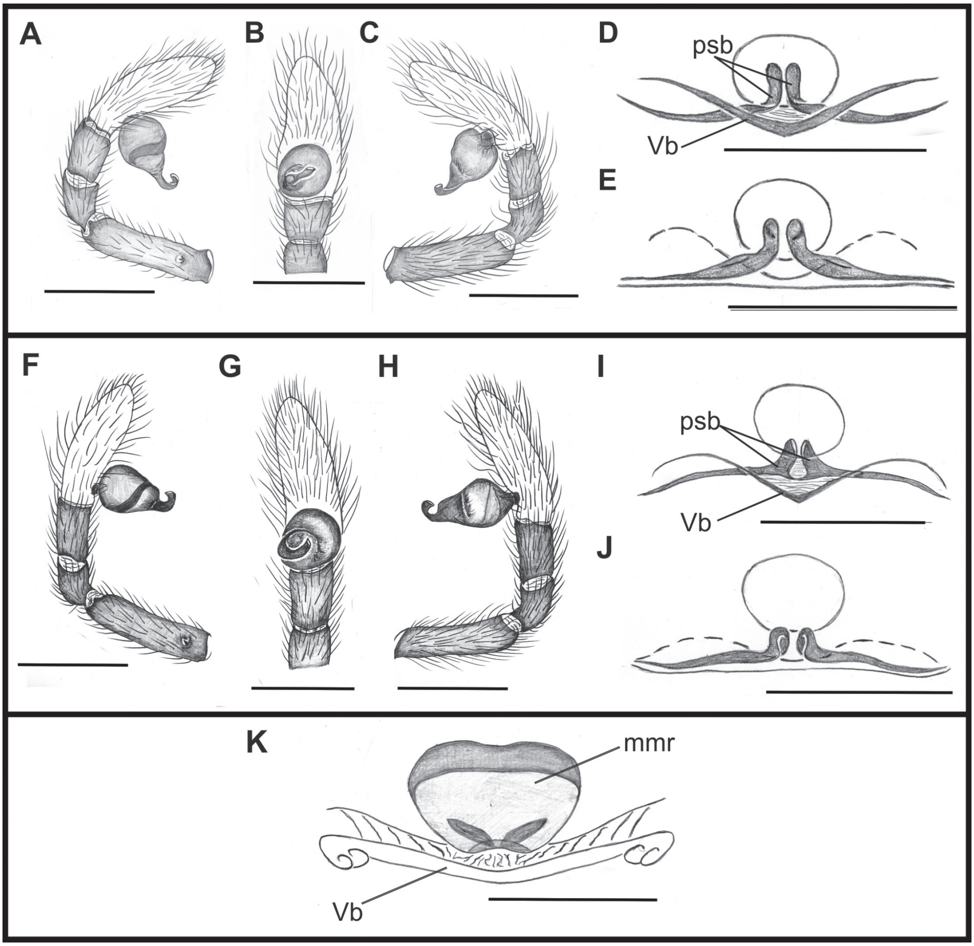

Figure 4. *Tisentnops mineiro* sp. n., male from Moeda, Minas Gerais (**A–C**), female from Santa Bárbara, Minas Gerais (IBSP 191313) (**D–E**), *Tisentnops onix* sp. n., male holotype **(F–H),** female paratype (**I–J**). *Taintnops paposo* sp. n. from Taltal, Antofagasta, Chile (**K**). **A** left pedipalp, prolateral view **B** same, ventral view **C** same, retrolateral view **D** sclerotized parts of internal genitalia, ventral view **E** same, dorsal view **F** left pedipalp, prolateral view **G** same, ventral view **H** same, retrolateral view **I** sclerotized parts of internal genitalia, ventral view **J** same, dorsal view **K** internal genitalia, ventral view (mmr = membranous anteromedian receptaculum; psb = pair of sclerotized bars; Vb = V-shaped bar). Scale bars: **A–C, F–H** = 1 mm, **D–E, I–K** = 0.5 mm.

Cave VL-29/30 (20°20'06"S, 43°56'19"W), 1♂ 1imm., 3-20/XI/2007, R. Andrade et al. (IBSP 97952); 1♀, 03-06/X/2011, J. Mascarenhas (IBSP 191320); 1♂, 29/III-03/IV/2012, J. Mascarenhas (IBSP 191321).

Distribution. Known only from the state of Minas Gerais, southeastern Brazil (Fig. 18A–B).

Natural history. All 79 specimens (7♂, 24♀, 48 immature) of *Tisentnops mineiro* sp. n. were collected in 33 caves distributed in rock outcrops in rupestrian fields found in mountain peaks of the Atlantic Forest and lowland areas of regenerated forest or grasslands. Unlike *T. onix* sp. n. from limestone caves, *T. mineiro* sp. n. was only found in iron caves. Additionally, *T. mineiro* sp. n. was found in palaeoburrows "*Paleotoca*" (natural shelter of extinct mammals, e.g. Giant Armadillos, see Bittencourt et al. 2015, figs 5–6) in Cave AP-38 in the municipality of Santa Bárbara. *T. mineiro* sp. n. were found on the ground, under rocks in aphotic zones with high relative humidity (≥ 98%). *Tisentnops mineiro* sp. n. is a troglobite spider restricted to caves from target mining areas and regions of iron formations with high economic interest.

Tisentnops onix sp. n.

http://zoobank.org/1EDE3574-70B1-43DC-8A92-0316D2C8A4CD
Figures 4F–J, 5, 17B–D

Types. Male holotype from Maciço da Gruta da Taboa, Cave 64 (19°28'35"S, 44°55'34"W), Sete Lagoas, Minas Gerais, Brazil, 26.II.2015, F. Bondezan col., deposited in IBSP 186339; female paratype from Gruta da Taboa (19°28'01"S, 44°19'0"W), Fazenda Taboa, Sete Lagoas, Minas Gerais, 31.IV.2014, L.S. Carvalho col., deposited in UFMG 15527.

Etymology. The specific name refers to the shape of the black spot on the ocular area which resembles a lozenge-shaped onyx jewel.

Diagnosis. *Tisentnops onyx* sp. n. differs from *T. mineiro* sp. n. by the presence of two eyes (Fig. 5E) and by a longer and more slender internal V-shaped dorsal fold in the female genitalia (Fig. 4F–G).

Description. Male (holotype). Total length 3.7. Carapace 1.8 long, 1.4 wide. Coloration as in *T. mineiro* sp. n., except cephalothorax red-brown, with black spot in the ocular area, and legs olive-brown. Leg measurements: I: femur 1.2/ patella 0.6/ tibia 1.0/ metatarsus 0.5/ tarsus 0.5/ total 3.8; II: 1.05/ 0.55/ 0.6/ 0.45/ 0.45/ 3.1; III: 0.9/ 0.4/ 0.6/ 0.5/ 0.5/ 2.9; IV: 1.2/ 0.6/ 1.2/ 0.6/ 0.7/ 4.3. Legs with long trichobothria. Elongate raised sockets as in *T. mineiro* sp. n. Palpal cymbium twice the length of the bulb, bulb enlarged distally, next to the base of the embolus. Embolus curved, half the length of bulb and narrow medially (Fig. 4F–H).

Female (paratype). Total length 4.7. Carapace 1.9 long, 1.4 wide. Coloration as in male, except sternum, endites and chelicerae red-brown (Fig. 5A–E). Leg measurements: I: femur 1.3/ patella 0.6/ tibia 1.0/ metatarsus 0.5/ tarsus 0.5/ total 3.9; II: 1.1/ 0.5/ 0.8/ 0.5/ 0.4/ 3.3; III: 0.9/ 0.5/ 0.6/ 0.6/ 0.4/ 3.0; IV: 1.2/ 0.5/ 1.2/ 0.9/ 0.7/ 4.5. Legs with tricobothria as in male (Fig. 5H). Elongated raised sockets as in male. External female genitalia weakly sclerotized, transparent so that receptaculum is visible (Fig. 5F). Internal female genitalia with a straight anterior margin of the hyaline membrane that covers the elongate sclerotized bars, an elongate, membranous anteromedian receptaculum with a narrow base, and a slender V-shaped dorsal fold (Fig. 4F–G).

Other material examined. None.

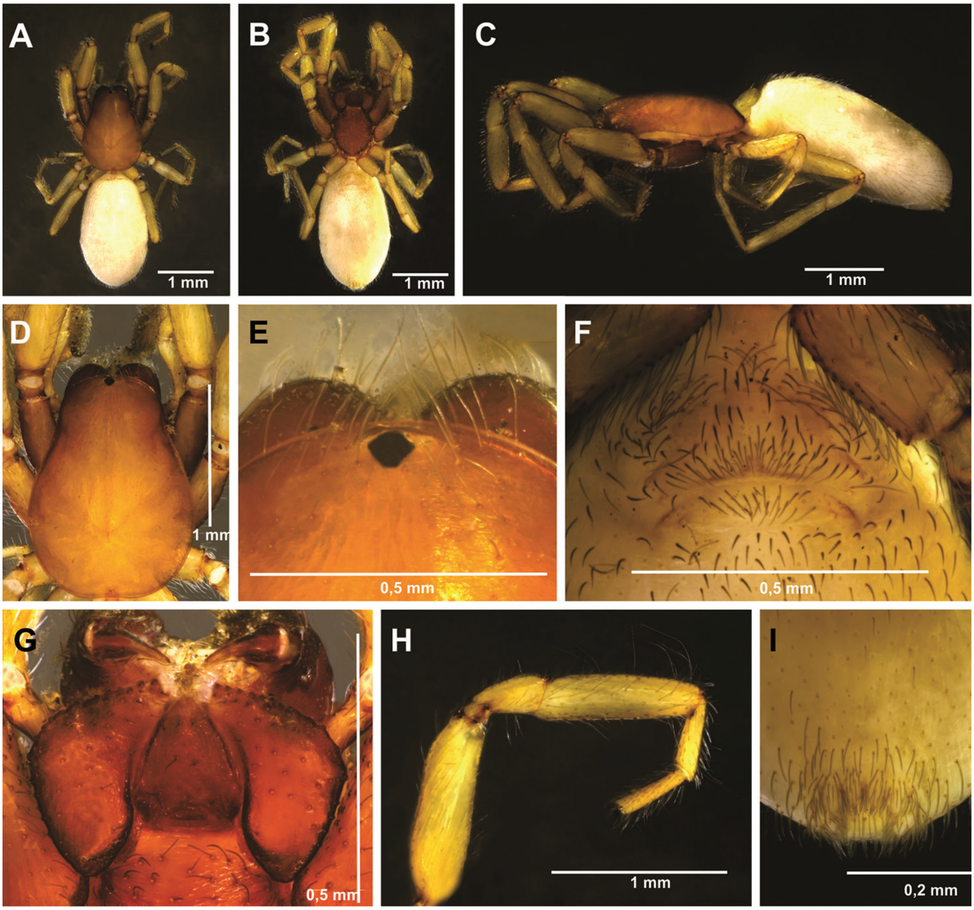

Figure 5. *Tisentnops onix* sp. n., female holotype (**A–I**). **A** habitus, dorsal view **B** same, ventral view **C** same, lateral view **D** carapace, dorsal view **E** ocular area, dorsal view **F** abdomen, genital area, ventral view **G** mouthparts, ventral view **H** leg I, prolateral view, showing long hairs **I** spinnerets, ventral view.

Distribution. Known only from the type locality in the state of Minas Gerais, southeastern Brazil (Fig. 18A).

Natural history. *Tisentnops onix* sp. n. is a troglobite spider. The female was collected from a cave, 15–20 meters from the entrance, under a rock in the aphotic area. The soil is very humid, composed of large and small rocks (Fig. 17A), is not sandy and lacks bat guano. Four people were collecting for at least 3 hours in this cave, and this was the only Caponiidae collected. Other arachnids were also captured: two species of spiders from the Ctenidae, *Enoploctenus* Simon and of *Ctenus* Keyserling, many specimens *Mesabolivar* aff. *togatus* (Pholcidae), and specimens of *Loxosceles similis* Moenkhaus (Sicariidae). Additionally, one species of *Charinus* Simon (Amblypygi) and Pseudoscorpiones of the family Cheliferidae were captured. No natural history data was obtained from the male specimen, but it was found in the aphotic area of Cave 64.

Taintnops Platnick

Taintnops Platnick, 1994b: 9 (type species by original designation *Taintnops goloboffi* Platnick).

Diagnosis. Members of *Taintnops* can be separated from other caponiids as follows: from Nopinae genera by having entire, rather than subsegmented tarsi, from *Caponia*, *Calponia*, *Carajas* gen n., *Nasutonops* gen. n. and *Notnops* by having only two eyes (Fig. 6B), from *Diploglena* and *Tisentnops* by the normal (rather than anteriorly expanded) palpal endites (Figs 6C, 7B), and from *Caponina* by the pear-shaped bulb and the short, distally situated embolus of males (Platnick 1994b, figs 22–24) and the distinct pad of shortened setae on the distodorsal surface of the female palpal tarsus (Figs 6E, 7D–E).

Description. Described by Platnick (1994b), but new details from SEM data and fresh specimens are presented here. Two eyes surrounded by a black area (Fig. 6B). Clypeus with at least six pairs of long setae (Figs 6B–C). Chelicerae (Fig. 7A) with short tooth-shaped tip on median lamina and white membranous lobe opposite the tip of the cheliceral fang. Endites acuminate, converging, not touching and not protuberant posteriorly (Figs 6C, 7B), serrula distal, with a single tooth row (Fig. 7C). Labium covered with plumose setae (Fig. 7B). Sternum oval, cuticle with long black setae (Fig. 6C). Female palp with dense patch of setae prolaterally and distinct distodorsal pad of shortened setae (Figs 6E–F, 7D–E). Legs pilose (Figs 6D, G), paired claws I-II with six teeth, and unpaired claw short without teeth (Fig. 7F), paired claws III-IV with five teeth (Fig. 7I), and unpaired claws short. Tarsal organ not found. Tibiae with row of five dorsal and two prolateral trichobothria; metatarsi and tarsi with two prolateral and two dorsal pairs of trichobothria, with a semicircular rim bearing few ridges (Fig. 7G), elongate and slightly sulcate sensilla (Fig. 7H). Six spinnerets in typical caponiid arrangement; anterior laterals greatly reduced and the same length as posterior laterals, females apparently with one major ampullate gland spigot and two smaller piriform gland spigots; posterior medians with single, enlarged, medially situated spigot presumed to serve the minor ampullate gland and 10–12 smaller, more peripheral spigots, arranged in a ring, presumed to serve the aciniform glands; posterior laterals with peripheral ring of 8–10 presumed aciniform gland spigots (Fig. 6I–J). External female genitalia with weakly sclerotized anterior plate. Internal female genitalia consisting of large, oval anteromedian membranous receptaculum, and V-shaped posterior bar with wide ends (Fig. 16E; Platnick 1994b: fig. 25).

Taintnops paposo sp. n.

http://zoobank.org/A882F6D3-9571-41F0-855E-30D498B58262
Figures 6, 7, 16E

Types. Holotype and paratype females from Reserva Nacional Paposo (24°57,82'S, 70°27,961'W), 52m asl, Taltal, Antofagasta Province, Chile, 16/VII/2012, A.D.

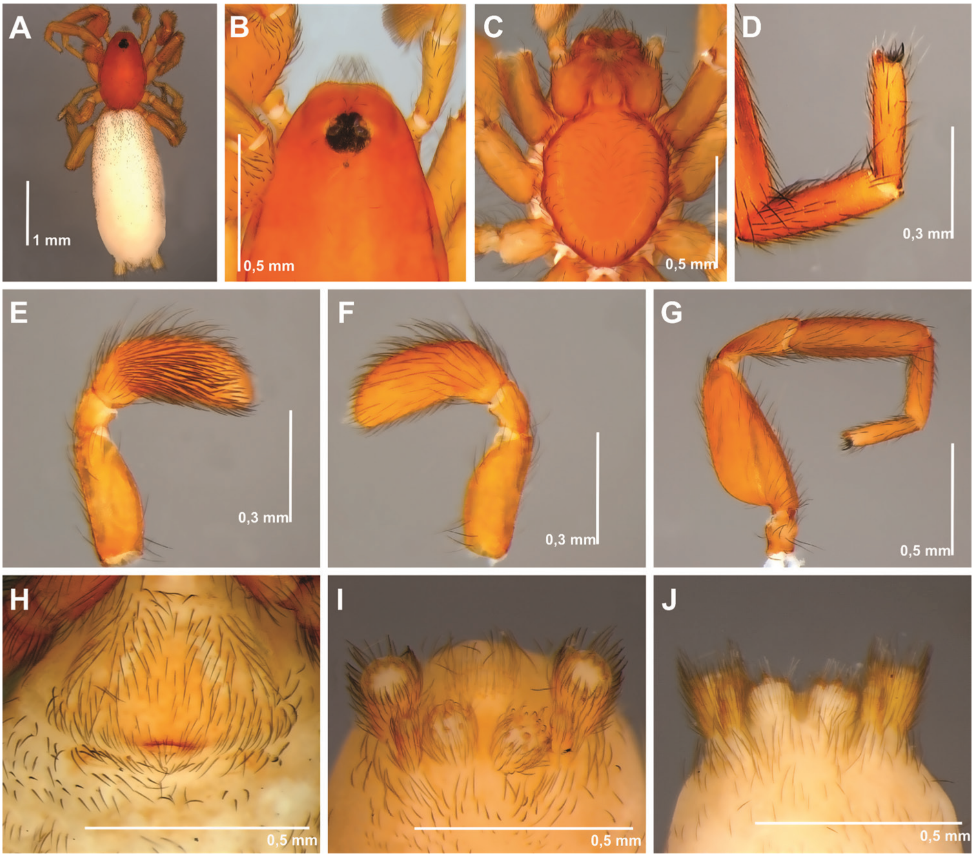

Figure 6. *Taintnops paposo* sp. n. from Taltal, Antofagasta, Chile, female paratype (**A–J**) **A** habitus, dorsal view **B** carapace, ocular area, dorsal view **C** carapace, ventral view **D** leg I, metatarsus and tarsus distal, retrolateral view **E** pedipalp, prolateral view **F** same, retrolateral view **G** leg I, prolateral view **H** genital area, ventral view **I** spinnerets, posterior view **J** same, ventral view.

Brescovit, A.J. Santos & A. Taucare-Rios col., deposited in IBSP 166983 and 166984, respectively.

Etymology. The specific name is a noun in apposition taken from the type locality.

Diagnosis. Females differ from those of *Taintnops goloboffi* Platnick (see Platnick 1994b: fig. 25) by the oval anteromedian receptaculum lacking posterior extensions (Fig. 16E)

Description. Male. Unknown.

Female (holotype). Total length 3.9. Carapace 1.3 long, 0.8 wide. Carapace, mouthparts and sternum reddish. Border of eyes black. Legs and pedipalp orange. Abdomen uniformly creamy white, with epyginal area orange (Fig. 6H). Leg measurements: I: femur 0.85/ patella 0.4/ tibia 0.55/ metatarsus 0.45/ tarsus 0.3/ total 2.55;

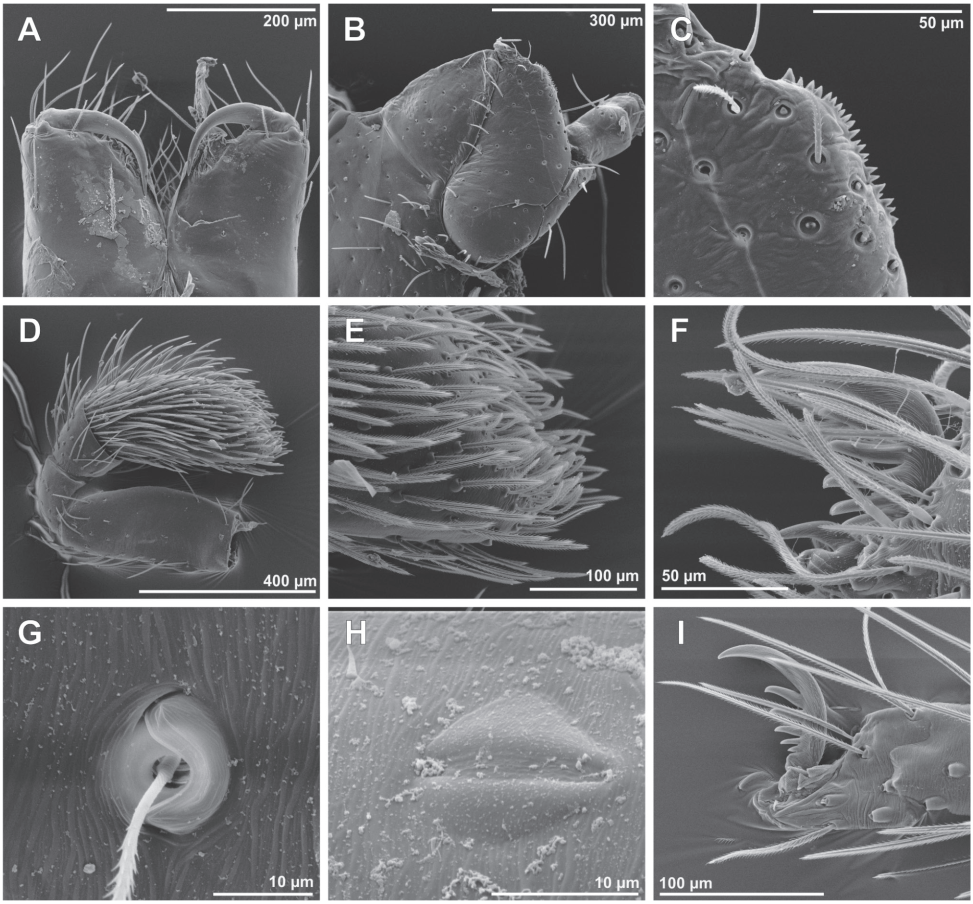

Figure 7. SEM images of *Taintnops paposo* sp. n., female paratype (**A–I**) **A** chelicerae, ventral view **B** left endite and labium, ventral view **C** left serrula, ventral view **D** left pedipalp**,** prolateral view **E** same, distal area, prolateral view **F** paired claws on right leg I, prolateral view **G** trichobotria base on leg II, dorsal view **H** sensilla on leg II, dorsal view **I** paired claws on right leg IV, prolateral view.

II: 0.75/ 0.4/ 0.55/ 0.45/ 0.25/ 2.40; III: 0.6/ 0.3/ 0.4/ 0.35/ 0.3/ 1.95; IV: 0.9/ 0.4/ 0.7/ 0.6/ 0.35/ 2.45. External female genitalia with weakly sclerotized anterior plate, and posterior border of genital opening strongly sclerotized (Fig. 6H). Internal genitalia with oval and elongate membranous anteromedian receptaculum not extending posteriorly, lacking sclerotized posterior extensions (Fig. 16E).

Other material examined. None.

Distribution. Known only from Taltal area, in the Antofagasta Region.

Natural history. Both specimens were collected under rocks during the day. Silk retreats were not observed in the area.

Nasutonops gen. n.

http://zoobank.org/DB6219F6-3347-4AFC-A52B-278E32FA652D

Type species. *Nasutonops xaxado* sp. n.

Etymology. The generic name comes from the Latin words *nasutus* (with a large nose) combined with *nops* (less eyes), and is masculine in gender.

Diagnosis. Males and females can be easily distinguished from all other known caponiids by the presence of a clypeal horn, projected distally (Fig. 8A, C, J). The genus resembles species of *Caponina* by having the palp with a globose bulb and an elongate and curved embolus in males (see Platnick 1994, figs 26–28) and by having a similar pair of boomerang-shaped sclerotized bars in the female genitalia (see Platnick 1994, figs 22–25); however, it differs by the flattened base of the embolus originating from the distal area of the male bulb (Fig. 11D–E), rather than the median area as in *Caponina*. The female differs by the strongly sclerotized transverse internal fold of the female genitalia, which is observed by transparecy on the posterior border of the anterior plate (Figs 8K, 11A–B, F–I; 12H–J), which is not apparent in any *Caponina* species. These three structures support the monophyly of *Nasutonops*.

Description. Moderate-sized caponiids with six eyes (Fig. 8A, G–H, J). Carapace oval, anteriorly narrowed to half its maximum width, pars cephalica depressed behind cephalic area, depressed between coxa of endite and coxa I, pars thoracica medially higher than laterally or posteriorly, gradually sloping laterally and posteriorly (Fig. 8B); cuticle smooth; few dorsally directed strong bristles on the clypeal area; carapace smooth; thoracic groove almost absent (Fig. 8A, G). Clypeal horn, distally conic, striated anteriorly and posteriorly, shorter in females (Figs 8C, J; 9A–F; 10E–F, H–J). Six eyes, medians largest and more elevated than laterals (Figs 8C, 9A–B), dark, separated by almost their radius, surrounded by black pigment; laterals white and oval, posteriors half the size of anteriors (Figs 8J, 10I). Cheliceral paturon with long and strong bristles medially (Figs 9E, 10F); base of fang unmodified; median lamina short, with irregular anteromedian tip; most of the space between the lamina and base of fang occupied by white membranous lobe; lateral surface with large stridulatory ridges in males and females (Figs 9G; 10G), pick on prolateral side of palpal femur, triangular, situated at approximately one-fifth of femur length (Figs 10K, 11C–D). Endites convergent, acuminate, not touching, covered with many long basal setae that shorten distally (Fig. 8I), with strong and long distal serrula consisting of a single tooth row with more than 20 teeth (Fig. 9H). Labium triangular, fused to sternum, covered with many scattered setae (Fig. 8H–I); labrum short, narrow, slightly elevated. Sternum longer than wide, smooth, without radial furrows between coxae, covered with scattered long setae, not fused to carapace (Fig. 8I); cephalothoracic membranes without epimeric sclerites, but long triangular sclerites extend from sternum between coxae I and II, II and III, and III and IV, shorter triangles extend to each coxae. Leg formula 4123; legs without spines; metatarsi and tarsi entire, without subsegmentation or membranous processes;

tarsi with three claws; paired claws with approximately ten teeth (more on leg I-II), distal teeth largest; unpaired claw shorter than paired ones, with five minuscule teeth (Fig. 10A–B). Tibiae with trichobothria in a double row, metatarsi and tarsi with trichobothria in single row, bases almost smooth, with strong external border (Fig. 10C); tarsal organ exposed, oval, not elevated, consisting of two oval, sclerotized laminae (Fig. 10D); female palpal tarsus elongate, prolateral surface densely covered with setae, without claw (Figs 10L; 12C). Abdomen immaculate and pilose; epigastric plate sclerotized (Figs 8G–H; 12A–B), two pairs of small respiratory spiracles. Six spinnerets (Figs 8L, 12G) in typical caponiid arrangement, anterior laterals shorter than posterior laterals, with one major ampullate gland spigot and at least three smaller piriform gland spigots; posterior medians with single, very thick, medially situated spigot presumed to serve minor ampullate gland, and 5-6 smaller, more peripheral spigots arranged in a ring, presumed to serve aciniform glands; posterior laterals with 8-10 central and peripheral aciniform gland spigots. Male palpal femur twice the length of the tibia, patella shorter than the tibia, unmodified; cymbium ovoid, prolateral surface densely covered with strong setae; bulb globose; embolus long, curved at base, flattened, with small teeth in the distal third, narrowed distally, with sinuous tip (Figs 8B–F; 9I–L). External female genitalia with large, rectangular, sclerotized anterior plate, and postepigastric scutum represented by a pair of narrowed sclerites, represented by a transparent area on an internal strongly sclerotized trasverse fold on the posterior border of the anterior plate (Figs 8K; 12 F). Internal female genitalia consist of a pair of boomerang-shaped sclerotized bars, that may or may not converge anteriorly, associated with the uterus externus short but with a wide base occupying almost the entire width of the sclerotized bars; strongly sclerotized transverse fold runs along nearly all of the epigastric area, reaching the posterior ends of the sclerotized bars (Figs 11A–B, F–I; 12H–J).

Distribution. Known only from Brazilian Caatinga in the states of Bahia and Pernambuco, Brazil.

Nasutonops xaxado sp. n.

http://zoobank.org/C40D5196-C43E-4B93-8EF6-7CA9F0BAA242

Figures 8, 9, 10, 11A–B, 12H–J

Types. Male holotype and female paratype from Serra Talhada (7°59'9"S, 38°17'45"W), Pernambuco, Brazil, 2008-2009, H. Amorin col., deposited in IBSP 166987 and 166988, respectively.

Etymology. The specific name is a nickname of the type locality, known as the ‘’Capital do Xaxado’’. The Xaxado is a popular dance in this region.

Diagnosis. Females of *Nasutonops xaxado* sp. n. resemble those of *N. chapeu* sp. n. in lacking the connection of a pair of sclerotized bars in the female internal genitalia (Fig. 11F–G), but can be distinguished by the enlarged anterior ends of the pair of elongate sclerotized bars and the short posterior ends (Fig. 11A–B). Males differ by their shorter embolus and curved tip (Figs 8F, 9J–K).

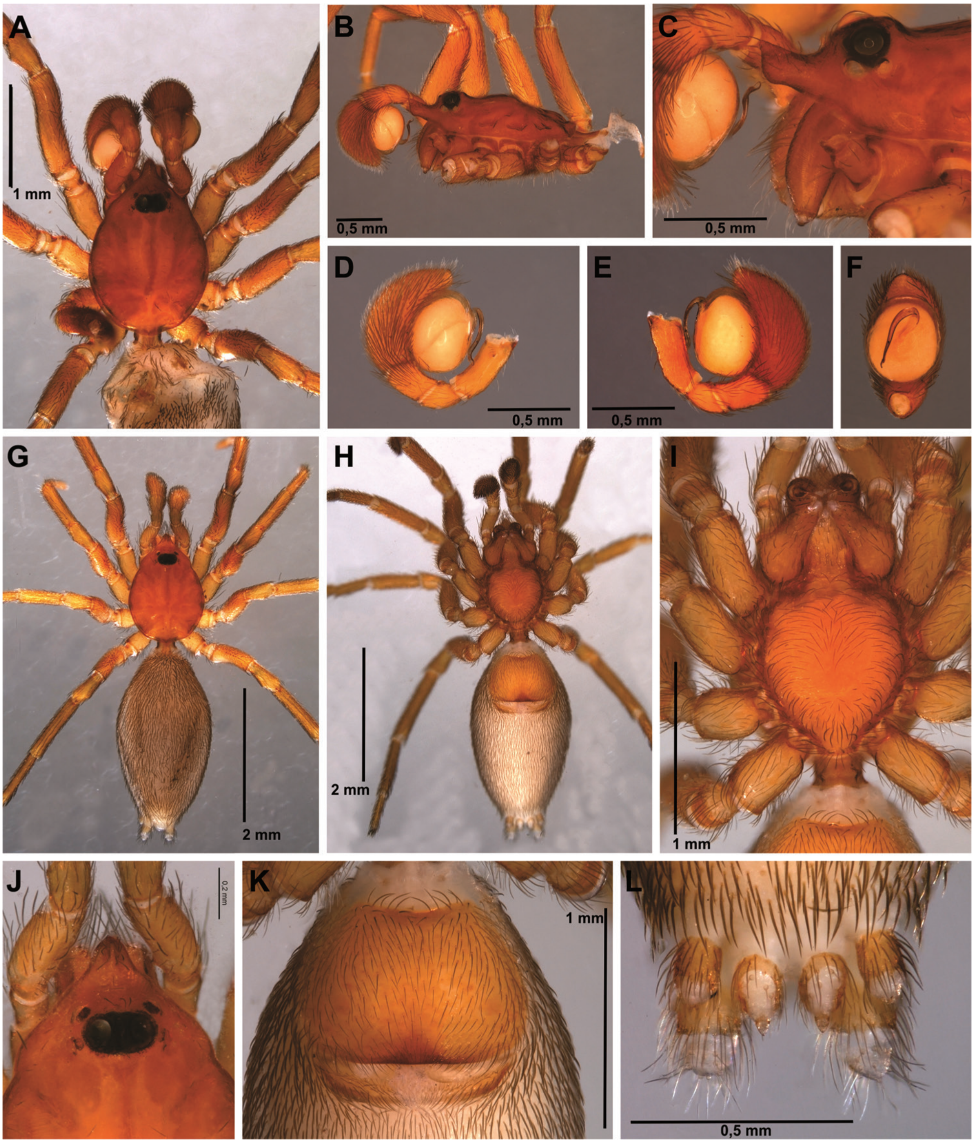

Figure 8. *Nasutonops xaxado* sp. n., male from Serra Talhada, Pernambuco (**A–F**) female, same locality (**G–L**) **A** habitus, dorsal view **B** carapace, lateral view **C** ocular area, lateral view **D** left pedipalp, prolateral view **E** same, retrolateral view **F** same, ventral view **G** habitus, dorsal view **H** same, ventral view **I** carapace, ventral view **J** ocular area, dorsal view **K** genital area, ventral view **L** spinnerets, ventral view.

Male (Holotype). Total length 3.80, with clypeal horn. Carapace 1.7 long, 1.2 wide. Coloration: carapace orange-reddish, except apex of endites and labium white, legs and palps orange. Eye median diameters 0.3, interdistances 0.15. Leg measurements: I: femur .1.1/ patella 0.5/ tibia 0.8/ metatarsus 0.7/ tarsus 0.4/ total 3.5; II: 1.1/ 0.5/ 0.7/ 0.7/ 0.4/ 3.4; III: 0.9/ 0.5/ 0.6/ 0.6/ 0.5/ 3.1; IV: 1.1/ 0.6/ 1.0/ 0.9/ 0.6/

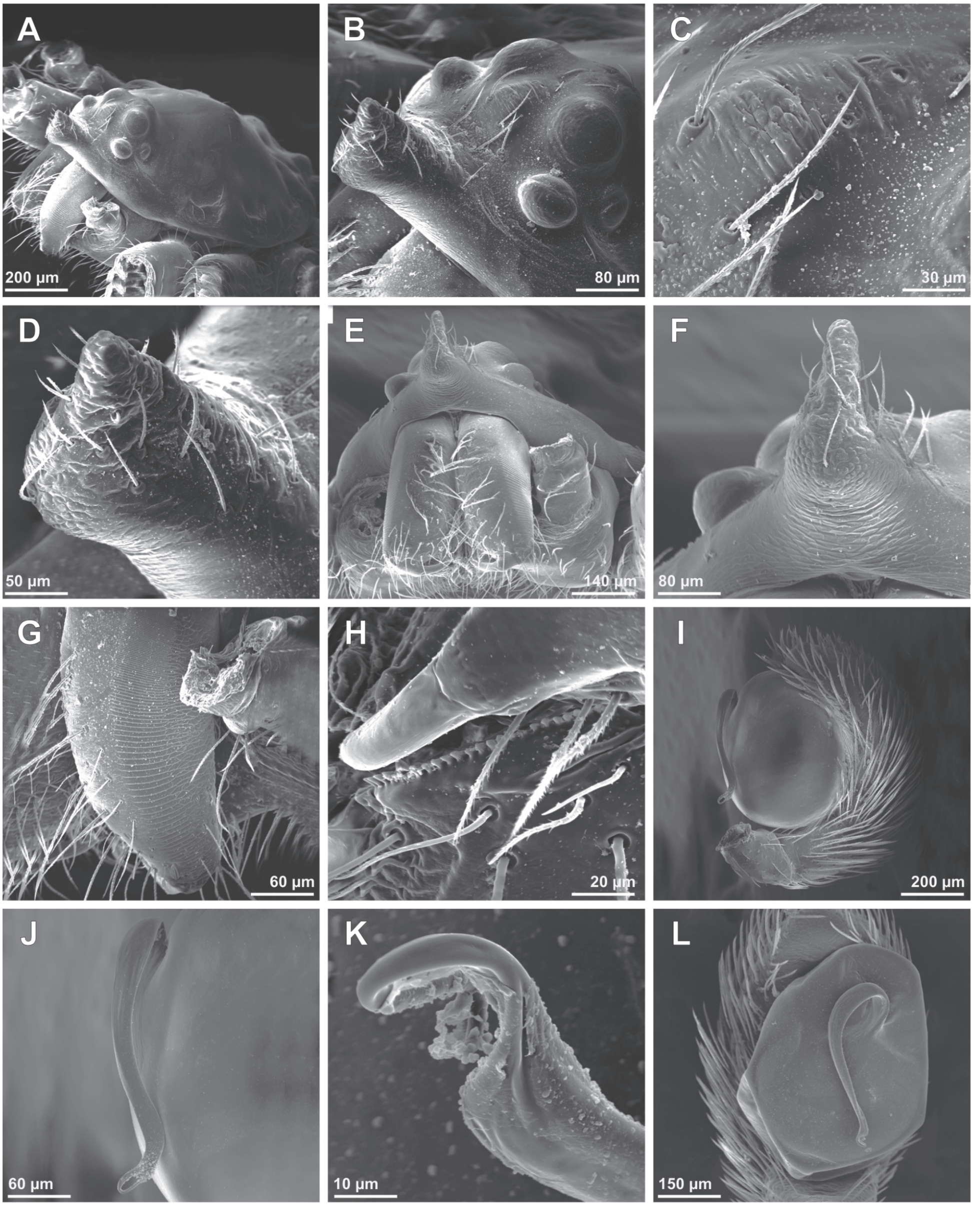

Figure 9. SEM images of *Nasutonops xaxado* sp. n., male from Serra Talhada, Pernambuco (**A–L**) **A** carapace, lateral oblique view **B** ocular area, lateral oblique view **C** striated area between posterior eyes, detail, dorsal view **D** clypeal projection, lateral view **E** same with chelicerae, anterior view **F** same, anterior view **G** chelicerae, stridulatory area, lateral view **H** serrula, lateral view **I** left pedipalp, retrolateral view **J** embolus, retrolateral view **K** tip of embolus, distal area **L** bulb, ventral view.

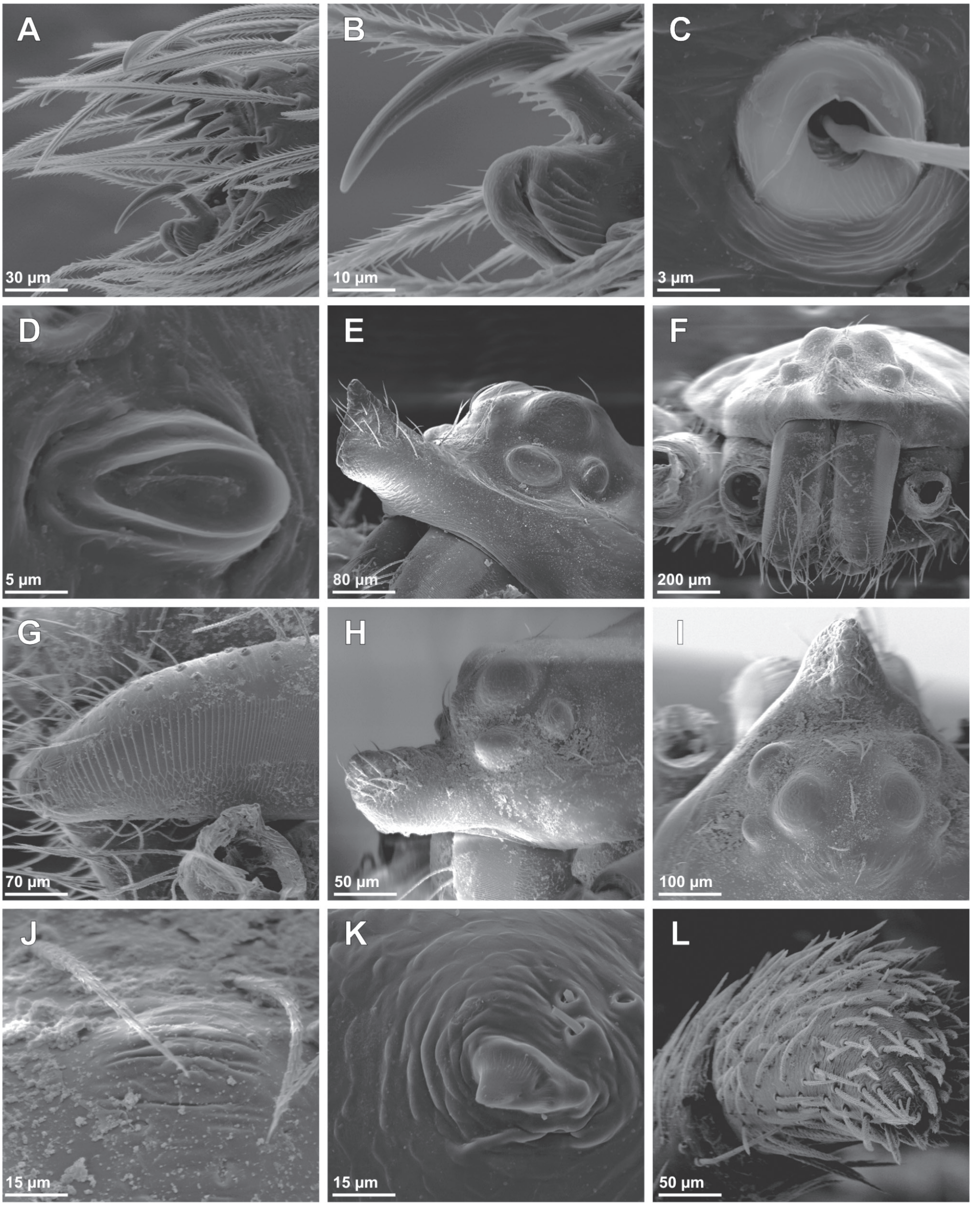

Figure 10. SEM images of *Nasutonops xaxado* sp. n., male (**A–D**) and female (**E–L**) from Serra Talhada, Pernambuco. **A** paired claws on right leg II, prolateral view **B** unpaired claw on right leg II, prolateral view **C** trichobothria base on right leg II, dorsal view **D** tarsal organ on right leg II, dorsal view **E** ocular area, lateral oblique view **F** same, anterior view **G** chelicerae, stridulatory area, lateral view **H** clypeal projection, lateral view **I** same, dorsal view **J** striated area between posterior eyes, detail, dorsal view **K** stridulatory pick on left pedipalp, prolateral view **L** distal area of left pedipalp, anterior view.

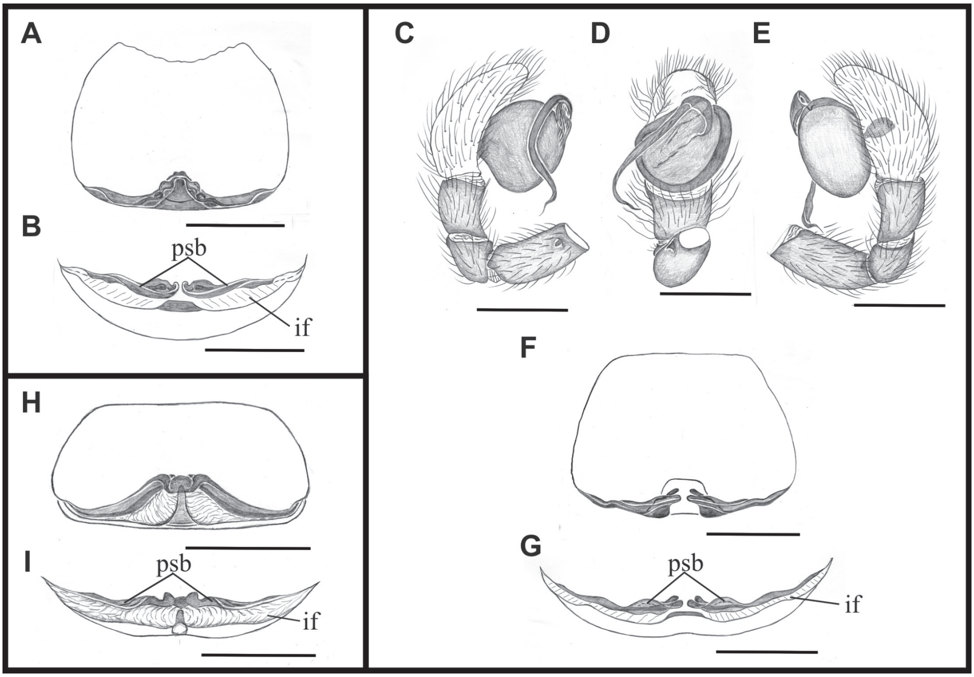

Figure 11. *Nasutonops xaxado* sp. n., female from Serra Talhada, Pernambuco (**A–B**) *Nasutonops chapeu* sp. n., male and female from Irecê, Bahia (**C–G**), *Nasutonops sincora* sp. n., female from Contendas do Sincorá, Bahia (**H–I**) (**A–B, F–G, H–I**) female internal genitalia **A, F, H** dorsal view **B, G, I** anterior view (**C–E**) male palp, A prolateral view **B** ventral view **D** prolateral view (if = internal transversal fold, psb = pair of sclerotized bars). Scale bars: **A–G** 0.5 mm.

4.2. Abdomen gray with epiandric plate and spinnerets orange. Palpal cymbium not covered with thick layer of distal setae (Fig. 9I).

Female (allotype). Total length 4.5, with clypeal horn. Carapace length 1.7 width 1.2. Coloration as in male. Eye median diameters 0.3, interdistances 0.2. Leg measurements: I: femur .1.0/ patella 0.5/ tibia 0.8/ metatarsus 0.6/ tarsus 0.5/ total 3.4; II: 1.0/ 0.5/ 0.7/ 0.7/ 0.5/ 3.4; III: 0.9/ 0.4/ 0.6/ 0.6/ 0.4/ 2.9; IV: 1.0/ 0.5/ 0.8/ 0.9/ 0.5/ 3.7. Internal genitalia with enlarged anterior ends and short posterior ends of the pair of sclerotized bars (Figs 11A–B, 12H–J).

Note. Left metatarsus and tarsus IV of male absent.

Other material examined. BRAZIL: **Pernambuco**, Serra Talhada (7°59'9"S, 38°17'45"W), 1♂ 1♀, 2008-2009, H. Amorin col. (IBSP 166989; 166990, respectively, both partially used in SEM).

Distribution. Known only from the type locality in the Brazilian Caatinga.

Natural history. The specimens were collected in soil with pitfall traps.

Nasutonops chapeu sp. n.

http://zoobank.org/CDDB6E7F-32DE-488A-9E4A-6F9E83D74711
Figure 11C–G

Types. Male holotype from Parque Estadual Morro do Chapéu (11°29'19,2"S, 41°15'27,6"W), Morro do Chapéu, Bahia, 21.I.2012, 1097 m asl., I.L.F. Magalhaes et al. col, and female allotype from Área da Mineradora Galvani, Irecê (11°18'14"S, 41°51'21"W), Bahia, 27.VI.-27.IX.2011, M.C. Nunes col., deposited in IBSP 161985 and 161986, respectively.

Note. Although the male and female were not collected from the exact same locality, both specimens were collected near one another in the state of Bahia, and they have the same body coloration.

Etymology. The specific name is an apposition to the type locality.

Diagnosis. Females of *Nasutonops chapeu* sp. n. resemble those of *N. xaxado* sp. n. in lacking the connection of the pair of elongate sclerotized bars in the female internal genitalia (Fig. 11F–G), but can be distinguished by the narrow anterior ends and slender posterior ends of the pair of sclerotized bars (Fig. 11F–G). Males differ by the elongate embolus with a slender and sinuous tip (Fig. 11C–E).

Description. Male (holotype). Total length 3.2, with clypeal horn. Carapace 1.3 long, 1.05 wide. Coloration of body as in *N. xaxado* sp. n., except abdomen grayish. Eye median diameters 1.0, inter distances 0.6. Leg measurements: I: femur 1.0/ patella 0.4/ tibia 0.75/ metatarsus 0.55/ tarsus 0.3/ total 3.0; II: 0.9/ 0.4/ 0.65/ 0.55/ 0.3/ 2.8; III: 0.75/ 0.35/ 0.5/ 0.5/ 0.25/ 2.35; IV: 0.95/ 0.4/ 0.8/ 0.7/ 0.45/ 3.3.

Female (allotype). Total length 4.3, with clypeal horn. Carapace 1.55 long, 1.1 wide. Coloration as in male. Eye median diameters 1.0, inter distances 0.8. Leg measurements: I: femur 1.1/ patella 0.45/ tibia 0.75/ metatarsus 0.65/ tarsus 0.4/ total 3.35; II: 1.0/ 0.4/ 0.75/ 0.6/ 0.45/ 3.2; III: 0.8/ 0.35/ 0.6/ 0.6/ 0.35/ 2.7; IV: 1.1/ 0.55/ 0.9/ 0.9/ 0.5/ 3.95. Internal genitalia with long pair of elongate sclerotized bars with narrow anterior ends and slender posterior ends, and with an enlarged area on the anterior third (Fig. 11G).

Other material examined. None.

Distribution. Known only from the type locality in the Brazilian Caatinga from the state of Bahia.

Nasutonops sincora sp. n.

http://zoobank.org/22845E0E-E92D-4F8C-B8D9-36CDD2FC3BC2
Figures 11H–I, 12A–G

Types. Female holotype from Floresta Nacional Contendas do Sincorá (13°46'–14°00'S, 41°03'–41°10'W), Contendas do Sincorá, Bahia, Brazil, X.2007–X.2008, Y.G. Santos col., deposited in IBSP 126918.

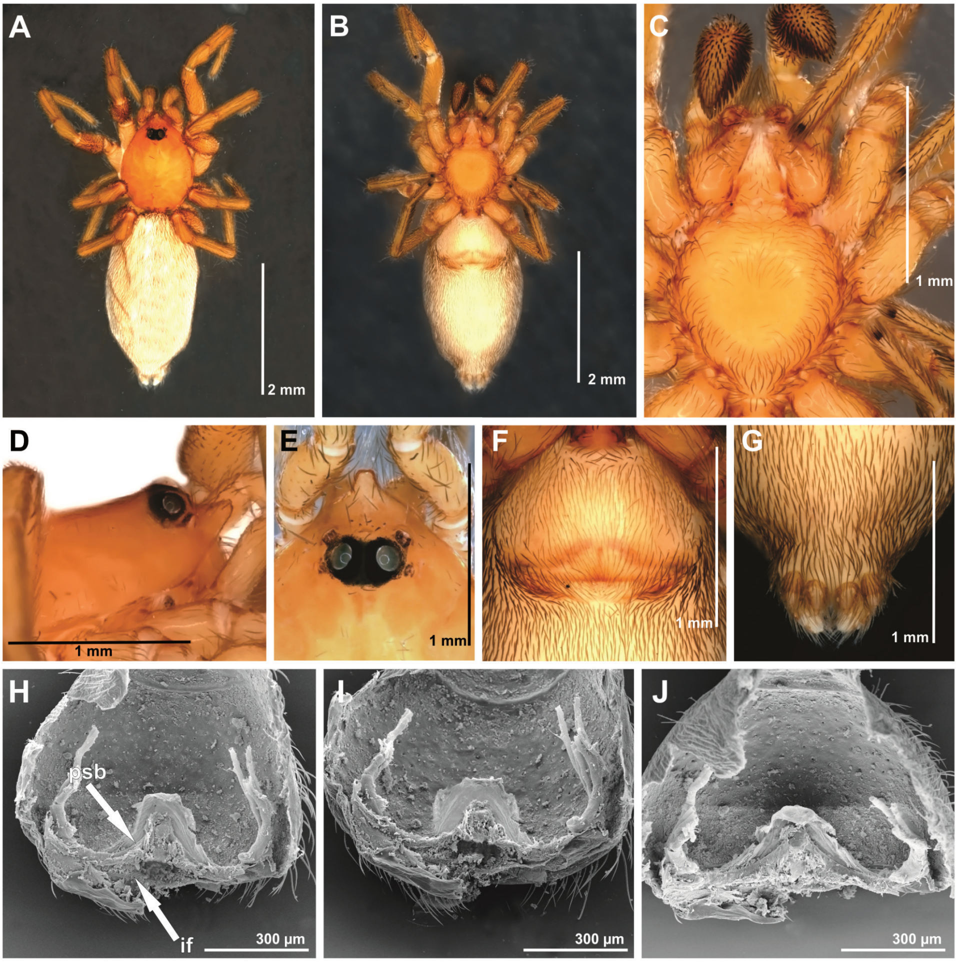

Figure 12. *Nasutonops sincora* sp. n., female from Contendas do Sincorá, Bahia (**A–G**). **A** habitus, dorsal view **B** same, ventral view **C** carapace, ventral view **D** ocular area, lateral view **E** same, dorsal view **F** genital area, ventral view **G** spinnerets, ventral view. *Nasutonops xaxado* sp. n. (**H–J**) **H** SEM images of internal genitalia, dorsal view **I** same, posterior view **J** same, anterior view (if = internal transversal fold; psb = pair of sclerotized bars). Scale bars: **A–G** 0.5 mm.

Etymology. The specific name is an apposition to the type locality.

Diagnosis. The female of *Nasutonops sincora* sp. n. differs from others females of the genus by the elevated area of the pair of transverse elongate sclerotized bars that are connected anteriorly, forming a rounded, small plate (11H–I) in the female genitalia.

Description. Male. Unknown.

Female (holotype). Total length 4.5, with shortest clypeal horn. Carapace 1.7 long, 1.2 wide. Coloration: cephalothorax and legs orange, ocular area black, abdomen cream, covered with gray hairs, genital area orange and spinnerets yellow (12 A–B). Clypeal horn truncate at tip (Fig. 12D–E). Eye median diameters 0.12, interdistances 0.8. Leg measurements: I: femur 1.1/ patella 0.55/ tibia 0.8/ metatarsus 0.65/ tarsus 0.45/ total 3.55; II: 1.05/ 0.5/ 0.8/ 0.6/ 0.4/ 3.35; III: 0.75/ 0.4/ 0.55/ 0.65/ 0.4/ 2.75; IV: 1.25/ 0.55/ 1/ 0.8/ 0.5/ 4.1. External genitalia with receptacula visible through transparent area (Fig. 12F). Internal genitalia with a pair of transverse elongate sclerotized bars, connected anteriorly, forming a rounded small plate; internal fold between the pair of sclerotized bars (Fig. 11I).

Other material examined. None.

Distribution. Known only from the type locality in the Brazilian Caatinga from the state of Bahia.

***Carajas* gen. n.**

http://zoobank.org/90E1A654-6D56-4276-97A7-6C85489B7975

Type species. *Carajas paraua* sp. n.

Etymology. The generic name is an apposition to the type locality where all known specimens were collected and is masculine in gender.

Diagnosis. Members of *Carajas* gen. n. can be easily separated from other caponiid genera by having anteriorly and posteriorly strongly projected endites (Figs 13J, 14D), a very short cheliceral fang (Fig. 15D–E), absence of unpaired claws on all legs, and the posterior paired claws with distal tip thickened and covered with dense and short bristles (Fig. 14G, 15H).

Description. Moderate-sized caponiids (Fig. 13A, I). Carapace oval, anteriorly narrowed to less than half of its maximum width, pars cephalica rounded, pars thoracica flat medially and sloping posteriorly; cuticle of carapace smooth, covered with short and uniform setae; clypeus almost smooth; thoracic groove inconspicuous, almost obsolete (Fig. 13A, I). Eyes absent (Figs 13A, I; 14A, 15A). Cheliceral paturon with long, weak bristles, mainly on frontal area; base of fang unmodified; fang short with large opening, median lamina short, occupying a small space by the white membranous lobe; lateral surface with small sulci of stridulatory ridges (Fig. 14C), pick small on prolateral basal side of palpal femur (Fig. 16A). Endites convergent, strongly projected, extending anteriorly far beyond the anterior margin of the labium, and posteriorly widened, extending far beyond the posterior margin of the labium (Figs 13J, 14D), covered with many small and long setae (Fig. 14D–E), with strong distal serrula consisting of a single tooth row. Labium triangular, strongly fused to sternum, not invaginated at base, covered with a few scattered setae, distal area hyaline (Figs 13B, 14E); labrum elongate, narrow, subtriangular, distally slightly elevated. Sternum longer that wide, without radial furrows between coxae, covered with small and uniform setae, not fused to carapace, with sclerotized lateral and posterior borders (Figs 13B, J; 14B); cephalothoracic membranes without epimeric sclerites, but short triangular sclerites extend from the sternum between coxae of endites and coxa I, I and II, II and III, and III and IV, shorter triangles extend to each coxae, straighter on coxae III and IV, posterior border triangular between coxae IV (Fig. 13B, J). Legs formula 4213, without spines, metatarsi and tarsi entire, without subsegmentation or membranous processes, tarsi with two claws, lack unpaired claws, surrounded with elongate hairs; paired claws I-II with approximately six teeth, distal tip of claw elongate (Fig.15G), III-IV weakly curved, with 3-4 short and well-separated teeth, distal tip of claw thickened, covered with dense and short bristles (Figs 14G, 15H). Tibiae, metatarsi, and tarsi with trichobothria in a single row, bothrium ridged (Fig. 14I), and very long bristles, several of them longer than metatrsus (Figs 13C–D, 14H); tarsal organ oval, exposed, with concentric ridges and two distal receptors (Fig. 15I); female palpal tarsus three times longer than the tibia, prolateral surface densely covered with setae, without claw (Figs 13G–H, 15B–C). Abdomen without scutum; covered uniformly with short setae, not striated (Fig. 13A–B, H–I). Epigastric region slightly protruding, with two pairs of respiratory spiracles, connected to large tracheal trunks directed anteriorly (Fig. 16D), posterior spiracles connected by rebordered groove extending parallel with the anterior spiracles; postepigastric scutum not fused to epigastric scutum. Males and females with six spinnerets in typical caponiid arrangement, anterior laterals with single, presumably major ampullate gland spigot, posterior medians with large, flattened minor ampullate gland spigot and posterior laterals with approximately ten aciniform gland spigots. Male palpal patella and tibia shorter that femur, unmodified; cymbium ovoid, elongate, prolateral surface densely covered with strong setae; bulb globose; embolus short, ribbon-like at base, slightly curved distally, tip enlarged and rounded (Figs 13E–F, 14J–L, 16A–C). External female genitalia with postepigastric scutum represented only by a basal sclerotized band and part of receptaculum visible through transparent area (Fig. 13K). Internal female genitalia with a membranous anteromedian receptaculum formed by a short unsclerotized median duct with a wide base leading to a large, globose sac. This sac is associated with elongate, sclerotized transverse bars with a dorsally projected anterior margin (Figs 15J–L, 16D).

Distribution. Known only from caves in Carajás region, in the state of Pará, Brazil.

Carajas paraua **sp. n.**

http://zoobank.org/DC7B7823-37B7-47A8-AA70-1D5BD4749DC1

Figures 13, 14, 15, 16A–D, 17E–I

Types. Male holotype and female allotype from Gruta N5S8 (06°06'29"S, 50°07'57"W), Flona de Carajás, Parauapebas, Pará, Brazil, 7-12.X.2008, R. Andrade, deposited in IBSP 191287.

Etymology. The specific name is a noun in apposition taken from the Brazilian Tupi Indian language that means parrot (‘‘Papagaio’’ in Portuguese) and refers to this common bird in the region of Parauapebas.

Diagnosis. With the characters of the genus and genitalia as above described.

Description. Male (holotype). Total length 4.2. Carapace 2.1 long, 1.5 wide. Coloration: cephalothorax uniformly orange-reddish, except border of sternum brown. Legs and palps yellow. Abdomen uniformly grayish. Leg measurements: I: femur 1.8/

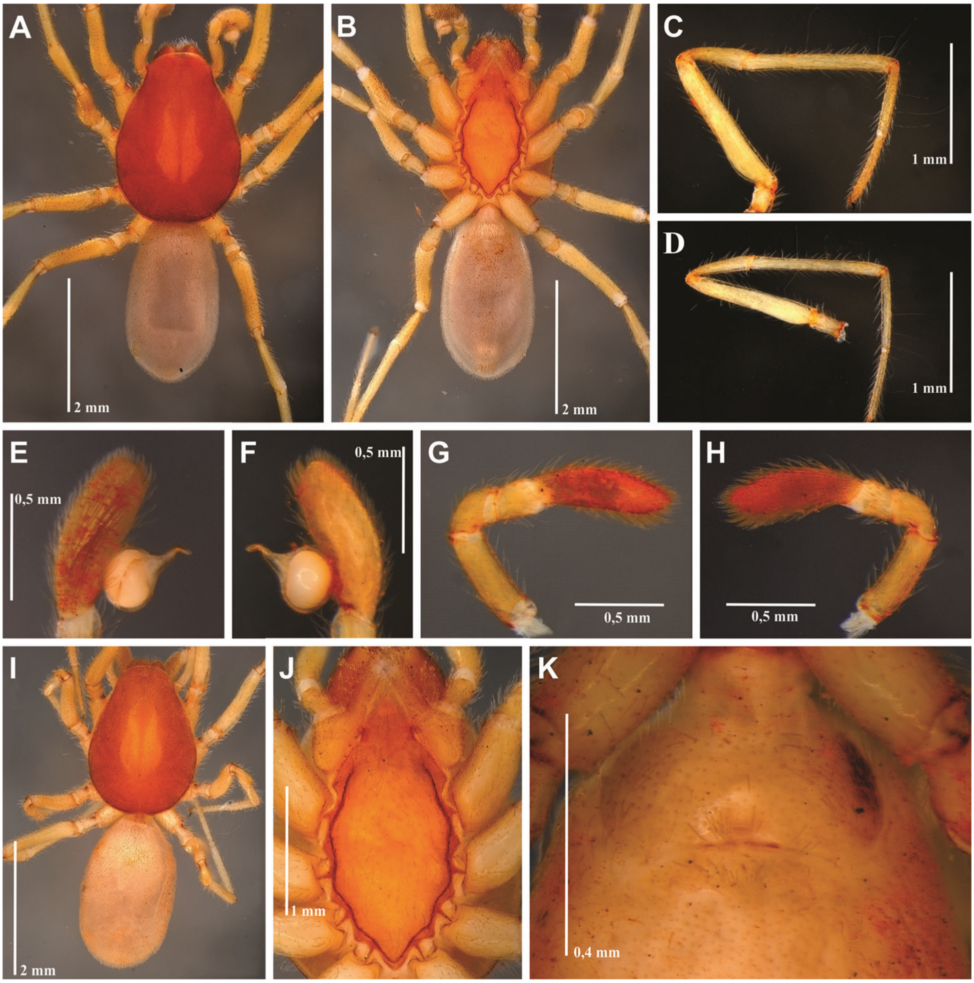

Figure 13. *Carajas paraua* sp. n., male (**A–F**) and female (**G–K**) from Parauapebas, Pará. **A** habitus dorsal view **B** same, ventral view **C** left leg I, prolateral view **D** left leg IV, prolateral view **E** left pedipalp, prolateral view **F** same, retrolateral view **G** left pedipalp prolateral view **H** same, retrolateral view **I** habitus, dorsal view **J** carapace, ventral view **K** genital area, ventral view.

patella 1.0/ tibia 1.4/ metatarsus 1.1/ tarsus 1.0/ total 6.3; II: 1.6/ 1.0/ 1.4/ 1.0/ 0.9/ 5.9; III: 1.5/ 0.7/ 1.1/ 1.0/ 0.8/ 4.1; IV: 2.0/ 1.0/ 2.1/ 1.3/ 1.0/ 7.4. Palp as in figures 13D–E, 14J–L and 16A–C.

Female (allotype). Total length 4.3. Carapace 2.1 long, 1.5 wide. Coloration as in male. Leg measurements: I: femur .1.3/ patella 0.7/ tibia 1.1/ metatarsus 0.7/ tarsus 0.6/ total 4.4; II: 1.1/ 0.6/ 0.9/ 0.7/ 0.6/ 3.9; III: 1.0/ 0.6/ 0.8/ 0.7/ 0.5/ 3.6; IV: 1.4/ 0.8/ 1.4/ 0.9/ 0.7/ 5.2. Internal genitalia as described for the genus (Fig. 16D).

Other material examined. BRASIL. **Pará**: Parauapebas, Flona de Carajás, Cave N1-15 (06°02'03"S, 50°16'17"W), Magangá, 2♀ 1imm., 28/IX-30/X/2007, R. Andrade col. (IBSP 97871); Cave N1-37 (06°01'51"S, 50°16'29"W), Bial, 1♀ 2imm., 28/IX-

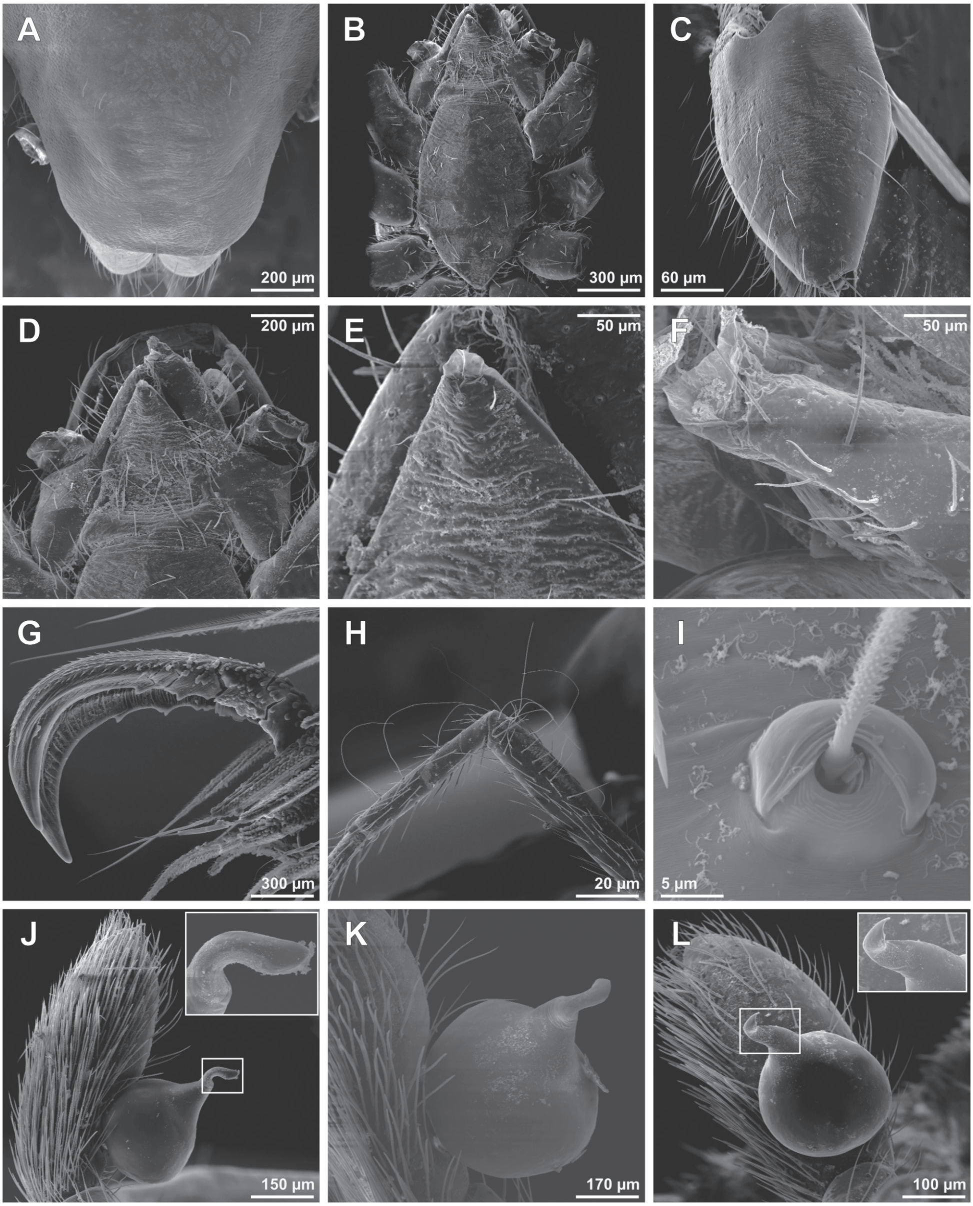

Figure 14. SEM images of *Carajas paraua* sp. n., male from type locality. **A** carapace, ocular area, dorsal view **B** carapace, ventral view **C** left chelicerae, prolateral view **D** mouthparts, ventral view **E** labium, distal area, ventral view **F** labium, distal area, prolateral view **G** paired claws on right leg IV, prolateral view **H** right tibiae and metatarsus I showing long trichobotria, prolateral view **I** tricobothria base on right leg I, dorsal view **J** pedipalp, prolateral view (inset: detail of embolus) **K** bulb, dorsal view **L** same,ventral view (inset: detail of embolus).

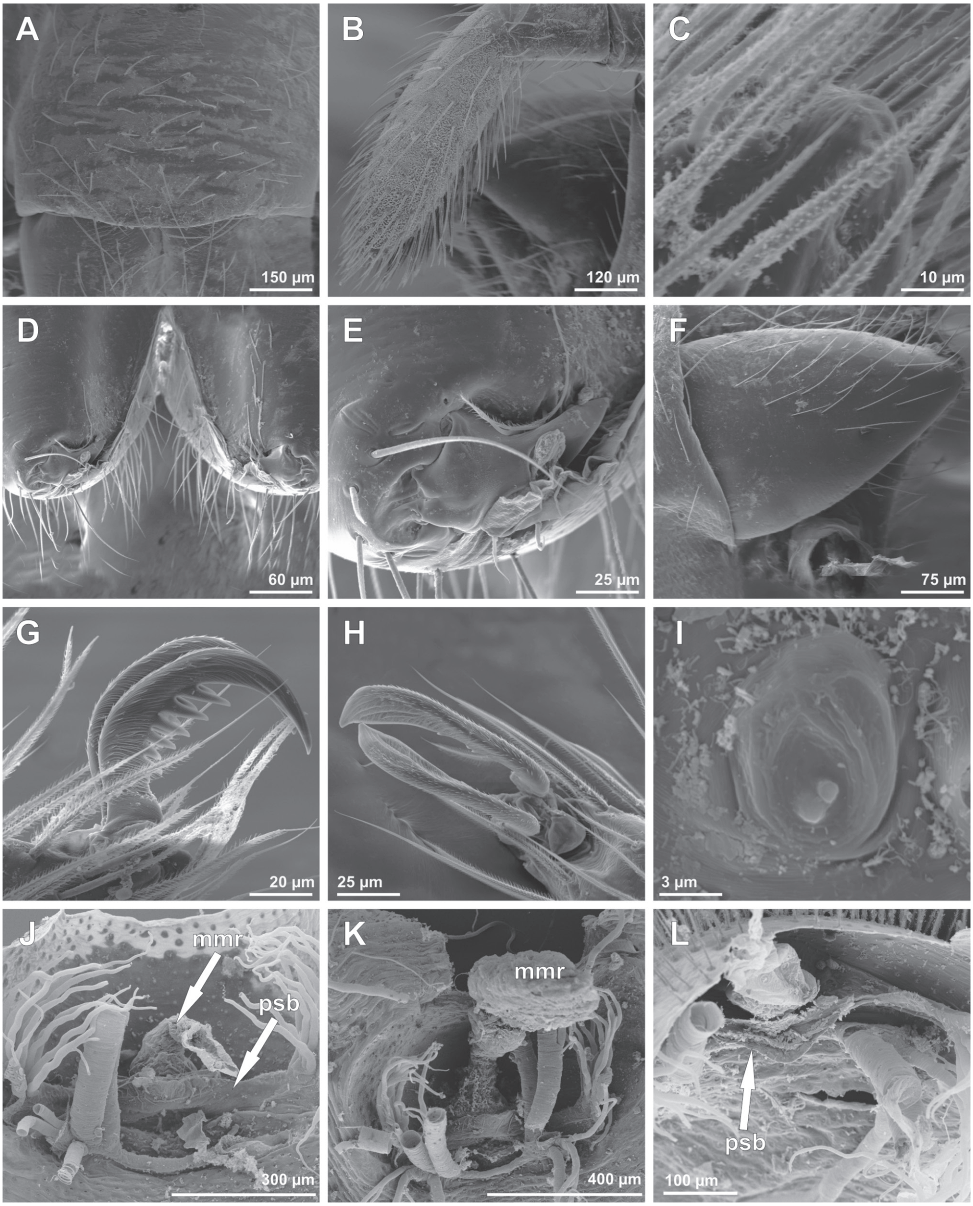

Figure 15. SEM images of *Carajas paraua* sp. n., three females (IBSP 161403) specimen 1 **(A–J),** specimen 2 **(K),** specimen 3 **(L) A** carapace, ocular area, dorsal view **B** pedipalp, retrolateral view **C** same, distal area, prolateral view **D** chelicerae, ventral view **E** same, distal area showing fang, ventral view **F** same, prolateral view **G** claws on left leg I, prolateral view **H** claws on left leg IV, dorsal view **I** tarsal organ on left leg IV, dorsal view **J** internal genitalia, dorsal view **K** same, dorsal view **L** same, anterior view (if = internal transversal fold; mmr = membranous anteromedian receptaculum; psb = pair of sclerotized bars).

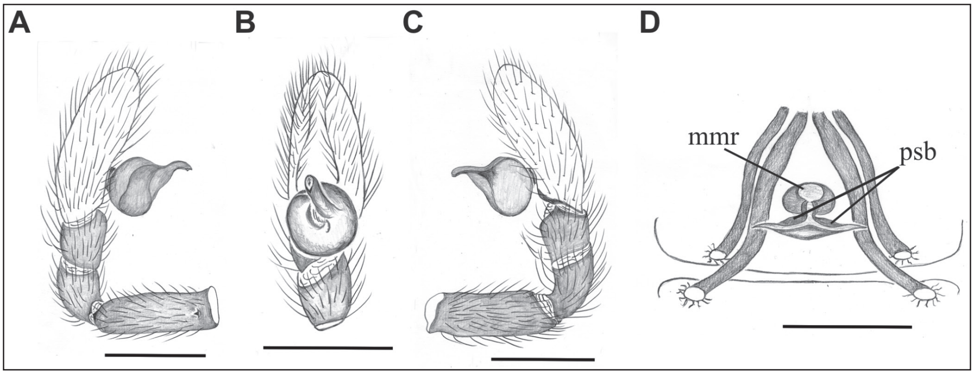

Figure 16. *Carajas paraua* sp. n., male from IBSP 161191 (**A–C**) and female from IBSP 191285 (**D**). **A** left pedipalp, prolateral view **B** same, ventral view **C** same, retrolateral view **D** internal genitalia and tracheae tubes, dorsal view (mmr = membranous anteromedian receptaculum; psb = pair of sclerotized bars). Scale bars: **A–D** 0.5 mm.

30/X/2007, R. Andrade col. (IBSP 97870); Cave N4E-08 (06°02'20"S, 50°09'36"W), 2 imm., 20/IV-04/V/2010, C.A.R. Souza col. (IBSP 191216); Cave N4E-15 (06°02'09"S, 50°09'35"W), 1♂ 1♀ 9imm., 20/IV-04/V/2010, D. B. Pedroso, D. Bebiano & I. Cizauskas col. (IBSP 191217-191220); Cave N4E-18 (06°02'02"S, 50°10'03"W), 2imm., 20/IV-04/V/2010, J. Mascarenhas (IBSP 191221); Cave N4E-22 (06°02'14"S, 50°10'02"W), 3♀ 4 imm., 20/X-04/V/10, R. Andrade, C.A.R. Souza & D. B. Pedroso (IBSP 97834; IBSP 191222-191223); Cave N4E-26 (06°02'24"S, 50°09'39"W), 1 imm., 18/VIII-03/IX/2009, I. Cizauskas (IBSP 191224); Cave N4E-31 (06°02'26"S, 50°09'36"W), 1 imm., 18/VIII-03/IX/2009, D. Bebiano (IBSP 191225); Cave N4E-33 (06°01'58"S, 50°09'38"W), 1♂ 1♀, 15-22/IX/2009, I. Cizauskas (IBSP 191226); Cave N4E-33 (06°01'58"S, 50°09'38"W), 3 imm., 15-22/IX/2009, D. B. Pedroso & I. Cizauskas (IBSP 191227-191228); Cave N4E-39 (06°02'22"S, 50°09'38"W), 1 imm., 19/II-04/III/2010, D. B. Pedroso (IBSP 191229); Cave N4E-51 (06°02'00"S, 50°09'12"W), 1 imm., 19/II-04/III/2010, D. Mello (IBSP 191230); Cave N4E-62 (06°01'57"S, 50°09'04"W), 2♀ 1imm., 19/II-04/III/2010, D. B. Pedroso & J. Mascarenhas (IBSP 191231-191232); Cave N4E-65 (06°01'54"S, 50°09'02"W), 1 imm., 24-30/VII/2009, D. Mello (IBSP 191233); Cave N4E-68 (06°01'56"S, 50°09'13"W), 1 imm., 19/II-04/III/2010, C.A.R. Souza (IBSP 191234); Cave N4E-73 (06°01'58"S, 50°09'20"W), 1♂ 2♀ 2 imm., 24-30/VII/2009-04/III/2010, D. Bebiano, J.B. Verdiani & R. Andrade (IBSP 191235-191237); Cave N4E-74 (06°01'57"S, 50°09'02"W), 1imm., 19/II-04/III/2010, I. Cizauskas (IBSP 191238); Cave N4E-77 (06°01'58"S, 50°09'04"W), 11 imm., 24/VII/2009-04/III/2010, I. Cizauskas, D. B. Pedroso & J. Mascarenhas (IBSP 191239-191242); Cave N4E-80 (06°01'58"S, 50°09'21"W), 2 imm., 24/VII/2009-04/III/2010, I. Cizauskas & D. B. Pedroso (IBSP 191243-191244); Cave N4E-82 (06°02'00"S, 50°09'13"W), 1♀, 24-30/VII/2009, D. B. Pedroso (IBSP 191245); Cave N4E-84 (06°02'05"S, 50°09'37"W), 1 imm., 24-30/VII/2009, R. Andrade (IBSP 191246); Cave N4WS-04 (06°04'21"S, 50°11'42"W), 1 imm., 18/XI-01/

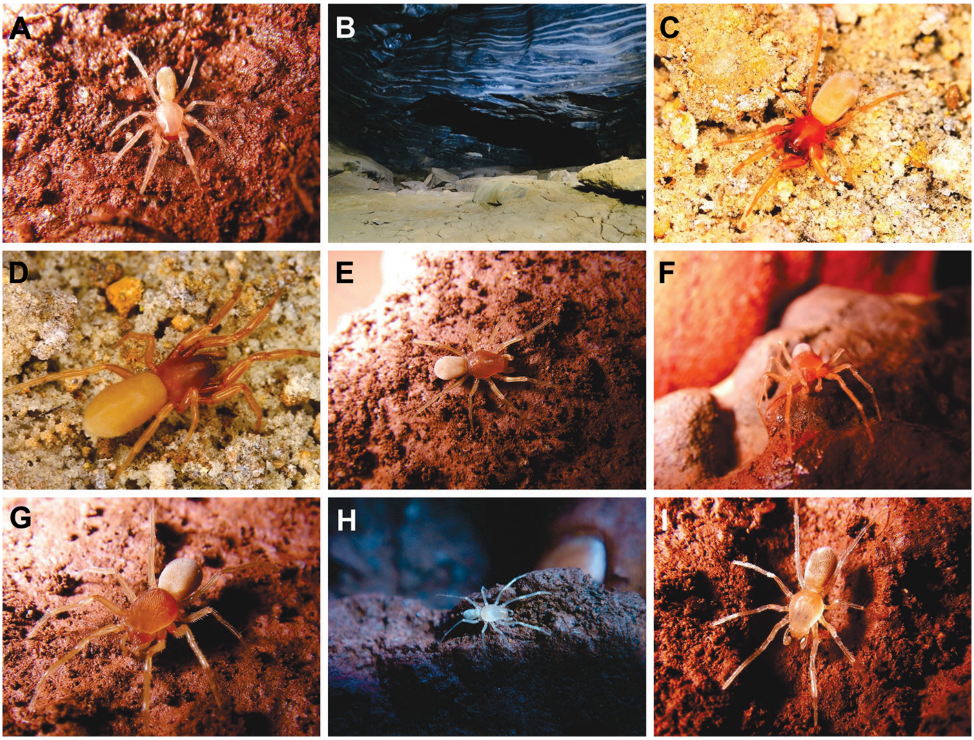

Figure 17. *Tisentnops mineiro* sp. n. (**A**), *Tisentnops onix* sp. n. (**B–D**), *Carajas paraua* sp. n. (**E–I**). **A** adult female on the soil **B** Gruta da Taboa, Minas Gerais, Brazil, showing the rocks on the soil where specimens of *T. onix* sp. n. were collected **C** adult female on the soil **D** same **E** adult female on rock **F** adult male on rock **G** adult female on rock **H** immature on rock **I** same.

XII/2010, L. Tunes col. (IBSP 191247); Cave N4WS-04 (06°04'21"S, 50°11'42"W), 2 imm., 10-19/V/2011, I. Cizauskas (IBSP 191248-191249); Cave N4WS-15 (06°03'57"S, 50°11'20"W), 2 imm., 20/IV-04/V/2010, C.A.R. Souza & D.B. Pedroso (IBSP 191250-191251); Cave N4WS-18 (06°04'01"S, 50°11'37"W), 1 imm., 18/XI-01/XII/2010, C.A.R. Souza (IBSP 191252); Cave N4WS-47 (06°04'34"S, 50°11'39"W), 1 imm., 18/XI-01/XII/2010, C.A.R. Souza (IBSP 191253); Cave N4WS-67 (06°04'21"S, 50°11'29"W), 1♀ 14 imm., 18/XI/2010-19/V/2011, V. Felice et al. (IBSP 191254-191259); Cave N4WS-73 (06°04'24"S, 50°11'37"W), 2 imm., 18/XI-01/XII/2010, V. Felice & C.A.R. Souza (IBSP 191260-191261); Cave N5S-03 (06°06'18"S, 50°08'04"W), 2♀, 14-23/X/2009, I. Cizauskas (IBSP 161138); Cave N5S-04 (06°06'19"S, 50°08'02"W), 1♂ 3♀ 10 imm., 14-23/X/2009, D.B. Pedroso & I. Cizauskas (IBSP 161140, IBSP 161189, IBSP 161191); Cave N5S-07 (06°06'20"S, 50°07'59"W), 1♀ 9 imm., 14-23/X/2009, I. Cizauskas, D.B. Pedroso & J.B. Verdiani (IBSP 161158, IBSP 161161, IBSP 161179, IBSP161182); Cave N5S-08 (06°06'20"S, 50°07'56"W), 4♂ 16♀ 49 imm., 7/X/2008-23/X/2009, R. Andrade, I. Cizauskas & J.B. Verdiani (IBSP 191262-191265, IBSP 161106, IBSP 161120, IBSP 161130, IBSP 161141, IBSP

161149, IBSP 161166, IBSP 161184; 1♂ 1♀ for SEM); Cave N5S-09 (06°06'21"S, 50°07'52"W), 1♂ 13♀ 14 imm., 14-23/X/2009, D. B. Pedroso, I. Cizauskas & J.B. Verdiani (IBSP 161108, IBSP 161127, IBSP 161133, IBSP 161215, IBSP 161226 IBSP 161231, IBSP 161233, IBSP 191266); Cave N5S-10 (06°06'20"S, 50°07'53"W), 9♀ 11 imm., 7/X/2008-23/X/2009, R. Andrade et al. (IBSP 161114, IBSP 161116, IBSP 161148, IBSP 161152, IBSP 161209-161210, IBSP 191267-191268); Cave N5S-11 (06°06'17"S, 50°07'46"W), 5♀, 14-23/X/2009, D. B. Pedroso (IBSP 161175); Cave N5S-13 (06°06'19"S, 50°08'01"W), 2♀ 5 imm., 14-23/X/2009, D. B. Pedroso & I. Cizauskas (IBSP 161113, IBSP 161154); Cave N5S-14 (06°06'19"S, 50°08'00"W), 2♂ 8♀ 12 imm., 14-23/X/2009, D. B. Pedroso & I. Cizauskas (IBSP 161132, IBSP 161203, IBSP 161218, IBSP 191269); Cave N5S-20 (06°05'15"S, 50°07'35"W), 2 imm., 25/VIII-03/IX/2009, I. Cizauskas & J.B. Verdiani (IBSP 161206, IBSP 161208); Cave N5S-21 (06°05'15"S, 50°07'33"W), 10♀ 16 imm., 7-12/X/2008, R. Andrade et al. (IBSP 161104, IBSP 161121, IBSP 161123, IBSP 161128, IBSP 161112, IBSP 160160 , IBSP 161170, IBSP 161174, IBSP 161216, IBSP 161169, IBSP 161194, IBSP 161197, IBSP 161207, IBSP 161234, IBSP 191270); Cave N5S-22 (06°05'15"S, 50°07'32"W), 2 imm., 25/VIII-03/IX/2009, I. Cizauskas & J. Mascarenhas (IBSP 161159, IBSP 161236); Cave N5S-26 (06°05'14"S, 50°07'37"W), 2 imm., 10-19/V/2011, D. Bebiano (IBSP 191271); Cave N5S-30 (06°05'18"S, 50°07'11"W), 1♀ 19 imm., 14/XII/2010-19/V/2011, I. Cizauskas et al. (IBSP 191272-191280); Cave N5S-31 (06°05'28"S, 50°07'08"W), 1imm., 10-19/V/2011, J. Mascarenhas (IBSP 191281); Cave N5S-37 (06°06'21"S, 50°07'56"W), 14♂ 33♀ 86 imm., 7/X/2008-04/IV/2010, J. Mascarenhas et al (IBSP 126125, IBSP 161105, IBSP 161110- 161111, IBSP 161115, IBSP 161124, IBSP 161126, IBSP 161131, IBSP 161134, IBSP 161139, IBSP 161145-161146, IBSP 161164, IBSP 161176- 161178; IBSP 161185-161186, IBSP 161190, IBSP 161192, IBSP 161200, IBSP 161211, IBSP 161213- 161214, IBSP 161221-161222, IBSP 161224-161225, IBSP 161237, IBSP 191282-191283, 2♂ for SEM/MPEG); Cave N5S-38 (06°06'21"S, 50°07'59"W), 1 imm., 14/III-04/IV/2010, C.A.R. Souza (IBSP 161181); Cave N5S-42 (06°06'21"S, 50°08'02"W), 3 imm., 25/VIII-03/IX/2009, D. Mello (IBSP 161109); Cave N5S-43 (06°06'21"S, 50°08'00"W), 1 imm., 14/III-04/IV/2010, J. Mascarenhas (IBSP 161117); Cave N5S-52/53 (06°06'27"S, 50°07'59"W), 1♂ 11♀ 24 imm., 25/VIII/2009-04/IV/2010, J.B. Verdiani et al. (IBSP 16111, IBSP 161118 -161119, IBSP 161143, IBSP 161168, IBSP 161198, IBSP 161219- 161220, IBSP 161227, IBSP 161232); Cave N5S-54 (06°06'28"S, 50°07'59"W), 1 imm., 25/VIII-03/IX/2009, D . Bebiano (IBSP 191284); Cave N5S-55 (06°06'29"S, 50°07'56"W), 2♂ 6♀ 22 imm., 25/VIII/2009-14/IV/2010, D. B. Pedroso et al. (IBSP 161122, IBSP 161155, IBSP 161163, IBSP 161201, IBSP 161212, IBSP 161238 – photography, IBSP 191285 epigynum drawed; IBSP 161403, MEV, internal epigynum); Cave N5S-56 (06°06'27"S, 50°07'57"W), 2 imm., 25/VIII-03/IX/2009, D. B. Pedroso (IBSP 191286); Cave N5S-62 (06°06'17"S, 50°08'06"W), 11 imm., 15/IX/2009-04/IV/2010, D. B. Pedroso & J. Mascarenhas (IBSP 161150, IBSP 161204, IBSP 191288); Cave N5S-63/64/65 (06°06'12"S, 50°08'07"W), 1♂ 5♀ 8 imm., 15/IX/2009-04/IV/2010, D.B. Pedroso, I. Cizauskas & J. Mascarenhas (IBSP 161127, IBSP 161135, IBSP 161144,

IBSP 161157, IBSP 161165, IBSP 161195); Cave N5S-66 (06°06'11"S, 50°08'07"W), 1 imm., 15-21/IX/2009, C.A.R. Souza (IBSP 191289); Cave N5S-70 (06°06'05"S, 50°08'03"W), 1♂ 2♀ 8 imm., 25/VIII/2009-04/IV/2010, I. Cizauskas & D. B. Pedroso (IBSP 161129-161230, IBSP 161156, IBSP 161196, IBSP 161205); Cave N5S-74 (06°06'01"S, 50°08'05"W), 3♀ 6 imm., 25/VIII/2009-14/III/2010, D. Mello, D. Bebiano, J.B. Verdiani & C.A.R.de Souza (IBSP 161107, IBSP 161142, IBSP 161151, IBSP 161171, IBSP 161187, IBSP 161228, IBSP 161235); Cave N5S-75 (06°06'02"S, 50°08'01"W), 1♀ 6 imm., 25/VIII/2009-04/IV/2010, R. de Andrade , C.A.R.de Souza & I. Cizauskas (IBSP 161137, IBSP 161162, IBSP 161167, IBSP 161172, IBSP 161183); Cave N5S-79 (06°06'09"S, 50°08'13"W), 4 imm., 15/IX/2009-14/III/2010, D. B. Pedroso & I. Cizauskas (IBSP 161153, IBSP 161199, IBSP 161223); Cave N5S-85 (06°05'11"S, 50°07'34"W), 1♀ 1 imm., 14/III-04/IV/2010, A.R.de Souza (IBSP 161173, IBSP 161229); Cave N5SM1- 031 (06°06'19"S, 50°08'18"W), 1♂ 1♀ 1imm., VIII/2010, M.P. A. Oliveira et al. (ISLA 3935); Cave N5SM2-021 (06°07'58"S, 50°07'51"W), 2♀ 3 imm., 27/X/2010, R. Zampaulo (IBSP 191290); Cave N5SM2-023 (06°08'06"S, 50°08'05"W), 2♀, 11/IV/2011, R. Zampaulo (IBSP 191291); Cave N5SM2-037 (06°07'58"S, 50°08'05"W), 1♂ 2imm., 19/X/2010, R. Zampaulo (IBSP 191292); Cave N5SM2_0001 (06°08'32"S, 50°08'01"W), 1 imm. (ISLA 12360); Cave N5SM2_0006 (06°08'27"S, 50°08'09"W), 1 imm. (ISLA 12370); Cave N5SM2_0016 (06°08'17"S, 50°07'59"W), 2♀ 8 imm. (ISLA 12357; ISLA 12382); Cave N5SM2_0023 (06°08'06"S, 50°08'05"W), 4♀ (ISLA 12378); Cave N5SM2_0026 (06°08'09"S, 50°08'06"W), 3♀ 7 imm. (ISLA 12354; ISLA 12362; ISLA 12377); Cave N5SM2_0027 (06°08'06"S, 50°08'12"W), 1 imm. (ISLA 12351); Cave N5SM2_0033 (06°08'02"S, 50°08'08"W), 1 imm. (ISLA 12350); Cave N5SM2_0037 (06°07'58"S, 50°08'05"W), 2♀ 4 imm. (ISLA 12366; ISLA 12385); Cave N5SM2_0039 (06°07'58"S, 50°08'06"W), 2 imm. (ISLA 12349; ISLA 12375); Cave N5SM2_0040 (06°07'58"S, 50°08'11"W), 11 imm. (ISLA 12347; ISLA 12383); Cave N5SM2_0041 (06°07'58"S, 50°08'12"W), 3 imm. (ISLA 12364; ISLA 12384); Cave N5SM2_0042 (06°07'57"S, 50°08'11"W), 3♀ 7 imm. (ISLA 12355; ISLA 12381); Cave N5SM2_0043 (06°07'56"S, 50°08'10"W), 1♀ 3imm. (ISLA 12358; ISLA 12388); Cave N5SM2_0045 (06°07'54"S, 50°08'05"W), 4♀ 11 imm. (ISLA 12365; ISLA 12387); Cave N5SM2_0046 (06°07'54"S, 50°08'06"W), 1 imm. (ISLA 12363); Cave N5SM2_0049 (06°07'52"S, 50°08'05"W), 2♀ 17 imm. (ISLA 12361; ISLA 12379); Cave N5SM2_0054 (06°07'48"S, 50°08'04"W), 1 imm. (ISLA 12368); Cave N5SM2_0057 (06°07'47"S, 50°08'05"W), 1 imm. (ISLA 12373), Cave N5SM2_0058 (06°07'46"S, 50°08'05"W), 2♀ 5 imm. (ISLA 12352; ISLA 12367); Cave N5SM2_0065 (06°07'41"S, 50°08'08"W), 3 imm. (ISLA 12348); Cave N5SM2_0076 (06°07'31"S, 50°07'54"W), 1 imm. (ISLA 12376); Cave N5SM2_0078 (06°07'23"S, 50°07'48"W), 3♀ 15 imm. (ISLA 12353; ISLA 12386); CaveN5SM2_0086 (06°07'16"S, 50°07'47"W), 3 imm. (ISLA 12356); Cave N5SM2_0089 (06°07'15"S, 50°07'44"W), 1 imm. (ISLA 12369), Cave N5SM2_0092 (06°07'17"S, 50°07'55"W), 1 imm. (ISLA 12372); Cave N5SM2_0095 (06°07'06"S, 50°07'54"W), 1♀ (ISLA 12380); Cave N5SM2_0098 (06°08'27"S, 50°08'03"W), 1 imm. (ISLA 12359; ISLA 12374); Cave N5SM2_0102 (06°07'17"S, 50°07'52"W), 3 imm. (ISLA 12371), all collected between 2014-2015 by Equipe UFLA; CaveN3_0047 (06°02'27"S, 50°13'40"W, 1 imm., 02-23/VIII/2013 (IBSP 186208); Cave N3_0076 (06°02'28"S, 50°13'36"W, 3 imm., 02-23/VIII/2013 (IBSP 186209, IBSP 186210); Cave N5W_0001 (06°04'47"S, 50°08'W), 1♂ 1 imm., 02-23/VIII/2013 (IBSP 186211); Cave N5W_0003 (06°04'53"S, 50°08'04"W), 2 imm., 04-07/XII/2013 (IBSP 186212; IBSP 186213); Cave N1_0015 (06°02'03"S, 50°16'17"W), 1 ♀ 7 imm., 11/VI-02/VII/2014 (IBSP 186214-IBSP 186218); Cave N1_0060 (06°01'12"S, 50°16'41"W), 1imm., 11/VI-02/VII/2014 (IBSP 186219); Cave N1_0064 (06°01'07"S, 50°16'45"W), 1 imm., 11/VI-02/VII/2014 (IBSP 186220); Cave N1_0156 (06°02'41"S, 50°16'22"W), 1imm., 11/VI-02/VII/2014 (IBSP 186221); Cave N1_0247 (06°01'14"S, 50°16'23"W), 1 imm., 11/VI-02/VII/2014 (IBSP 186222); Cave N1_0073 (06°01'13"S, 50°17'17"W), 1 imm., 16/VII-06/VIII/2014 (IBSP 186223); Cave N1_0170 (06°01'23"S, 50°17'58"W), 1 imm., 16/VII-06/VIII/2014 (IBSP 186224); Cave N8_0038 (06°10'24"S, 50°08'49"W), 1 imm., 16/VII-06/VIII/2014 (IBSP 186225); Cave N1_0025 (06°01'49"S, 50°16'20"W), 1 imm., 04/IX-06/X/2014 (IBSP 186226); Cave N1_0037 (06°01'51"S, 50°16'29"W), 2 imm., 04/IX-06/X/2014 (IBSP 186227; IBSP 186228); Cave N1_0101 (06°01'09"S, 50°16'46"W), 1 imm., 24/II-13/III/2015 (IBSP 186229); Cave N8_0004 (06°10'06"S, 50°09'27"W), 1 imm., 24/II-13/III/2015 (IBSP 186230); Cave N1_0119 (06°01'16"S, 50°18'06"W), 1 imm., 02-29/IV/2015 (IBSP 186231), Cave N8_0008 (06°10'05"S, 50°09'32"W), 1 imm., 02-29/IV/2015 (IBSP 186232), all collected by Equipe Carste.

Distribution. Known only from caves in the state of Pará, northern Brazil (Fig. 19).

Natural history. All 767 specimens (34♂, 179♀, 554 immatures) of *Carajas paraua* sp. n. were collected in 104 caves distributed in rock outcrops covered by canga vegetation (details in Mota et al. 2015) surrounded by the Amazon Forest. This species is restricted to the underground environment of iron caves that exist in canga, in the ore (a rock with more than 60% iron and little or no silica, carbonates, or sulfides) and iron formations (designated for itabirites, ferruginous dolomites, hematitic phyllites, jaspilitos, and hematite) from Flona of Carajás. The specimens were found on the ground, under rocks in aphotic zones with high relative humidity (≥ 98%) and frequently in caves with bat colonies. The tiny size of the fangs of this species seems to indicate that their diet is based on micro invertebrates such as mites, Collembola and Diptera larvae, often found in high abundance in soil areas with bat guano. *Carajas paraua* sp. n. is a troglobite spider with a distribution restricted to iron caves in target areas of mining and regions of iron formation with high economic interest.

Discussion

The phylogenetic relationships of Caponiidae are unknown, although some studies have inferred the relationship of certain genera of the family (Platnick 1993; Platnick 1994a, b; Platnick and Jager 2008; Platnick and Lise 2007). A study including all genera of the family is being prepared by the authors, and the discussion here is premature.

Among the genera described here, the most remarkable is *Nasutonops* gen. n. All species have a distally projected clypeal horn, not found in other Caponiidae. Despite this interesting modification, the ocular area and genital structures link this species to *Caponina* (see Platnick 1994a). The disposition of the six eyes are similar in both genera, with the median eyes larger than the others (see Platnick 1994a: fig. 19); however, no *Nasutonops* species have an ocular reduction as do some *Caponina* species. The configuration of the male palp is also similar (compare Fig. 11C with Platnick 1994a: fig. 26), with the differences in the position and base of the embolus, which has a flattened base and protrudes distally in *Nasutonops* species (Fig. 11C–E) rather than protruding medially as in *Caponina* (Platnick 1994a, fig. 27). Whether the embolus protrudes from the bulb distally or medially could be a synapomorphy for each genus. The female internal genitalia of *Caponina* species (see Platnick 1994a, figs 22–25; Brescovit and Sánchez-Ruiz 2013, fig. 10) resembles the genitalia of *Nasutonops* species, but species of *Caponina* have a distinctive pair of curved sclerotizations arising from the posterior wall of the bursa copulatrix (see Platnick 1994a, figs 22–25) and is considered a synapomorphy of the genus. Externally, the genitalia are quite different: *Nasutonops* species have a strongly sclerotized trasverse internal fold (absent in *Caponina*), which can be observed externally via a transparent area. This transverse fold runs along nearly the entire epigastric area, reaching the posterior ends of the sclerotized bars in the internal genitalia, and in *N. sincora* is very wide. The clypeal horn, the distal origin of the embolic base in the male palps, and the sclerotized trasverse internal fold of the female internal genitalia may be synapomorphies supporting the monophyly of *Nasutonops*.

The first blind caponiids described here are also remarkable (*T. mineiro* sp. n. and *C. paraua* sp. n.). They were found only in caves and are totally eyeless. Furthermore, they have other troglobitic adaptations, such as very long trichobothria (Figs 3A,13C, D; 14H) and some modifications to the tarsal claws. Particularly, *C. paraua* sp. n. lacks unpaired claws on all tarsi (Figs 14G; 15G, H), and the paired claws on the posterior tarsi have the distal tip thickened and covered with dense and short bristles (Figs 14G, 15H). These dramatic modifications of the tarsal claws, as well as the anteriorly and posteriorly strongly projected endites (Figs 13J, 14D), are unique among caponiids, and may also be related to the cave environment. Specimens of *C. paraua* sp. n. and *T. mineiro* sp. n. were extensively collected in caves from the Brazilian states of Pará and Minas Gerais respectively (Figs 18–19), but were never found outside these caves, where only specimens of *Nops* MacLeay were collected. The other new *Tisentnops* described here (*T. onix* sp. n.) was also found in a cave, and although it is not eyeless, it has a much reduced single pair of eyes almost on the front of carapace (Fig. 5D–E) and similar distinct trichobothria (Fig. 5H). Diagnostic characters of the genus, such as the uniquely modified endites, and the elongate raised sockets of setae on endites and anterior legs, could be other troglobitic modifications, suggesting that representatives of Brazilian *Tisentnops* apparently live only in caves. However, when Platnick (1994b) redescribed the type species *Tisentnops leopoldi* (Zapfe), he mentioned that a major collection effort to obtain additional material was made without success on two separate

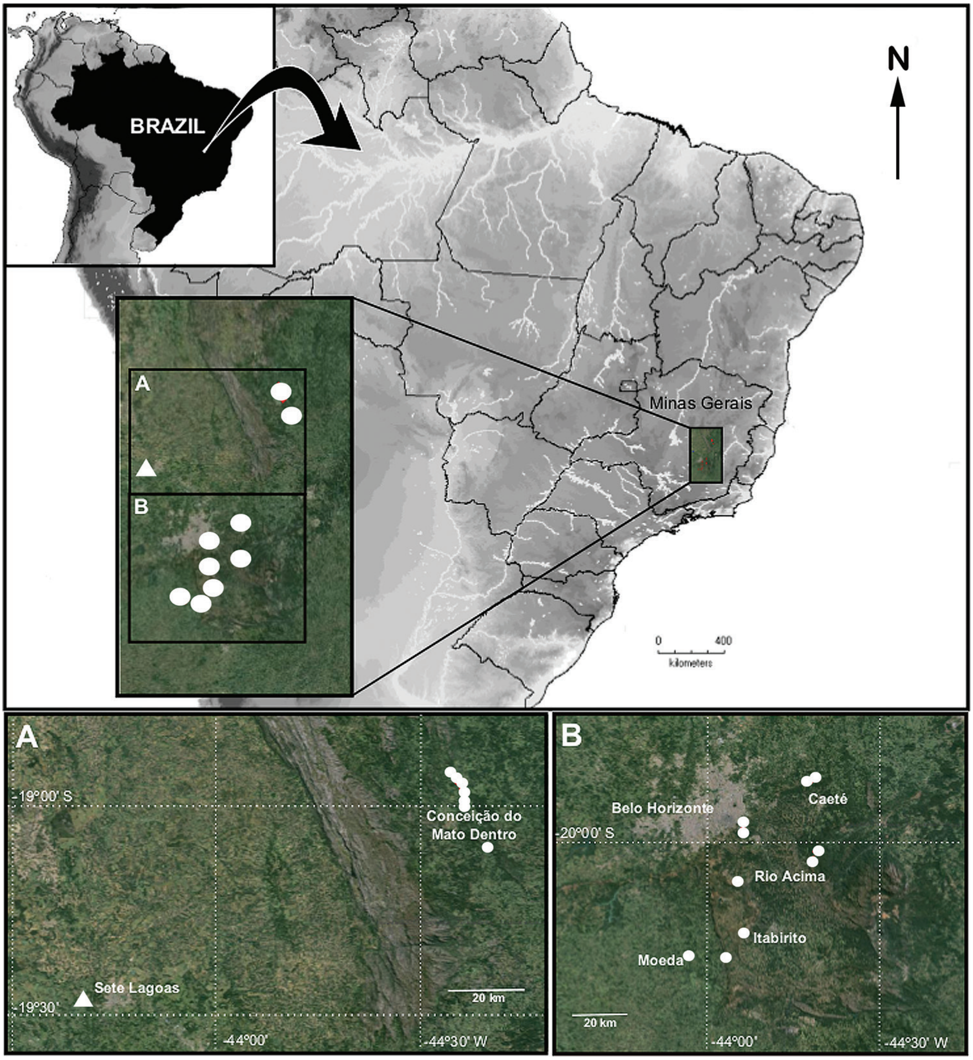

Figure 18. Distribution maps of *Tisentnops mineiro* sp. n (white circles) and *Tisentnops onix* sp. n. (white triangles) from the state of Minas Gerais, Brazil.

occasions at the type and nearby localities from Chile; however, there are no caves in these areas. Therefore, it is unlikely that the Chilean type species is a troglobite.

The description of these two new *Tisentnops* species allowed us to increase the knowledge of this genus. Specifically, the configuration of the female internal genitalia was studied for the first time. The female genitalia of *Tisentnops* resembles that found in *Calponia*, *Carajas* gen. n., *Diploglena*, *Notnops*, *Laoponia* and *Iraponia*, with an elongate membranous anteromedian receptaculum formed by an anteriorly directed median tubular duct leading to a globose sac (see Figs 3G, 15K; Platnick 1993: fig 17; Platnick 1994b: figs 20–21; Platnick and Jager 2008: figs 31–34; Kranz-Baltensperger

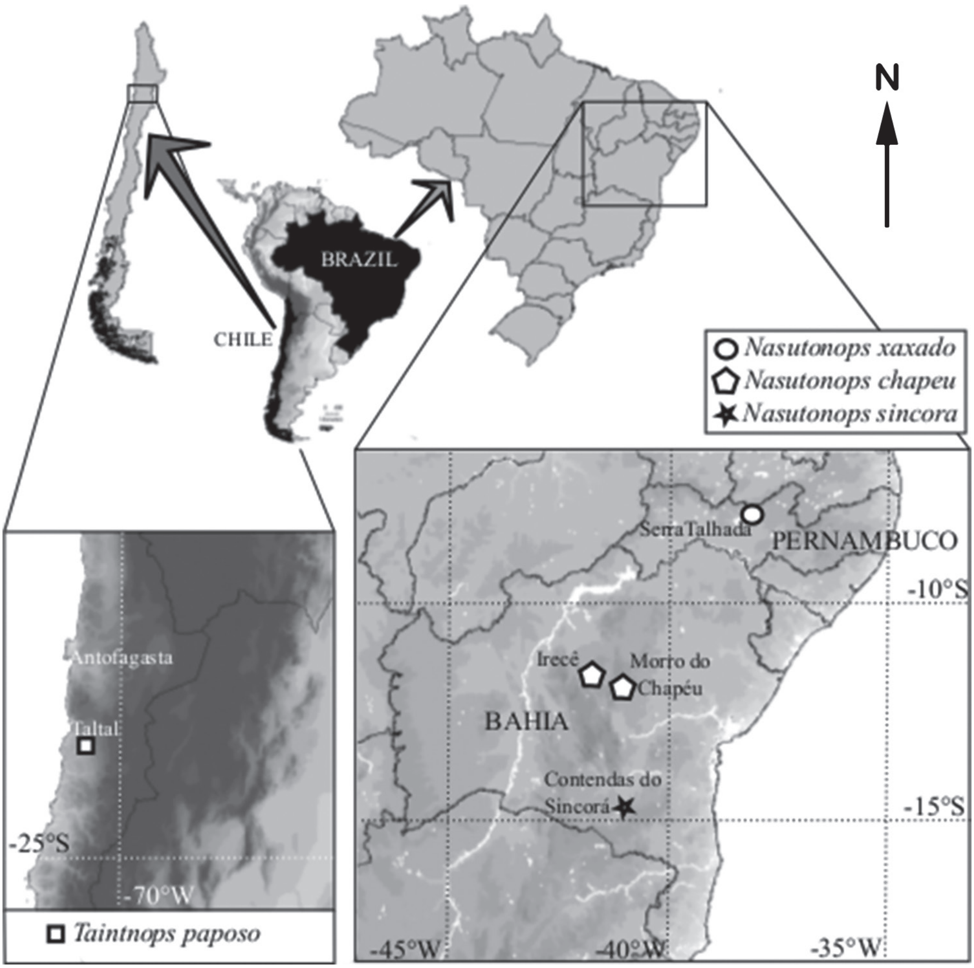

Figure 19. Distribution maps of *Nasutonops* species from the states of Bahia and Pernambuco, Brazil, and *Taintnops paposo* sp. n. from Chile.

et al. 2009: figs 47–48; Haddad 2015: fig. 24). The main differences among all genera are in the presence or absence, position and shape of the sclerotized structures forming the transverse bars and folds. Interestingly, *Taintnops* species also have a large, oval anteromedian receptaculum (see Fig. 4H and Platnick 1994b: fig. 25), but lack the anteriorly directed median duct. *Caponina* and *Nasutonops* gen. n. apparently form a separate group with a wide and short uterus externus that is not globose and lacks a median duct; however, they retain the pair of elongate sclerotized bars, which are covered by a transparent hyaline membrane (Fig. 4D–E).

In summary, the female internal genitalia of non-nopine genera may indicate a monophyletic group formed by those genera with a median duct and a globose sac on the membranous anteromedian receptaculum. In this case, *Diploglena* and *Tisentnops* belong to this group and would be closely related as suggested by Platnick and Jager

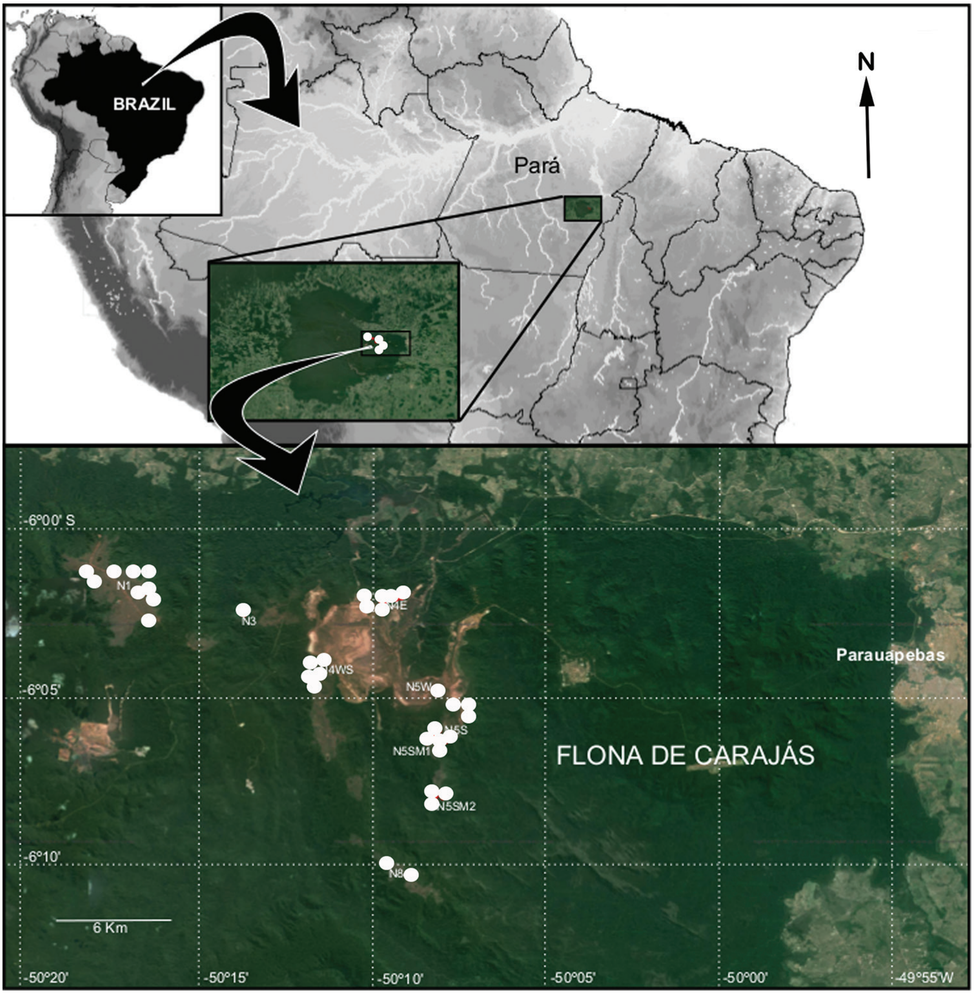

Figure 20. Distribution map of *Carajas paraua* sp. n. (white circles) from the Carajás area, northern Brazil.

(2008) due to the anteriorly expanded palpal endites. Unfortunately, the male palp appears to be uniform among the non-nopine genera, having a globose bulb with a tubular or lamelliform embolus (Figs 1E–F, 9J). The exception occurs in the genera *Caponia* and *Diploglena* whose bulbs have a tegular apophysis and a membranous conductor (see Purcell 1904: figs 28–35; Haddad 2015: figs 46–47, 64–66).

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RESEARCH ARTICLE

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The leafhopper genus *Onukigallia* Ishihara, 1955 with descriptions of two new species from southern China (Hemiptera, Cicadellidae, Megophthalminae, Agalliini)

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Abstract

Two new Chinese species of the leafhopper genus *Onukigallia*, *O. neoonukii* **sp. n.** from Sichuan and Guangdong Provinces, and *O. tumida* **sp. n.** from Hubei and Hunan Provinces are described and illustrated. A key and an updated checklist with distributions of *Onukigallia* species are provided.

Keywords

Auchenorrhyncha, China, distribution, morphology, *Onukigallia*

Introduction

The leafhopper genus *Onukigallia* is a small group in the tribe Agalliini of the subfamily Megophthalminae (Hemiptera: Auchenorrhyncha: Cicadellidae) with a distribution in the Oriental region, and well-known by its similarity to the type genus *Agallia* Curtis, 1833, both sharing stout setae on the male subgenital plates but *Onukigallia* differs from the latter in having hairlike setae on the male pygofer and subgenital plates and in the structure of the aedeagus and subgenital plates. It was established by Ishihara (1955) for *Agallia onukii* Matsumura, 1912 (type species). Later, other authors (Viraktamath 1973, 2011; Anufriev and Emeljanov 1988; Zhang and Li 1999; Zhang 2011) proposed new combinations, described new species, provided identification keys and distribution data, and brought the total species number of the genus to five.

The present paper deals with two new species: *Onukigallia neoonukii* sp. n. from Sichuan and Guangdong Provinces, China and *O. tumida* sp. n. from Hubei and Hunan Provinces, China which are described and illustrated. A key to species is provided for identification, and the checklist is updated with distributions.

Material and methods

The higher classification of Cicadellidae and morphological terminology used in this work follow Dietrich (2005) and Viraktamath (2011). Leg chaetotaxy follows Rakitov (1998). Examination of *Onukigallia fanjingensis* Zhang & Li follows Li et al. (2014, 2015). The body length is measured from the apex of the head to the end of the forewings and is given in millimeters (mm).

The type material and other material examined are deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Taxonomy

Genus *Onukigallia* Ishihara, 1955

Type species. *Agallia onukii* Matsumura, 1912 by original designation.

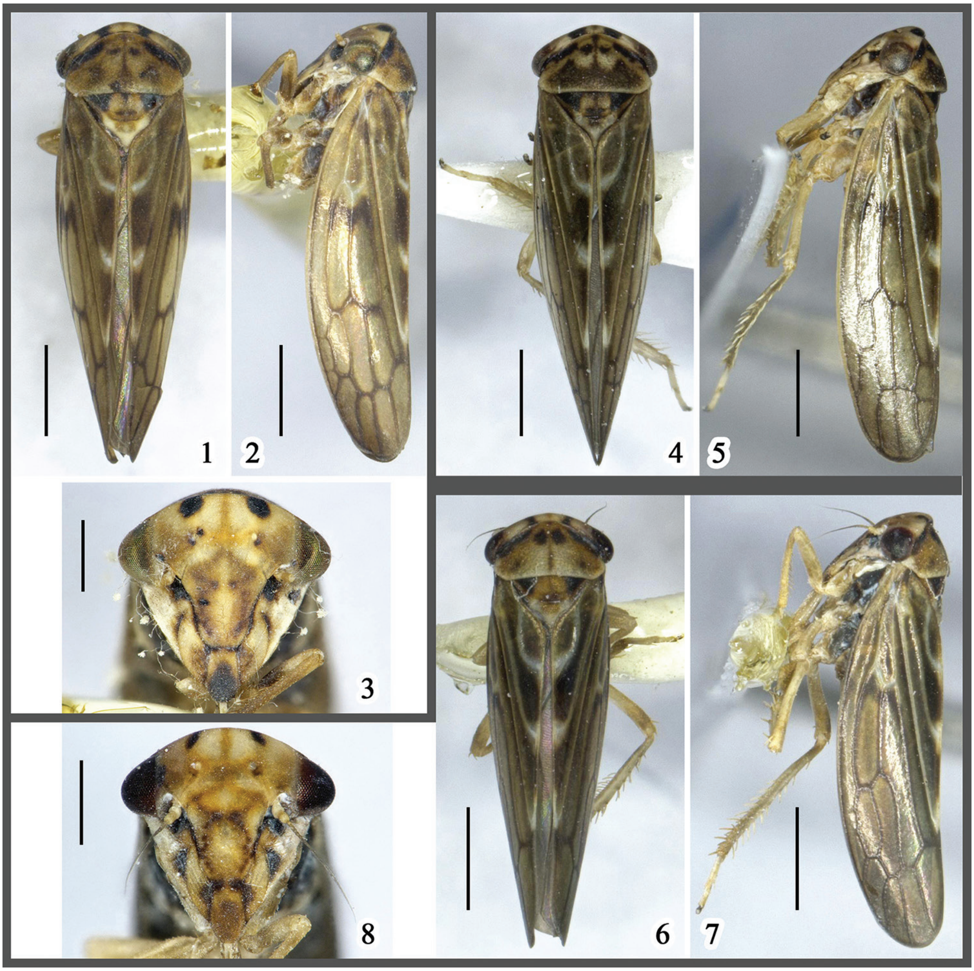
Remarks. After Viraktamath (2011). This genus is similar to other two Agalliini genera, *Agallia* Curtis, 1833 and *Formallia* Viraktamath, 2011: it closely resembles *Agallia* in having stout setae on the ventral margin of the male subgenital plate but differs in having hairlike setae on the male pygofer side and subgenital plate and in the shapes of the aedeagus and subgenital plates; it is also similar to *Formallia* in body appearance but differs in having setae both dorsally and ventrally on the subgenital plates and also in the shapes of the male pygofer, connective, and aedeagus.

Distribution. Oriental and Palearctic regions: China, Japan, Korea and Russia.

Onukigallia neoonukii sp. n.

http://zoobank.org/68AE9AD3-19B8-4301-80E9-2536E59D3D9C
Figures 1–3, 9–17

Measurements. Body length including tegmina in repose: ♂, 5.32–5.36 mm; ♀, 5.45–5.85 mm.



Figures 1–8. Species of *Onukigallia*, male habitus, dorsal (**1, 4, 6**) and lateral (**2, 5, 7**) views, and face (**3, 8**) **1–3** *O. neoonukii* sp. n. **4–5** *O. onukii* (Matsumura, 1912) **6–8** *O. tumida* sp. n. Scale bars: 1.0 mm (**1–2, 4–7**), 0.5 mm (**3, 8**).

Description. *Body coloration*. Body background color yellowish brown (Figs 1–3). Crown with darker yellowish stripe on midline, and with one pair of black spots separating crown into three equal parts. Face (Fig. 3) upper part with two black spots contiguous with those on crown, midline with yellow stripe extending to base of postclypeus, both sides of midline with white halo; small dark brown macula present ventrolaterad of ocellus; eyes brown, scattered with yellow markings; area below antennal fossa black; lateral frontal suture pale yellow, clypeal sutures dark brown; anteclypeus, distal half black; gena white. Pronotum yellowish brown, anterior margin with black maculae near eyes, midline dark brown, both sides of midline with small and larger paired dark brown maculae. Mesonotum dark brown, lateral angles and basal part of midline black, sides of midline with two small dark brown maculae on distal part.

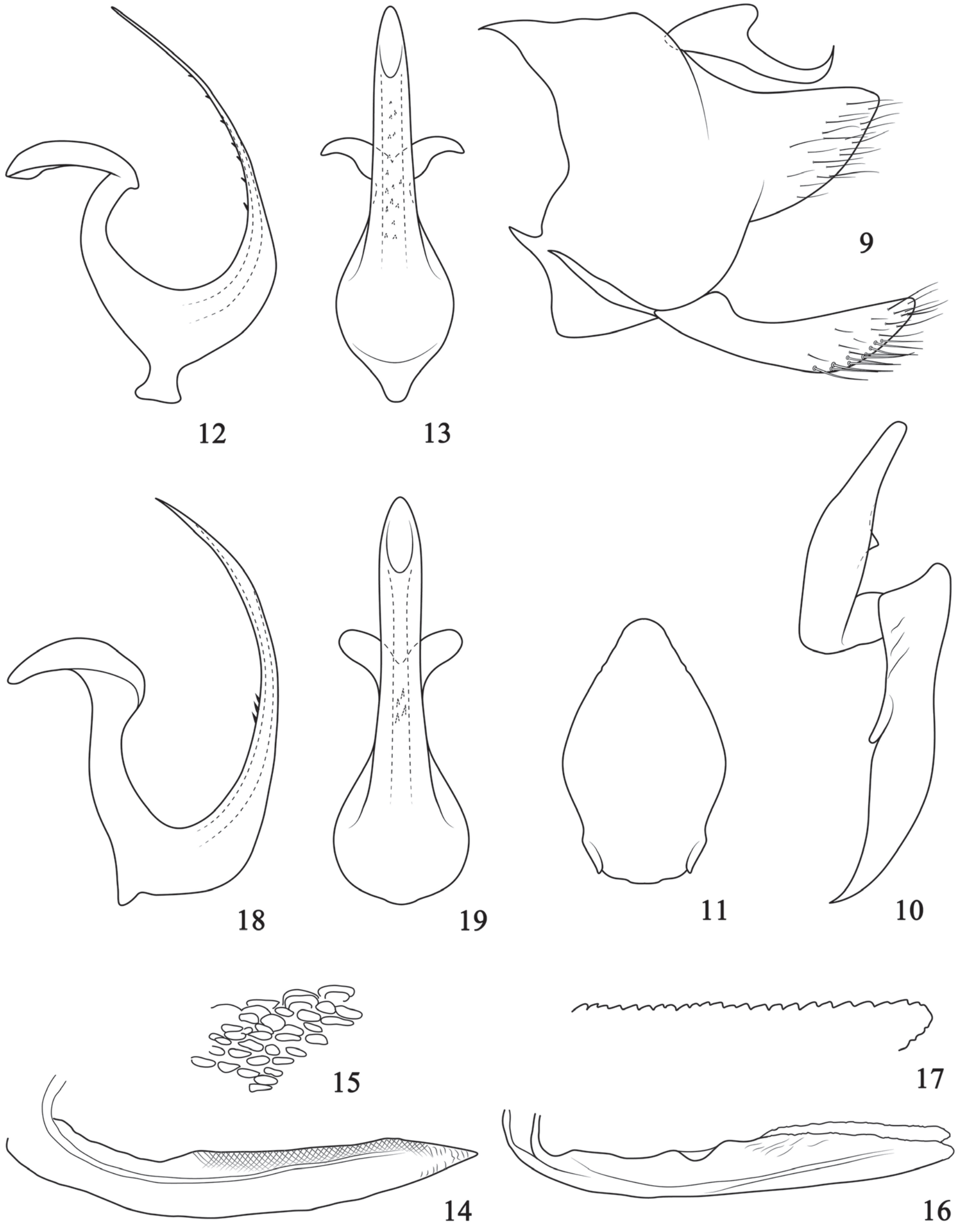
Scutellum with end and lateral angles cream. Forewing claval veins and basal corial veins cream, other veins dark brown. Legs dark brown. Female body color and pattern similar to male but lighter.

External morphology. Body appearance (Figs 1–2) typical, slender. Head shorter medially than laterally. Face (Fig. 3) across eyes as long as wide; ocelli transparent, closer to eyes than to each other; anteclypeus round and slightly widened distally, projected beyond lora and gena; transclypeal suture complete. Pronotum nearly 2.0 × wider than broad, oblique frontally and laterally, fore margin prominent, projecting forwards and slightly depressed near eyes, hind margin nearly straight. Scutellum triangular, 1.5 × longer than broad, as long as pronotum. Forewings opaque, venation clearly prominent especially on clavus, with three anteapical and four apical cells, inner anteapical cell closed basally, inner claval vein strongly curved. Hind femoral macrosetae 2+1; hind tibia with 11 macrosetae on PD row, six on AD row, eight on AV row; hind basitarsus with two platellae on distal transverse row.

Male genitalia. Pygofer (Fig. 9), basally broad, in lateral view, dorsocaudal and ventrocaudal margins strongly excavated, lobe strongly narrowed and tapering to end, ventrocaudal surface with hairlike setae. Valve wider than long. Subgenital plates (Fig. 9) elongate, slightly exceeding pygofer side, distal half surface with filamentous setae, ventral margin prominent medially and with stout setae in one row. Anal collar process well developed, basally broad, then sharply narrowed and tapered to acute tip twisted dorsally. Style (Fig. 10), robust, inner arm much longer than outer arm, slightly inflated at middle, with small triangular process medially on outer margin, distal half narrowed, end round. Connective (Fig. 11) simple, longer than broad, caudal margin prominent medially, lateral margins expanded near base. Aedeagus (Figs 12–13) broad basally, twisted dorsally, shaft with distal 75% strongly compressed, filiform in lateral aspect, dorsal margin with many small teeth subbasally to subapically, in ventral view, shaft with margin parallel sided, subacute apically; gonopore apical on ventral margin; dorsal apodeme elongate, slender, tip expanded in bilateral direction; preatrium weakly developed.

Female genitalia. 7th sternite nearly 1.5 × wider than long, and nearly 2.0 × longer than 6th sternite, hind margin slightly excavated and ridged medially. Ovipositor projecting beyond pygofer. First pair of valvulae (Figs 14–15), in lateral view, relatively broad, slightly curved dorsally from base, tapering, tip sharpened, dorsal half with sculpturing imbricate. Second pair of valvulae (Figs 16–17) dorsally curved slightly from base in lateral view, slightly inflated subapically, then tapering to subacute point; dorsal hyaline area (DHA) clear, dorsal prominence (AP) pronounced, apical half of dorsal margin with dense teeth gradually from base to apex.

Material examined. HOLOTYPE: ♂, CHINA: Sichuan Province, Yaan City, Baoxing, Fengtongzhai, 1500 m, 03.VIII.2005, collected by Zhou Zhong-Hui. PARATYPES: 2 ♀♀, Same data as holotype. 1 ♂ 5 ♀♀, CHINA: Guangdong Province, Nanling, Ruyang management station, 850–1500 m, 04–06.VIII.2006, collected by Zhou Zhong-Hui. 4 ♀♀, CHINA: Guangdong Province, Nanling, Longshan Power Station, 500 m, 07–09.VIII.2006, collected by Yang Zai-Hua.



Figures 9–19. *Onukigallia* species **9–17** *O. neoonukii* sp. n. **18–19** *O. onukii* (Matsumura, 1912) **9** Pygofer side and subgenital plate, lateral view **10** Style, dorsal view **11** Connective, dorsal view **12, 18** Aedeagus, lateral view **13, 19** Same, caudal view **14–15** First valvulae **16–17** Second valvulae **15, 17** partial enlarged view.

Distribution. China (Sichuan and Guangdong Provinces).

Remarks. The new species is similar to *O. onukii* (Matsumura) (Figs 4–5, 18–19) but can be distinguished from the latter by the large-sized body (male body length including tegmina in repose of *O. onukii* is 4.30–4.55 mm), the different color pattern particularly on the pronotum, the more slender aedeagal shaft, and the larger number and wider distribution of teeth on dorsal margin of the aedeagal shaft.

Etymology. The new species name is derived from the Latin words "*neo-*" and "*onukii*", refers to the similarity to *O. onukii* (Matsumura).

Onukigallia tumida sp. n.

http://zoobank.org/B2BC9011-8481-4C2D-8F10-6E99852A9B8F
Figures 6–8, 20–24

Measurement. Body length including tegmina in repose: ♂, 4.48–4.50 mm.

Description. *Body coloration and external morphology*. Body (Figs 6–7) relatively darker and more slender than *O. neoonukii* sp. n. Face (Fig. 8), anteclypeus distal half not black; gena with black macula medially. Pronotum 2.1 × wider than broad. Scutellum with end and lateral angles pale, 1.1 × longer than pronotum and 1.3 × wider than long. Other color pattern and external morphology similar to *O. neoonukii* sp. n.

Male genitalia. Pygofer (Fig. 20), basally broad, in lateral view, lobe strongly narrowed, with dorsal and ventral margins parallel, apex round, ventrocaudal surface of lobe with hairlike setae. Valve broader than long. Subgenital plates (Fig. 20) widened, exceeding pygofer side, surface with filamentous setae, and uniseriate stout setae ventrally. Anal collar process simple, relatively stout, basally broad, then tapered to acute tip twisted caudally. Style (Fig. 21) typical of genus, inner arm 2.0 × longer than outer arm, slightly inflated in middle, with clear triangular process medially on outer margin, apex blunt. Connective (Fig. 22) anterior margin with medial lobe, caudal margin prominent medially, lateral margins slightly expanded near apex, and clearly excavated near base. Aedeagus (Figs 23–24), in lateral view, broad basally, curved dorsally, shaft with small hump near midlength on dorsal margin, ventral margin below gonopore slightly depressed, apex subacute; in ventral view, shaft expanded laterally on lateral margins near base, then tapered, subapex slightly widened and apex round; gonopore apical on ventral margin; dorsal apodeme elongate, tip expanded in bilateral direction.

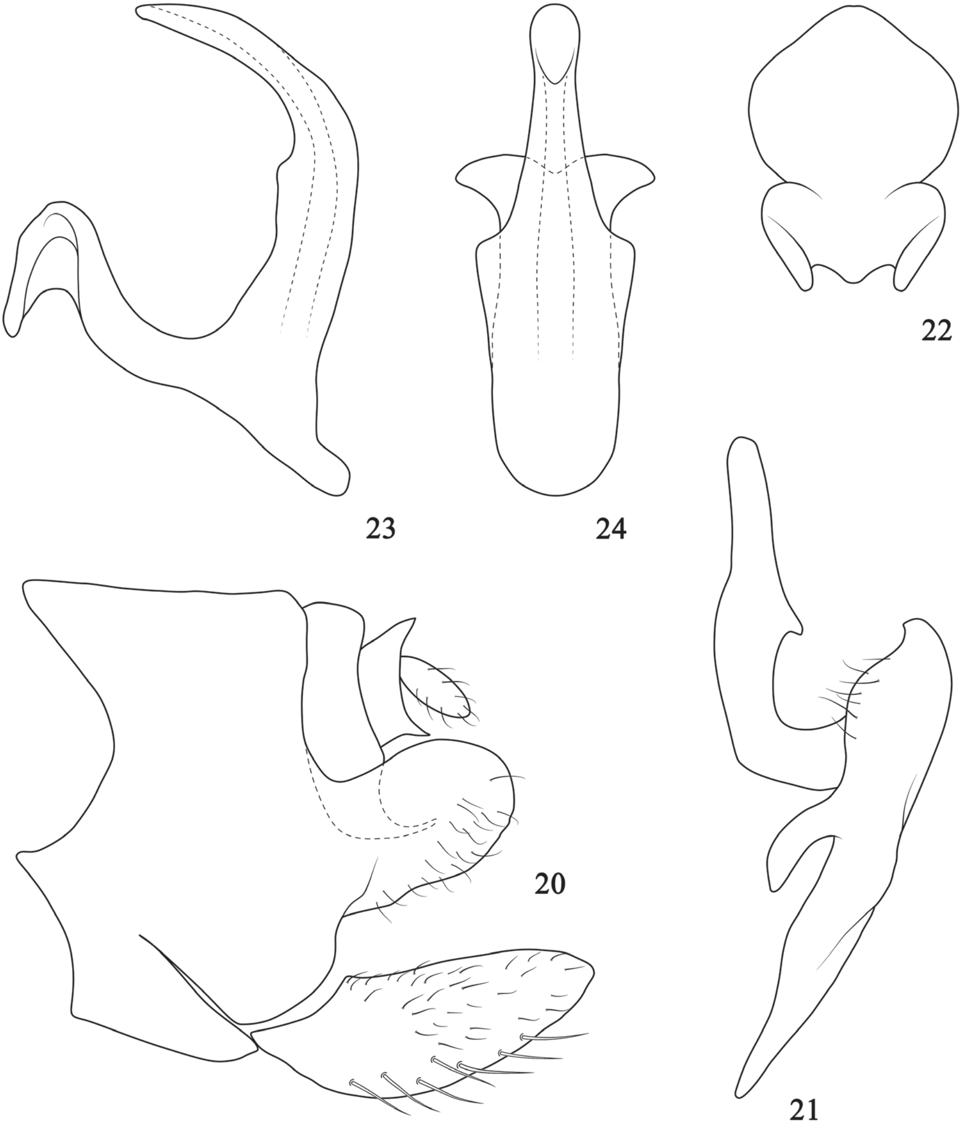
Female genitalia. Unknown.

Material examined. HOLOTYPE: ♂, CHINA: Hubei Province, Shennongjia, 17.VII.2013, collected by Chang Zhi-Min. PARATYPES: 1 ♂, CHINA: Hunan Province, Badagongshan, 03.VIII.2013, collected by Li Hu.

Distribution. China (Hubei and Hunan Provinces).

Remarks. This new species is similar to *O. fanjingensis* Zhang & Li but can be distinguished from the latter by the different shape of the pygofer lobe and the anal collar process, the aedeagal shaft with an apophysis on its dorsal margin near the base in lateral view, and expanded laterally near base in ventral aspect.

Etymology. The new species name is derived from the Latin word "*tumidus*", refers to the swollen structure of aegeagal shaft.



Figures 20–24. *Onukigallia tumida* sp. n. **20** Pygofer side and subgenital plate, lateral view **21** Style, dorsal view **22** Connective, dorsal view **23** Aedeagus, lateral view **24** Same, caudal view.

Key to species of *Onukigallia*

Based on the original descriptions, illustrations, and examinations of specimens the following key (largely based on the male genitalia) distinguishes the species of *Onukigallia* except *O. tenuis* (Matsumura) which is only known by its female.

1 Aedeagal shaft with teeth on dorsal margin **2**
– Aedeagal shaft without teeth on dorsal margin **3**
2 Aedeagal shaft slender and with several teeth on dorsal margin near middle.. .... ***O. onukii* (Matsumura)**
– Aedeagal shaft strongly slender and with more teeth on dorsal margin from subbasally to subapically .... ***O. neoonukii* sp. n.**
3 Aegeagal shaft with hump on dorsal margin in lateral view near midlength, and expanded laterally near base in ventral view................ ***O. tumida* sp. n.**
– Aegeagal shaft without apophysis on dorsal margin in lateral view, and not expanded laterally in ventral view 4
4 Preatrium of aedeagus elongate; pronotum darkly pigmented...................... .... ***O. arisana* (Matsumura)**
– Preatrium of aedeagus short and poorly developed; pronotum paler **5**
5 Aedeagus lacking preatrium; anal collar process with inflated subapex and round tip .... ***O. matsumurai* Zhang**
– Aedeagus with weakly developed preatrium; anal collar process with tapered subapex and acute tip...................................... ***O. fanjingensis* Zhang & Li**

Updated checklist and distributions of species of *Onukigallia*

Species name	**Distribution**
O. arisana (Matsumura, 1912)	China (Taiwan)
O. fanjingensis Zhang & Li, 1999	China (Shaanxi, Hubei, Guangxi, Guizhou, Fujian, Anhui, Zhejiang)
O. matsumurai Zhang, 2011	China (Yunnan)
O. neoonukii sp. n.	China (Sichuan, Guangdong)
O. onukii (Matsumura, 1912)	China (Gansu, Shaanxi, Ningxia, Shanxi, Liaoning, Jilin, Hebei, Henan, Anhui, Hubei, Hunan, Zhejiang, Guizhou, Sichuan, Yunnan), Japan, Korea, Russia
O. tenuis (Matsumura, 1912)	China (Taiwan)
O. tumida sp. n.	China (Hubei, Hunan)

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Viraktamath CA (1973) Some species of Agalliinae described by Dr. S. Matsumura. Kontyû 41(3): 307–311.

Viraktamath CA (2011) Revision of the Oriental and Australian Agalliini (Hemiptera: Cicadellidae: Megophthalminae). Zootaxa 2844: 1–118.

Zhang YZ, Li ZZ (1999) Two new species of Agalliinae (Homoptera: Cicadellidae) from Guizhou, China. Entomotaxonomia 21(2): 107–110.

Zhang B (2011) Revision of the leafhopper genus *Onukigallia* Ishihara, 1955 (Hemiptera: Cicadellidae: Megophthalminae). Zootaxa 2915: 52–60.

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New species of *Bidessonotus* Régimbart, 1895 with a review of the South American species (Coleoptera, Adephaga, Dytiscidae, Hydroporinae, Bidessini)

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Abstract

The South American species of the New World genus *Bidessonotus* Régimbart, 1895 are reviewed with descriptions of seven new species. This brings the total number of valid *Bidessonotus* species to 37, making it the largest Bidessini genus in the New World. The new species are *B. annae* **sp. n.** (Venezuela), *B. josiahi* **sp. n.** (Venezuela), *B. palecephalus* **sp. n.** (Venezuela), *B. reductus* **sp. n.** (Venezuela), *B. septimus* **sp. n.** (Venezuela), *B. spinosus* **sp. n.** (Venezuela), and *B. valdezi* **sp. n.** (Guyana, Suriname). New distribution records are provided for many other South American *Bidessonotus* species. The main diagnostic features of *Bidessonotus* species are in the male genitalia, and these are illustrated for all South American species. Diagnostic features, distributions (including distribution maps), and additional comments are provided for all South American species.

Resumen

Las especies sudamericanas del género del Nuevo Mundo *Bidessonotus* Regimbart, 1895 (Coleoptera: Adephaga: Dytiscidae: Hydroporinae: Bidessini) se revisan con descripciones de siete especies nuevas. Se eleva el número total de especies válidas en *Bidessonotus* a 37, el género más grande de Bidessini en el Nuevo Mundo. Las especies nuevas son *B. annae* **sp. n.** (Venezuela), *B. josiahi* **sp. n.** (Venezuela), *B. palecephalus* **sp. n.** (Venezuela), *B. reductus* **sp. n.** (Venezuela), *B. septimus* **sp. n.** (Venezuela), *B. spinosus* **sp. n.** (Venezuela), y *B. valdezi* **sp. n.** (Guyana, Surinam). Se incluyen nuevos registros distribucionales para la mayoría de las otras especies de *Bidessonotus* en América del Sur. Los principales caracteres diagnósticos para las especies de *Bidessonotus* están en los órganos genitales de los machos, los cuales se ilustran para todas las especies sudamericanas. También se incluyen caracteres diagnósticos, mapas de distribución, y comentarios adicionales para todas las especies sudamericanas.

Keywords
Water beetles, taxonomy, classification, Neotropical, *Bidessonotus*, Dytiscidae, Coleoptera

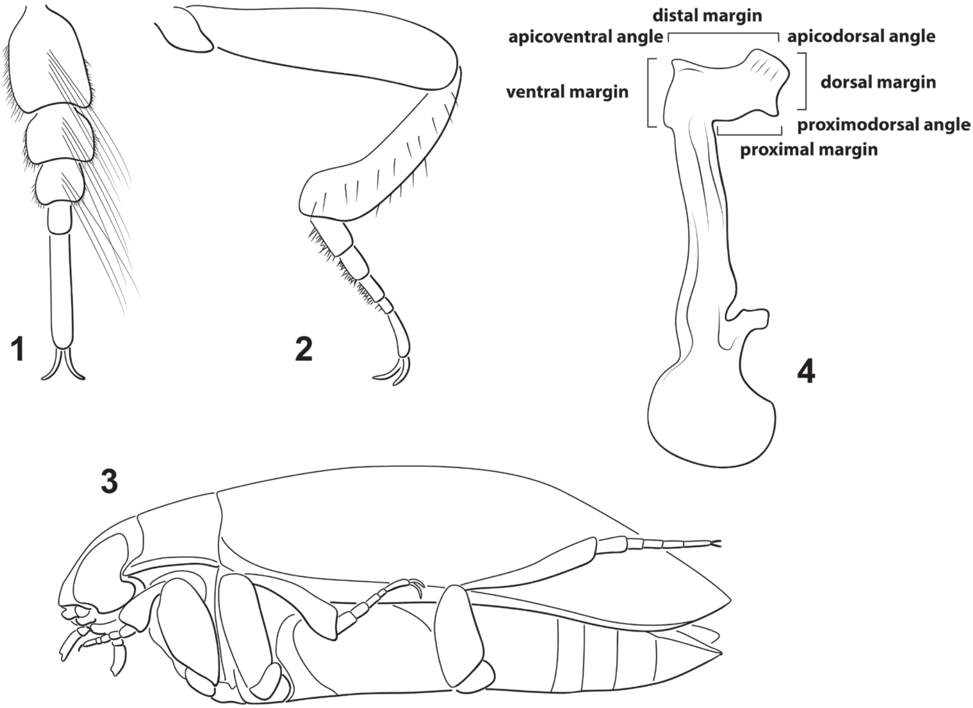
Introduction

The New World Bidessini genus *Bidessonotus* Régimbart (Coleoptera: Dytiscidae: Hydroporinae) included, prior to this paper, 30 species, making it one of the largest genera in the tribe in the New World with only *Neobidessus* Young (30 species) and *Liodessus* Guignot (27 species) comparable in size. There are three species in eastern and southern North America, numerous species in Central America and the Caribbean and additional species in South America. Although many *Bidessonotus* species are widespread, others are relatively narrowly distributed, and new species are likely to be discovered with additional collecting efforts in undercollected areas of South America.

Bidessonotus are easily diagnosed by the presence of relatively distinctively pentamerous pro- and mesotarsi (Fig. 1) whereas in other Bidessini these are pseudotetramerous with tarsomere IV small and concealed in the lobes of III. Males are characteristic, too, with strongly curved mesotibiae (Fig. 2) and a distinctly concave ventral surface (Fig. 3). The male median lobe is strongly asymmetrical and laterally flattened with a broadly expanded and characteristically shaped apex (like a "hatchet," e.g Fig. 4). Species differ especially in the shape of this apex along with body size and coloration. Otherwise, species are relatively similar to each other, typically elongate oval, mottled gray and brown with the head and pronotum yellow, and females of many species, and occasionally males also, purplish iridescent.

The genus was originally described by Régimbart (1895) to include seven species, three of which were new, with a few names treated as junior synonyms. Earlier species were placed in *Hydroporus*, but later in *Bidessus* by Sharp (1882). Blatchley (1919) next described a new species from Florida placing it in *Bidessus*, however J. Balfour-Browne (1947) later transferred it to *Bidessonotus*, who revised the genus clarifying a number of the described species and adding eleven new ones. After this, little was done in the genus for several decades except for one new species described by Guignot (1957). A significant contribution was made, however, by Young (1990), who revised the entire genus and added nine new species. Finally, a new species was described by Miller (1997).

Collecting in poorly known areas of northern South America during the past decade has led to discovery of seven previously undescribed species of *Bidessonotus*, and these are described here. This brings the number of known species to 37. New records of other South American species are also presented here along with brief diagnostic descriptions, illustrations, additional comments, and distributions. Young (1990) was unable to write a suitable key because the diagnostic features of species are coloration,



Figures 1–4. 1–2 *Bidessonotus obtusatus* male. **1** Left protarsomeres, dorsal aspect **2** Left mesoleg, anterior aspect **3** *B. tibialis* male, habitus, lateral aspect **4** *B. rubellus*, male median lobe, right lateral aspect showing regions referenced in diagnoses and descriptions.

size and male genitalia, and come in such combinations as to make a key difficult. That problem persists, and no key is presented here. The best way to identify species is to compare male genitalia against the illustrations and use distribution information.

Materials and methods

Measurements. Measurements were made with an ocular scale on a Zeiss Discovery V8 dissecting microscope. Emphasis was placed on getting the diagnostic range of measurements of structures rather than finding the average or taking a random sample. Measurements include: 1) total length (TL), 2) greatest width across elytra (GW), 3) greatest width of pronotum (PW), 4) greatest width of head (HW), and 5) distance between eyes (EW). The ratios TL/GW, HW/EW and FW/FL were also calculated.

Images. Illustrations were made using a drawing tube on a Zeiss Discovery V8 dissecting scope. Sketches were first done in pencil then scanned, placed into an Adobe Illustrator artboard and "inked" digitally using vector lines. The illustration of the male median lobe of *B. bicolor* was redrawn from Guignot (1957).

Material. Specimens were examined from the following collections:

CSBD	Center for Biological Diversity, University of Guyana (type specimens currently reposed with KUNHM)
FSCA	Florida State Collection of Arthropods, University of Florida, Gainesville, FL, USA (P. Skelley)
KBMC	Kelly B. Miller Collection, Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM, USA
KUNHM	University of Kansas Natural History Museum, University of Kansas, Lawrence, Kansas, USA (A.E.Z. Short)
MIZA	Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez, Universidad Central de Venezuela, Maracay, Venezuela (L. Joly)
MSBA	Museum of Southwestern Biology Division of Arthropods, University of New Mexico, Albuquerque, NM, USA (K.B. Miller)
NZCS	National Zoological Collection of Suriname, Paramaribo, Suriname (P. Ouboter)
USNM	United States National Collection of Insects, Smithsonian Institution, Washington, DC, USA (T. Erwin)

Label data for holotype specimens are reported verbatim. All other label data, including for paratypes, are reported in a standardized format. All paratypes have a blue label with a black line border bearing the species name attached to them.

Distribution maps. Dot maps presented here are derived from examined specimens and specific localities reported by Young (1990) and J. Balfour-Browne (1947).

Taxonomic characters

Bidessonotus are superficially extremely similar to each other with a similar body shape and coloration. There are some distinctive character systems, however, that require some explanation.

Head. The anterior surface of the clypeus of some *Bidessonotus* has a moderately distinctive transverse shallow sulcus which may be interrupted medially. Young (1990) used this character, but I have found it to be somewhat variable within species and difficult to assess, so it is not emphasized here.

Pronotum. The basal pronotal plicae are somewhat variably impressed with some species deeply and others more shallowly. However, Young (1990) found the relative length of the pronotal plicae to the elytral plicae to be about the same length and not variable between South American species, so this comparative feature is not used here.

Prosternal process. The prosternal process in *Bidessonotus* is elongate and slender. There is some variability in the relative width and the apex that ranges from sharply pointed to rounded. The surface may be convex to flat to somewhat sulcate, features emphasized by Young (1990), but emphasized less here given lack of variability in the South American species.

Male genitalia. Dytiscid male genitalia are rotated in such a way as to make describing orientation of structures difficult. This paper follows Miller and Nilsson (2003) in the way these features are described. The male median lobe is bilaterally asymmetrical with the base typically very large and complex and the apical portion developed into a flattened, dorsally directed, roughly rectangular "blade" (something like a hatchet blade) with a highly variable and species-specific shape that is the most reliable diagnostic feature for *Bidessonotus*. The dorsal, distal, ventral and proximal margins have variable shapes, spines and teeth (e.g. Fig. 4). The lateral lobes are bilaterally asymmetrical with the apical segments, in particular, often species specific and useful for species diagnostics.

Sexual dimorphism. All *Bidessonotus* species are distinctively sexually dimorphic. The metaventrite and medial portions of the metacoxae are distinctly concave in males (Fig. 3), possibly to correspond to the convex dorsal surface of females when mating. Also, the male mesotibiae are abruptly curved in males (Fig. 2), but straight in females. Other sexual dimorphisms are more variable. Young (1990) emphasized lateral impressions on abdominal ventrite VI that are more distinctly impressed in males. However, South American species have only indistinct, and more medial, modifications to the ventrite. Females of some species have the elytra more abruptly rounded apically with the apicolateral margins broadly lobed (Figs 6b, 7b) and others have a distinct subapical spine on the margin of the elytron (Fig. 10b) whereas males have the apicolateral margins evenly curved (e.g. Figs 6a, 7a, 10a). Finally, coloration and dorsal microsculpture can be somewhat variable with females often matte and/or dorsally purplish iridescent, though in some cases males may also have such coloration.

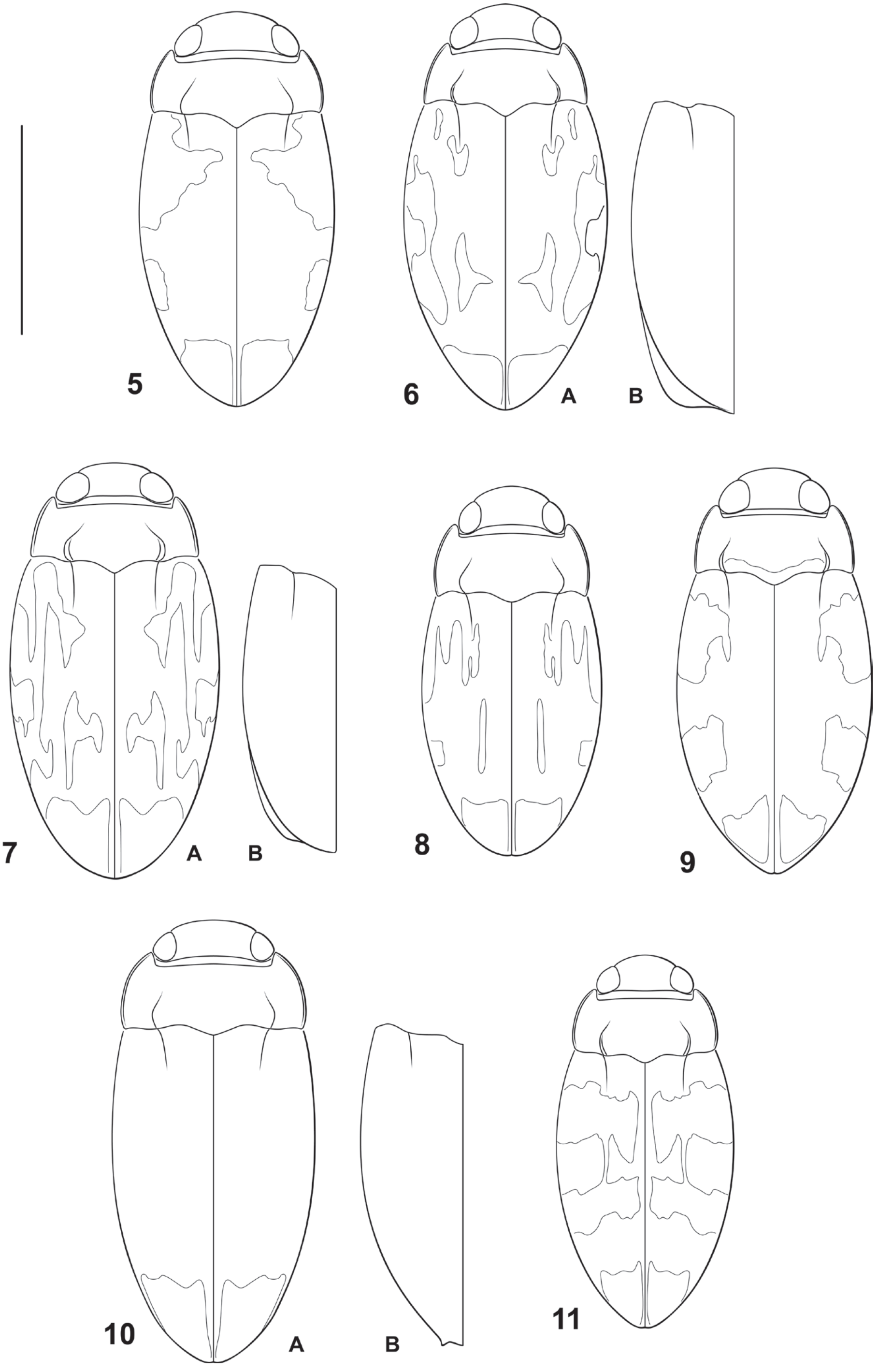
Taxonomy

Bidessonotus annae Miller, sp. n.

http://zoobank.org/9BEB8E25-1EE8-46F8-A78E-F7D7CC5A2ABD
Figs 5, 12, 30

Type locality. Venezuela, Apure State, Communidad Caño Gato, on Rio Sipapo, 4°58.838'N, 67°44.341'W.

Diagnosis. Specimens of this species are brown with irregular, indistinct paler regions. The prosternal process is laceolate, shallowly sulcate and apically pointed. The female elytron is unmodified. The apical blade of the male median lobe is slender and curved with an elongate, curved, apically narrowly rounded process at the apicoventral angle, and the dorsal margin narrowly truncate (Fig. 12a). The lateral lobes are nearly bilaterally symmetrical (Fig. 12b, c), though the left lateral lobe has the apex somewhat more broad with a more distinctive, angulate expansion on the ventral margin (Fig. 12c). Male genitalia are similar to those of *B. tibialis* but the apical blade in *B. annae* is more slender, more strongly curved, and more truncate along the dorsal margin, and



Figures 5–11. *Bidessonotus* species, dorsal habitus. **5** *B. annae* **6** *B. josiahi* **A** male **B** female, left elytron **7** *B. palecephalus* **A** male **B** female, left elytron **8** *B. reductus* **9** *B. septimus* **10** *B. spinosus* **A** male **B** female, left elytron **11** *B. valdezi*. Scale bar: 1.0 mm.

the anteroventral process is very slender, strongly curved and directed ventrad whereas it is somewhat broader and directed apically in *B. tibialis*.

Description. *Measurements*. TL = 1.7–1.8 mm, GW = 0.8–0.9 mm, PW = 0.7–0.8 mm, HW = 0.5–0.6 mm, EW = 0.3 mm, TL/GW = 2.0–2.1, HW/EW = 1.9. Body shape elongate, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 5). Head yellow orange. Pronotum yellow orange, darker along posterior margin. Elytron base color orange brown with pale diffuse areas anteriorly and medially, and a distinctive pale macula apically (Fig. 5); without purplish iridescence. Ventral surfaces orange on all surfaces, some sutures darker.

Sculpture and structure. Head with anterior clypeal margin evenly rounded; surface smooth and shiny, impuncate, slightly microreticulate; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins evenly curved; basal striae moderately impressed, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface overall shiny, slightly microreticulate, finely punctate. Elytron with lateral margins broadly curved; basal stria distinct, elongate, moderately impressed; surface of elytron covered with fine punctation, surface between punctures matte, microreticulate. Prosternal process elongate, lanceolate, apically pointed, surface broadly convex throughout length. Metaventrite with distinctive carinae extending from medial apex of metaventrite process posteriorly to near posterior margin at anterior terminus of metacoxal lines; anteriorly very closely approximated, divergent to posterior margin; surface of metaventrite shiny with few micropunctures. Metacoxae shiny with few micropunctures; metacoxal lines distinct, broad apically, broadly curved with external surface convex, convergent anteriorly. Basal abdominal ventrites punctate, other surfaces of abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with apical blade narrow, curved, with apicoventral elongate, curved process, ventral margin subtruncate, proximal margin curved (Fig. 12a). Right lateral lobe in lateral aspect with apical segment longer than proximal segment; apical segment expanded medially, apex rounded (Fig. 12b); left lateral lobe with apical segment similar to right, but broader and more distinctly and prominently angulate along ventral margin (Fig. 12c).

Variation. Only a single male specimen examined.

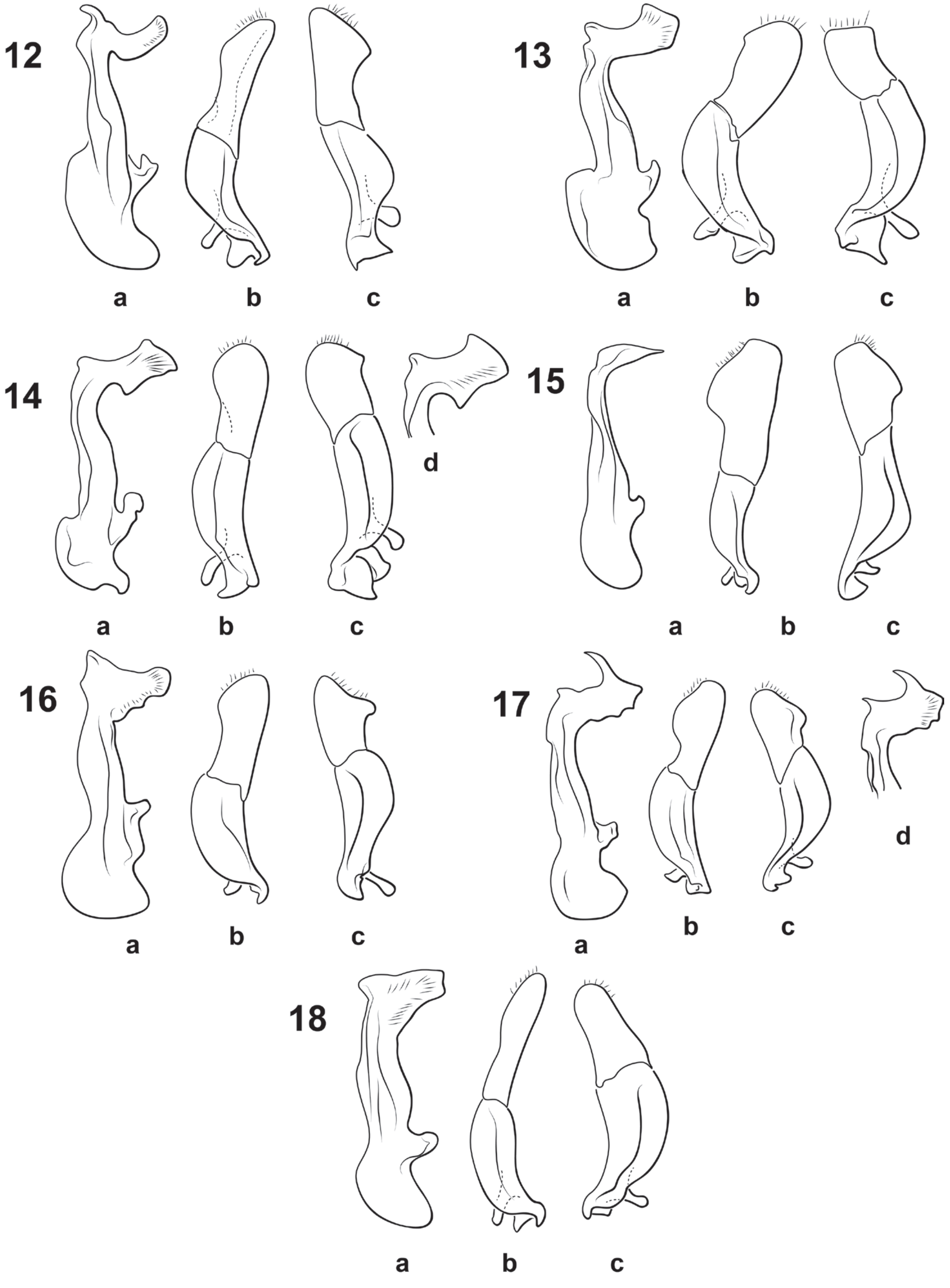
Sexual dimorphism. Only a single male specimen examined.

Etymology. This species is named *annae* after the author's daughter, Annie Miller.

Distribution. This species is known from one locality in Apure State, Venezuela (Fig. 30).

Habitat. The habitat where the type series was collected is a sandy forest stream with large deposits of leaf pack along the margins.

Type material. Holotype in MIZA, male labeled, "VENEZUELA: Apure State 4°58.838'N, 67°44.341'W, 95m Communidad Caño Gato, on Rio Sipapo: 16.i.2009; leg. Short, Miller, Camacho, Joly, & García VZ09-0116-01X; along stream/ SM0842863 KUNHM-ENT [barcode label]/ HOLOTYPE *Bidessonotus annae* Miller, 2016 [red label with black line border]." No other specimens examined.



Figures 12–18. *Bidessonotus* species, male genitalia **A** median lobe, right lateral aspect **B** right lateral lobe, right lateral aspect **C** left lateral lobe, apical segment, left lateral aspect **D** median lobe apex, oblique right lateral aspect **12** *B. annae* **13** *B. josiahi* **14** *B. palecephalus* **15** *B. reductus* **16** *B. septimus* **17** *B. spinosus* **18** *B. valdezi*.

Bidessonotus josiahi **Miller, sp. n.**

http://zoobank.org/49A491B8-9C3B-4D3C-868E-8F2F0B185DD0
Figs 6, 13, 31

Type locality. Venezuela, Apure State, between "La Ye" and Bruzual, 7.644°N, 69.300°W.

Diagnosis. Specimens of this species are brown with moderately distinctive maculae. The prosternal process is lanceolate and flat with the apex pointed. The female elytron is apicolaterally broadly lobed (Fig. 6b). The apical blade of the male median lobe is broad with the apicoventral angle developed into a rounded prominence, a broad apicodorsal tooth, the proximal margin straight without a tooth, and the ventral margin broadly pointed (Fig. 13a). The apical portions of the lateral lobes are broad with the apical segment of the right lateral lobe longer and broader with the apex very broadly rounded (Fig. 13b). The apical segment of the left lateral lobe is somewhat shorter and narrower than the right and the apex is very broadly truncate (Fig. 13c). The male genitalia are not similar to any other species. The proximal margin is nearly straight, without undulations or teeth. The apex is strongly obliquely truncate.

Description. *Measurements*. TL = 2.2–2.3 mm, GW = 1.1–1.2 mm, PW = 0.9 mm, HW = 0.6 mm, EW = 0.3 mm, TL/GW = 2.0, HW/EW = 2.0. Body shape elongate, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 6). Head orange. Pronotum yellow, dark along posterior margin. Elytron evenly dark brown except apex broadly pale (Fig. 6); without purplish iridescence in either sex. Ventral surfaces orange, darker orange laterally.

Sculpture and structure. Head with anterior clypeal margin evenly rounded; surface smooth and shiny, with few punctures medially; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins evenly curved; basal striae strongly impressed, especially basally, broad, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface overall slightly matte, but shiny, medial surface finely punctate. Elytron with lateral margins broadly curved; basal stria distinct, elongate, well impressed basally; surface of elytron covered with fine punctation, surface between punctures shiny. Prosternal process elongate, lanceolate, apically pointed, surface broadly convex throughout length. Metaventrite with distinctive carinae extending from medial apex of metaventrite process posteriorly to near posterior margin at anterior terminus of metacoxal lines; anteriorly very closely approximated, divergent to posterior margin; surface of metaventrite shiny with few micropunctures. Metacoxa shiny with few micropunctures; metacoxal lines distinct, broad, broadly curved with external surface convex, slightly convergent anteriorly. Basal abdominal ventrites punctate, other surfaces of abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with apical blade broad, with apicoventral rounded prominence, broad apicodorsal tooth, proximal margin straight, without tooth, ventral margin broadly pointed (Fig. 13a). Right lateral lobe in lateral aspect with apical segment about as long as proximal segment; apical segment apically slightly expanded, apex broadly rounded (Fig. 13b); left lateral lobe with apical segment shorter than basal segment, broad with apex very broadly truncate (Fig. 13c).

Variation. Specimens are variable in the extent of the pale markings on the elytron.

Sexual dimorphism. With typical *Bidessonotus* dimorphism. Males with apicolateral margin of elytron evenly curved (Fig. 6a); females apically with distinctive, subapical broad lobe (Fig. 6b).

Etymology. This species is named *josiahi* after the author's son, Josiah Miller.

Distribution. The species is known from northern Venezuela (Fig. 31).

Habitat. The type specimens were collected from a "lagoon."

Type material. Holotype in MIZA, male labeled, "VENEZUELA: Apure State 7.644°N, 69.300°W, 90, between "La Ye" & Bruzual 18.i.2009: Short, Camacho, & García: VZ09-0118-03X: lagoon/ SM0845741 KUNHM-ENT [barcode label]/ HOLOTYPE *Bidessonotus josiahi* Miller, 2016 [red label with red line border]." Paratypes 44; **Venezuela:** Anzoategui, Transect 1, 9.33°N, 64.196°W, 12 Aug 2009, Cordero, R (1, SEMC); Apure, between La Ye and Bruzual, 7.644°N, 69.300°W, 18 Jan 2009, Short, Camacho, Miller (6, SEMC); Guarico, N of Palenque, 9.113°N, 66.993°W, 08 Jan 2009, Short, Camacho, Garcia, Joly, Miller (3, SEMC); Monagas, El Guamo Reservoir, 10.102°N, 63.690°W, 28 Jan 2010, Short & Garcia (34, SEMC).

Bidessonotus palecephalus Miller, sp. n.

http://zoobank.org/4E6CCE60-C5C0-46B6-8229-6A30BB98E398

Figs 7, 14, 30

Type locality. Venezuela, Guarico, N of Palenque, 9.113°N, 66.993°W.

Diagnosis. This is a relatively pale brown species. The head color in specimens of *B. palecephalus* is overall pale, unlike *B. melanocephalus* which has the base of the head darkened. The prosternal process is flat and apically pointed. Females have the apicolateral elytral margins developed into a prominent lobe (Fig. 7b). Males of this species have the median lobe shape similar to those of *B. melanocephalus* with a tooth medially on the dorsal margin near the apical base of the shaft as well as a tooth at each end of the distal margin (Fig. 14a), though the overall shapes are different in the two species. The lateral lobes are moderately similar in shape with the apical segments broad, but the right apical segment (Fig. 14b) is apically broadly rounded and the left apical segment is distinctly angulate along the ventral margin (Fig. 14c).

Description. *Measurements*. TL = 1.9–2.0 mm, GW = 1.0 mm, PW = 0.8–0.9 mm, HW = 0.5–0.6 mm, EW = 0.3 mm, TL/GW = 1.8–2.0, HW/EW = 1.8–2.0. Body shape elongate oval, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 7). Head, including all appendages and ventral surface, entirely pale yellow to yellow-orange. Pronotum yellow to yellow-orange. Elytron base color brown with large irregular yellow fasciae and maculae (Fig. 7); dorsal surfaces not purplish or iridescent in either sex. Ventral surfaces, including all legs and mouthparts, yellow, slightly darker along some sutures.

Sculpture and structure. Head with anterior clypeal margin slightly thickened, evenly rounded; surface smooth and shiny; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins evenly curved; basal striae strongly impressed, broad, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface overall slightly matte, but shiny, surface mediad of striae distinctly punctate. Elytron with lateral margins broadly curved; basal stria distinct, elongate, well impressed basally; surface of elytron covered with fine punctation, surface between punctures shiny. Prosternal process elongate, apically pointed, surface broadly convex throughout length. Metaventrite with distinctive carinae extending from medial apex of metaventrite process posteriorly to near posterior margin at anterior terminus of metacoxal lines; surface of metaventrite shiny with few micropunctures. Metacoxae shiny with few micropunctures; metacoxal lines distinct, broad, broadly curved with external surface convex, slightly convergent anteriorly. Basal abdominal ventrites punctate, other surfaces of abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with blade elongate, with apicoventral tooth, submedial broad tooth on distal margin and broad tooth along proximal margin, dorsal margin broad and obliquely truncate (Fig. 14a, d). Right lateral lobe in lateral aspect with apical segment about as long as proximal segment; apical segment apically broadly expanded, apex broadly rounded (Fig. 14b) left lateral lobe with apical segment very broad, apically very broadly rounded and with a distinct angulation along the ventral margin (Fig. 14c).

Variation. Specimens vary in the extent and intensity of the elytral fasciae and maculations.

Sexual dimorphism. With typical dimorphism found in *Bidessonotus*. Males with apicolateral margin of elytron evenly curved (Fig. 7a); females apically shortened, more abruptly rounded with distinctive, broadly rounded posterolateral expansion (Fig. 7b). Males with elytra shiny and smooth between punctures; females with elytra opaque and microreticulate.

Etymology. The species is named *palecephalus* from the Greek words *pale*, meaning "pale," and *cephalus*, meaning "head," for the pale head of specimens in comparison with the somewhat similar species *B. melanocephalus*.

Distribution. The species is known from Apure and Guarico, Venezuela (Fig. 30).

Habitat. Nothing is known of the habitat of this species.

Type material. Holotype in MIZA, male labeled, "VENEZUELA: Guarico State 9.113°N, 66.993°W, 152m, Stream @ [sic] road crossing, N. of Palenque; 6.i.2009; leg. Short, García, Miller, Camacho, Joly VZ09-0108-03X; stream/ SEMC0854983 KUNHM-ENT [barcode label]/ HOLOTYPE *Bidessonotus palecephalus* Miller, 2016 [red label with black line border]." Paratypes, 31 total from the following localites: **Venezuela**: Apure, between La Ye and Bruzual, 7.644°N, 69.300°W, 18 Jan 2009, Short, Camacho, Miller (6, SEMC); Guarico, N of Palenque, 9.113°N, 66.993°W, 08 Jan 2009, Short, Camacho, Garcia, Joly, Miller (25, SEMC).

***Bidessonotus reductus* Miller, sp. n.**

http://zoobank.org/6EEEE867-0465-44F6-BA7A-BC0E964097A8
Figs 8, 15, 31

Type locality. Venezuela, Bolivar State, Gran Sabana, N Santa Elena, Rio Guara at Rt. 10, 04°37.362'N, 61°05.679'W.

Diagnosis. Specimens of this species are small and pale (Fig. 8). The prosternal process is lanceolate and slightly sulcate with the apex pointed. The male genitalia in the species are quite unique. The apical blade of the male median lobe is narrowed and elongate-triangular with the dorsal margin sharply pointed (Fig. 15a). The right lateral lobe has the apical portion very large and broad with a very broad expansion along the ventral margin (Fig. 15b). The right lateral lobe has the apical portion somewhat smaller relative to the basal segment but also broad and distinctly expanded along the ventral margin (Fig. 15c). Females have the apicolateral elytral margins unmodified.

Description. *Measurements*. TL = 1.8–2.0 mm, GW = 0.9–1.0 mm, PW = 0.8 mm, HW = 0.5 mm, EW = 0.3 mm, TL/GW = 2.0, HW/EW = 1.7–1.8. Body shape elongate oval, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 15). Head orange yellow. Pronotum yellow. Elytron base color light brown with diffuse, irregular pale fasciae, oriented more-or-less longitudinally, apex pale; female with indistinct purplish iridescence. Ventral surfaces yellow on all surfaces.

Sculpture and structure. Head with anterior clypeal margin evenly rounded; surface smooth and shiny, with few micropunctures medially; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins evenly curved; basal striae distinctly impressed, especially basally, elongate, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface shiny, medial surface finely punctate. Elytron with lateral margins broadly curved; basal stria distinct, elongate, well impressed; surface of elytron covered with fine punctation, surface between punctures somewhat shiny but microreticulate. Prosternal process moderately broad, broadly oval, apex rounded, surface broadly convex throughout length. Metaventrite with distinctive carinae extending from medial apex of metaventrite process posteriorly to near posterior margin at anterior terminus of metacoxal lines; anteriorly very closely approximated, strongly divergent to posterior margin; surface of metaventrite shiny, impunctate. Metacoxae shiny, nearly impunctate; metacoxal lines distinct, broadly separated, anteriorly slightly divergent. Abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with blade reduced, slender, sharply pointed at dorsal margin (Fig. 15a). Right lateral lobe in lateral aspect with apical segment much longer than proximal segment; apical segment apically very broadly expanded medially, apex broadly rounded (Fig. 15b); left lateral lobe with apical segment shorter than basal segment, broad with apex truncate and with distinct expansion along ventral margin (Fig. 15c).

Variation. The two specimens vary somwhat in the extent and intensity of the pale elytral areas.

Sexual dimorphism. Specimens of this species with typical *Bidessonotus* sexual dimorphism and female more matte dorsally than male. Without other evident dimorphisms.

Etymology. This species is named *reductus*, Latin for "reduced," for the relatively small apical blade of the male median lobe.

Distribution. Known only from the Gran Sabana, Bolivar State, Venezuela (Fig. 31).

Habitat. Specimens have been collected from "marshy areas."

Type material. Holotype in MIZA, male labeled, "VENEZUELA: Bolivar State 04°37.362'N, 61°05.679'W, 876 m Gran Sabana, N. Santa Elena Rio Guara at Rt. 10. 17.VII.2010 Leg. Short, Tellez & Arias marshy area; VZ10-0717-02A/ SEMC0908509 KUNHM-ENT [barcode label]/ HOLOTYPE *Bidessonotus reductus* Miller, 2016 [red label with double black line border]." Paratype, 1 female, **Venezuela**, Bolivar State, 04°41.878'N, 61°04.246'W, 815m, Gran Sabana, N Santa Elena, marshy area along Rt 10, Short, Tellez and Camacho, legs. 17 Jul 2010, VZ10-0717-03A, SEMC0908642.

Bidessonotus septimus Miller, sp. n.

http://zoobank.org/7D5AC872-4A0C-4351-B079-64132D28A150
Figs 9, 16, 32

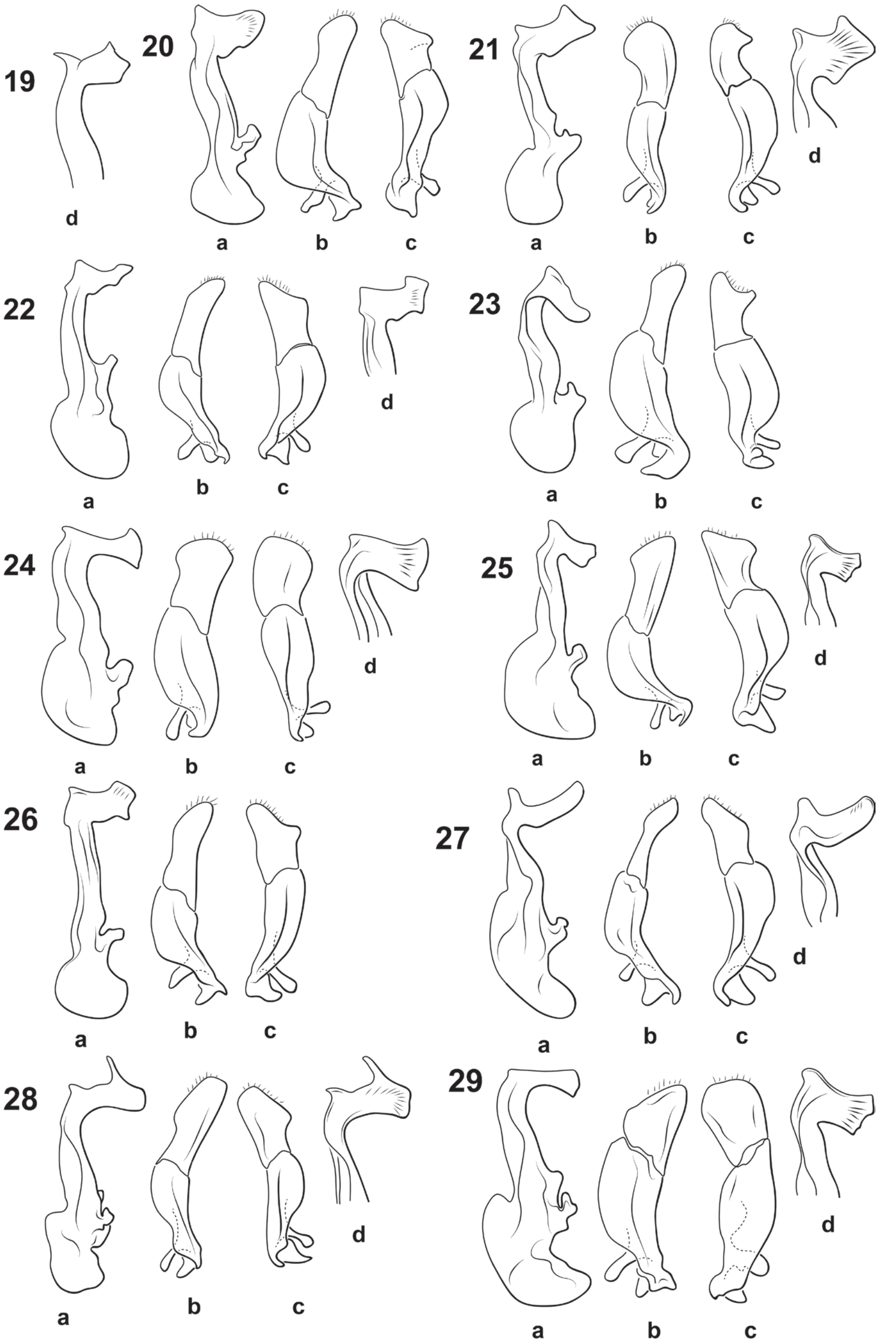
Type locality. Venezuela, Apure, Bruzual, edge of town, 8.042°N, 69.342°W.

Diagnosis. Specimens of this species are medium-sized and dark with moderately well-developed, but somewhat diffuse maculae. The prosternal process is moderately broad, sulcate and apically pointed. The male genitalia are characteristic with the apical blade of the median lobe broad with a moderately well-developed apicoventral triangular prominence, the dorsal margin rounded, and the proximal margin oblique and distinctly undulate (Fig. 16a). The lateral lobes have the apical segments rather different in shape with the right lateral lobe apically elongate, apically rounded and expanded along the ventral margin (Fig. 16b). The left lateral lobe has the apical segment short, broad and apically distinctly concave making an obliquely bilobed margin (Fig. 16b). This shape is somewhat similar to that of *B. dubius* (Fig. 20), but is more elongate with the dorsal margin distinctly rounded.

Description. *Measurements*. TL = 2.0 mm, GW = 1.0 mm, PW = 0.8 mm, HW = 0.6 mm, EW = 0.2 mm, TL/GW = 2.0, HW/EW = 2.3. Body shape elongate, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 9). Head yellow. Pronotum yellow, darker along posterior margin. Elytron base color dark brown with diffuse, irregular pale maculae antero- and mediolaterally, apex pale (Fig. 9); purplish iridescence not evident in male specimen. Ventral surfaces yellow orange on all surfaces.

Sculpture and structure. Head with anterior clypeal margin evenly rounded; surface smooth and shiny, with few micropunctures medially; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins



Figures 19–29. *Bidessonotus* species, male genitalia; **A** median lobe, right lateral aspect **B** right lateral lobe, right lateral aspect **C** left lateral lobe, apical segment, left lateral aspect **D** median lobe apex, oblique right lateral aspect **19** *B. bicolor* (redrawn from Guignot, 1957) **20** *B. dubius* **21** *B. melanocephalus* **22** *B. obtusatus* **23** *B. otrerus* **24** *B. paludicolus* **25** *B. ploterus* **26** *B. rubellus* **27** *B. tibialis* **28** *B. truncatus* **29** *B. vicinus*.

evenly curved; basal striae strongly impressed, especially basally, elongate, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface shiny, medial surface finely punctate. Elytron with lateral margins broadly curved; basal stria distinct, elongate, well impressed; surface of elytron covered with fine punctation, surface between punctures matte, microreticulate. Prosternal process narrow, elongate, lanceolate, apex pointed, surface broadly convex throughout length. Metaventrite with carinae extending from medial apex of metaventrite process posteriorly, effaced and indistinct for much of length, marked mainly by smooth longitudinal area; anteriorly very closely approximated, strongly divergent to posterior margin; surface of metaventrite shiny, impunctate. Metacoxae shiny, nearly impunctate; metacoxal lines distinct, moderately separated, subparallel, slightly curved anteriorly forming slight lateral bulge. Abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with blade broad, with apicoventral tooth, ventral tooth near apical base of shaft, angulate, oblique proximal margin, dorsal margin rounded, produced (Fig. 16a). Right lateral lobe in lateral aspect with apical segment about as long as proximal segment; apical segment apically slightly expanded, apex rounded (Fig. 16b); left lateral lobe short, broad, apically obliquely concave making margin obliquely and broadly bilobed (Fig. 16c).

Variation. Only a single specimen was examined.

Sexual dimorphism. Only a single specimen was examined.

Etymology. This species is named *septimus*, Latin for "seventh," since there are seven species described in *Bidessonotus* herein.

Distribution. The single specimen was found in Apure State, Venezuela.

Habitat. The holotype was collected from a "large marsh."

Type material. Holotype in MIZA, male labeled, "VENEZUELA: Apure State 8°2.534'N, 69°20.530' 83m edge of Bruzual; 18.i.2009 leg, Short, García, Camacho VZ09-0118-04X; large marsh/ SM0844586 KUNHM-ENT [barcode label]/ HOLOTYPE *Bidessonotus septimus* Miller, 2016 [red label with black line border]."

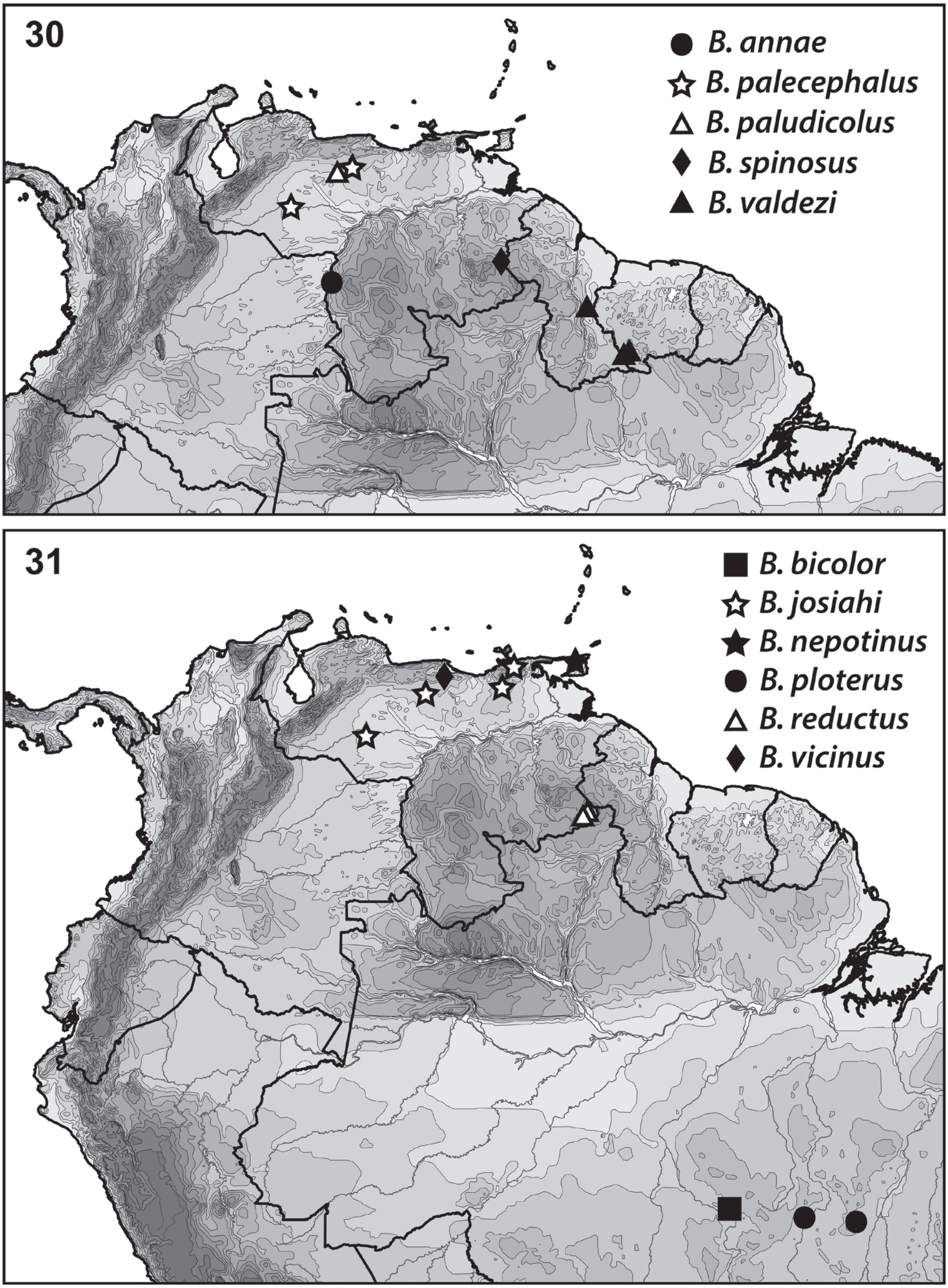
***Bidessonotus spinosus* Miller, sp. n.**

http://zoobank.org/17890E01-A262-4AF8-B28C-D991C756071E

Figs 10, 17, 30

Type locality. Venezuela, Bolivar, Gran Sabana, Rio Aponwao at Rt 10, 5.847°N, 61.467°W.

Diagnosis. Individuals have brown elytra with diffuse, poorly defined paler regions. The prosternal process is broadly oval, apically rounded and not sulcate. The female elytron has the apicolateral margin developed into a distinctive spine (Fig. 10b). The apical blade of the male median lobe is very broad with a spinous process at the anteroventral angle, a long, spinous process medially on the distal margin, and the dorsal margin irregularly subtruncate (Fig. 17a). The right lateral lobe has the apical segment broadly expanded along the ventral margin and about as long as the basal segment



Figures 30–31. *Bidessonotus* species, South American distributions.

(Fig. 17b). The left lateral segment is shorter and broader with a distinct, rounded angulation along the ventral margin (Fig. 17c). The male genitalia (Fig. 17a,d) are similar to *B. truncatus* (Fig. 28a,d) in having a distinctive spine along the apical margin. The apical blade is much broader and shorter with the proximal margin irregularly toothed (Fig. 17a,d).

Description. *Measurements*. TL = 2.0 mm, GW = 1.0 mm, PW = 0.8–0.9 mm, HW = 0.6 mm, EW = 0.3 mm, TL/GW = 2.0, HW/EW = 1.7–1.8. Body shape elongate oval, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 10). Head orange. Pronotum entirely yellow. Elytron base color brown with broad, diffuse, somewhat transverse slightly paler regions, margin of regions vague and indistinct (Fig. 10); without purplish dorsal iridescence. Prosternal surface yellow; other thoracic ventrites orange except metacoxa darker orange.

Sculpture and structure. Head with anterior clypeal margin slightly thickened laterally, broadly rounded; surface smooth and shiny; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins evenly curved; basal striae moderately impressed, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface overall shiny, surface mediad of striae slightly punctate. Elytron with lateral margins broadly curved; basal stria distinct, moderately elongate, well impressed basally; surface of elytron covered with punctation, surface between punctures shiny but with distinctive microreticulation. Prosternal process elongate, lanceolate, apically pointed, surface broadly convex throughout length. Metaventrite with carinae extending from medial apex of metaventrite process posteriorly to posterior margin at anterior terminus of metacoxal lines; lines narrowly separated anteriorly, slightly divergent posteriorly and somewhat effaced; surface of metaventrite shiny with few micropunctures. Metacoxa shiny with few micropunctures; metacoxal lines distinct, nearly parallel, width slightly increased near anterior margin making lines slightly undulate anteriorly. Basal abdominal ventrites punctate, other surfaces of abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with apical blade broad, with apicoventral sharp tooth, long spinous apicodorsal tooth, dorsal margin broadly subtruncate, proximal margin irregular (Fig. 17a). Right lateral lobe in lateral aspect with apical segment about as long as proximal segment; apical segment very broadly expanded with rounded lobe along ventral margin, apex broadly rounded (Fig. 17b); left lateral lobe lateral aspect with apical segment broader and shorter than right with distinct, angulate expansion along ventral margin (Fig. 17c).

Variation. The two specimens vary in the extent and intensity of the elytral fasciae and maculations.

Sexual dimorphism. With typical sexual dimorphism for *Bidessonotus*. Male with anteroapical margin of elytron evenly curved; female with anteroapical margin produced into small spine (Fig. 10b).

Etymology. This species is named *spinosus*, Latin for “thorny,” for the long apical spine on the apex of the male median lobe.

Distribution. Known from one locality in Bolivar State, Venezuela (Fig. 30).

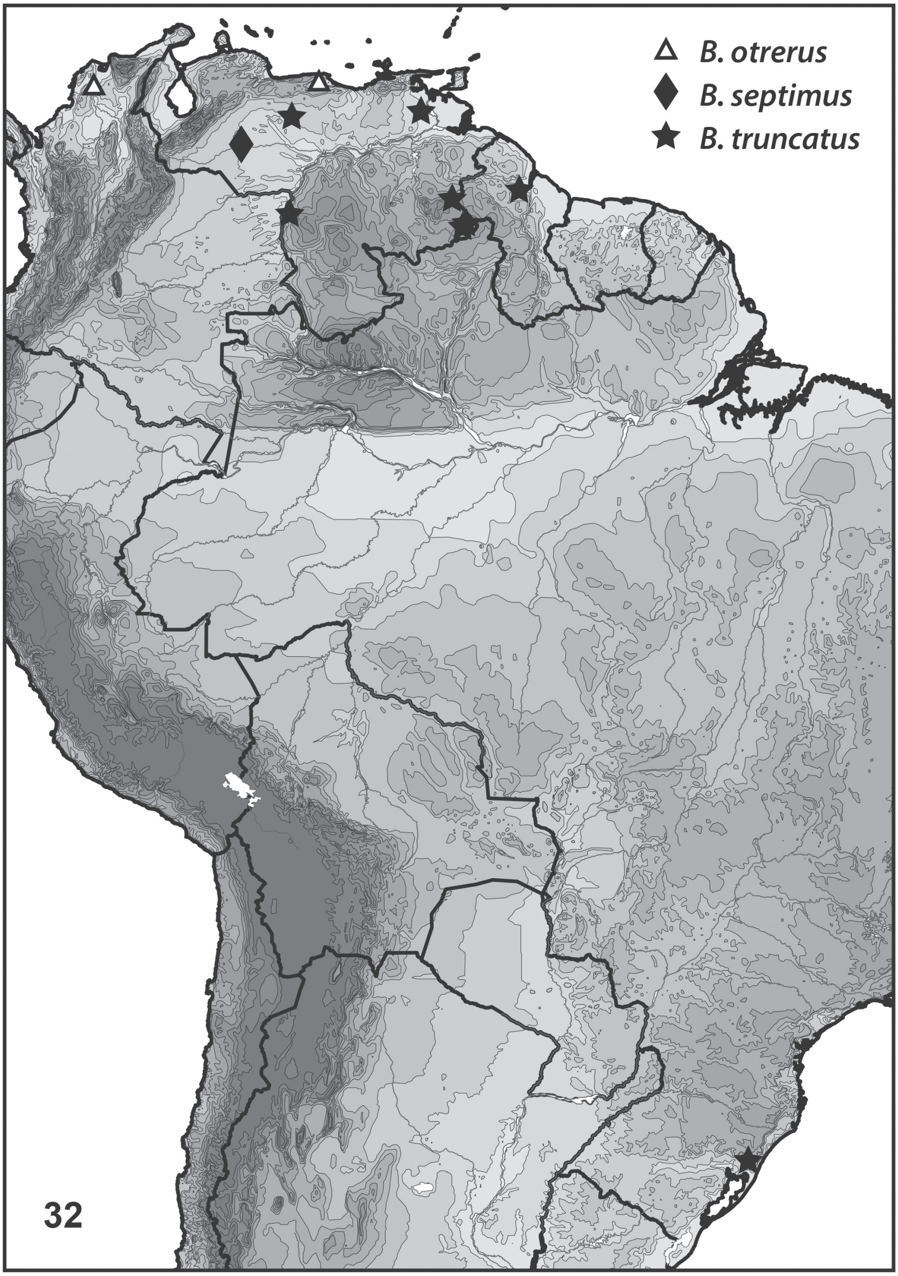


Figure 32. *Bidessonotus* species, South American distributions.

Habitat. Specimens were collected from a "small vegetated pool" and a "small streamlet."

Type material. Holotype in MIZA, male labeled, "VENEZUELA: Bolivar State 6°50'49.2"N, 61°28.2'2.4"W, 1340m Rio Agonwao @ [sic] Hwy 10 31.vii.2008; leg.

A.Short, M. García AS-08-060a; small vegetated pool/ SM0827643 KUNHM-ENT/ HOLOTYPE *Bidessonotus spinosus* Miller, 2016 [red label with red line border].” Paratypes, 1, **Venezuela:** Bolivar State, 6°50'49.2"N, 61°28.2'2.4"W, Rio Aponwao, 1340m, 31 Jul 2008, small streamlet, A. Short, M. García, legs., AS-08-060b, SM0830163.

Bidessonotus valdezi Miller, sp. n.

http://zoobank.org/5837C9C7-606B-4F1B-9082-59EED7A0610F
Figs 11, 18, 30

Type locality. Guyana, Region 6, Upper Berbice, ca 1km S Basecamp 1, 4°09.289'N, 58°12.274'W.

Diagnosis. Specimens of *B. valdezi* are relatively pale brown with the elytral maculae indistinct and vague. The prosternal process is lanceolate, shallowly sulcate and apically pointed. The apical blade of the male median lobe is broad with a moderately developed apicoventral triangular prominence, the distal margin sublinear, the proximal margin obliquely linear, and the dorsal margin narrowly truncate (Fig. 18a). The lateral lobes are distinctive, the right lateral lobe has the apical segment long, slender and apically rounded (Fig. 18a). The left lateral lobe is shorter, broader with the lateral margins evenly convergent to a rounded apex (Fig. 18c). Females have the apicolateral margin of the elytron unmodified. The male median lobe is somewhat similar in shape to the species *B. peregrinus* J. Balfour-Browne, but that species (known from Panama) is smaller (<1.8mm) and there are some differences in the male genitalia. In *B. peregrinus* the apical blade of the median lobe is much more narrow and the lateral lobes are broader with the apical segments on each side differently shaped between the two species. Specimens of *B. valdezi* are not dorsally iridescent, whereas females of *B. peregrinus* usually are.

Description. *Measurements*. TL = 1.8–1.9 mm, GW = 0.9 mm, PW = 0.7 mm, HW = 0.5 mm, EW = 0.3 mm, TL/GW = 2.0–2.1, HW/EW = 1.8. Body shape elongate oval, lateral outline discontinuous between pronotum and elytron.

Coloration (Fig. 11). Head, including all appendages and ventral surface, entirely pale yellow to yellow-orange. Pronotum entirely yellow. Elytron base color brown with broad, diffuse, somewhat transverse slightly paler regions, margin of regions vague and indistinct (Fig. 11); without purplish iridescence. Prosternal surface yellow; other thoracic ventrites orange except metacoxa darker orange.

Sculpture and structure. Head with anterior clypeal margin slightly thickened laterally, broadly rounded; surface smooth and shiny; antennomeres III-X moderately broad, slightly asymmetrical. Pronotum widest near posterior angles, lateral margins evenly curved; basal striae moderately impressed, extending anteriorly more than halfway across surface; posterior margins distinctly undulate; surface overall shiny, surface mediad of striae slightly punctate. Elytron with lateral margins broadly curved; basal stria distinct, moderately elongate, well impressed basally; surface of elytron covered with punctation, surface between punctures shiny but with distinctive microreticulation. Prosternal process elongate, lanceolate, apically pointed, surface broadly convex throughout length. Metaventrite with carinae extending from medial apex of metaventrite process posteriorly to posterior margin at anterior terminus of metacoxal lines; lines narrowly separated anteriorly, slightly divergent posteriorly and somewhat effaced; surface of metaventrite shiny with few micropunctures. Metacoxae shiny with few micropunctures; metacoxal lines distinct, nearly parallel, width slightly increased near anterior margin making lines slightly undulate anteriorly. Basal abdominal ventrites punctate, other surfaces of abdominal ventrites smooth, relatively shiny.

Male genitalia. Apex of median lobe in lateral aspect with apical blade moderately broad, with anteroventral triangular prominence, dorsal margin truncate, proximal margin obliquely curved (Fig. 11a). Lateral lobe in lateral aspect with apical segment about as long as proximal segment; apical segment relatively narrow, apex rounded (Fig. 11b).

Variation. Specimens vary in the extent and intensity of the elytral fasciae and maculations. In some specimens the lighter regions of the elytra are somewhat more intensely pale and slightly more distinctly defined.

Sexual dimorphism. With typical sexual dimorphisms for *Bidessonotus* species. Females with dorsal surface more matte than in males.

Etymology. The species is named *valdezi* after the good friend of the author and eminent biologist, Dr. Ernest Valdez.

Distribution. Known from Guyana and Suriname (Fig. 30).

Habitat. Specimens have been found in “muddy detrital pools” in a drying creek bed,“detritus pools” in a dry creek bed, and a “pooled up creek.”

Type material. Holotype in CSBD, male labeled, “GUAYANA: Region 6 4°09.289'N, 58°12.274'W, 108m Upper Berbice, ca. 1 km S. Basecamp 1 detrius pools in dry creekbed leg. Short, Salisbury, La Cruz 26.ix.2014; GY14-0825-01D/ SECM1358746 KUNHM-ENT [barcode label]/ HOLOTYPE *Bidessonotus valdezi* Miller, 2016 [red label with black line border].” paratypes 12, **Guyana:** Region 6, Upper Berbice, Basecamp 1, 4°09.289'N, 58°12.274'W, 72m, muddy detrital pools in drying creekbed near camp, Short, Salisburg, La Cruz, legs., 21 Sep 2014, GY14-0821-02A (2, SEMC); Region 6, Upper Berbice, ca 1km S Basecamp 1, 4°09.241'N, 58°10.627'W, detritus pools in dry creekbed, Short, Salisbury, La Cruz, legs, 26 Sep 2014, GY14-0925-010 (7, SEMC); Region 6, Upper Berbice, 3km W Basecamp 1, 4°09.297'N, 58°00.431'W, pooled up creek, Short, Salisbury, La Cruz, legs, GY14-0923-01A (3, SEMC). **Suriname:** Sipaliwini, Camp 2, on Sipaliwini river, 2.182°N, 56.787°W, 28 Aug 2010, Short & Kadosoe (5, SEMC); Sipaliwini, Camp 3, Wehepai, 2.362°N, 56.697°W, 03 Sep 2010, Short & Kadosoe (16, SEMC).

Bidessonotus bicolor Guignot, 1957

Figs 19, 31

Bidessonotus bicolor Guignot, 1957: 36; Young 1969: 2; 1990: 378; Biström 1988: 18; Nilsson 2016: 99.

Diagnosis. *Bidessonotus bicolor* is inadequately known and a diagnosis is difficult to establish. The apical blade of the male median lobe is relatively small with a spinous process at the apicoventral angle, a triangular prominence medially on the distal margin, and a pointed dorsal apex (Fig. 19).

Discussion. The type was not found and no other specimens were examined by Young (1990), who thought the species might be based on a teneral specimen of *B. melanocephalus*. No specimens were examined for this study either.

Distribution. Known only from the type locality, Brazil, Pará, Cachimbo (Fig. 31).

Bidessonotus dubius **Young, 1990**

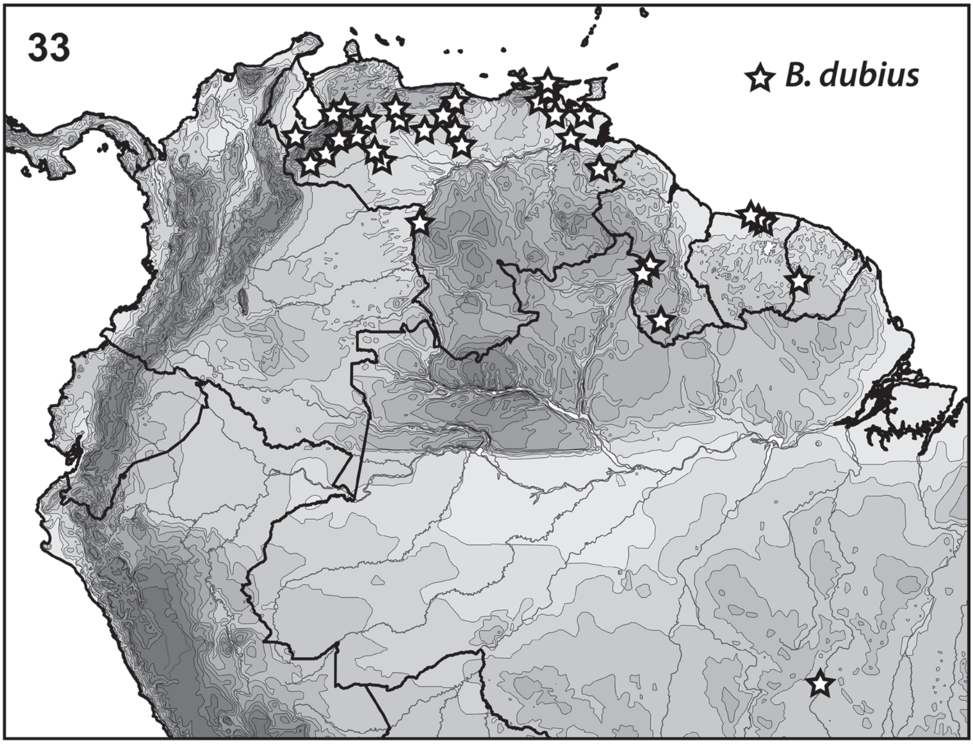
Figs 20, 33

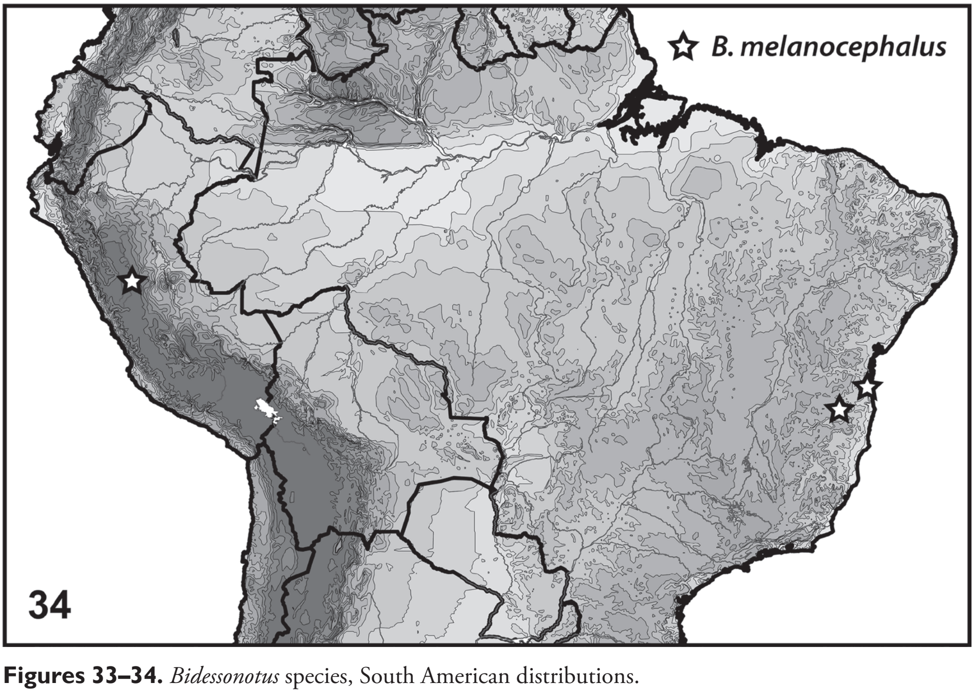
Bidessonotus dubius Young, 1990a: 364; Nilsson 2016: 99.

Diagnosis. Specimens of *Bidessonotus dubius* are moderately darkly colored with fairly well defined pale maculae on the elytra. The prosternal process is narrow and not or slightly sulcate and apically pointed. The apical blade of the male median lobe is diagnostic with a weakly developed apicoventral prominence and the dorsal apex broadly rounded with an undulating proximal margin (Fig. 20a). The male right lateral lobe has the apical segment relatively narrow and as long as the basal segment (Fig. 20b). The left lateral lobe has the apical segment shorter with the apex broadly obliquely truncate with a small distinctive lobe along the ventral margin (Fig. 20c).

Discussion. Young (1990) thought this species is similar to *B. obtusatus*. The species is one of the most common in northern South America and is found especially in marshes and ponds.

Distribution. Known from throughout northern South America (Fig. 33). Young (1990) reported *B. dubius* from numerous sites in Brazil, French Guyana, Suriname and Venezuela. Examined specimens include the following: **Guyana:** Region 9, Karanambo, 3.749°N, 59.299°W, 02 Apr 1994, PJ Spangler (2, USNM); Region 9, Karanambo, Simoni Lake, 3.749°N, 59.299°W, 02 Apr 1994, PJ Spangler (2, USNM); Region 9, Parabara, at N. edge of village, 2.095°N, 59.239°W, 03 Nov 2013, Short, Isaacs, Salisbury (2, SEMC); Pirara Ranch, Pirara River, 3.535°N, 59.675°W, 24 Apr 1995, Spangler & Perry (6, USNM). **Suriname:** Para, Paramaribo, 25 km S, 5.578°N, 55.192°W, 12 Jul 1969, PJ Spangler (1, USNM); Suriname: Saramacca, Sidiredjo, 1 km E, 5.830°N, 55.533°W, 5 Mar 2012, Short & Kadosoe (11, SEMC). **Venezuela:** Amazonas, Puerto Ayacucho, approx 15 km S, nr. Campamento Canturama, 5.510°N, 67.601°W, 08 Aug 2008, AE Short (1, SEMC); Apure, between La Ye and Bruzual, 7.644°N, 69.300°W, 18 Jan 2009, Short, Camacho, Miller (8, SEMC); Apure, Bruzual, edge of town, 8.042°N, 69.342°W, 18 Jan 2009, Short, Camacho, Miller (7, MIZA); Apure, Mantecal, approx 10 km W, side road, 7.621°N, 69.061°W, 18 Jan 2009, Short, Camacho, Miller (32, SEMC); Barinas, SW of Batatuy, 8.170°N, 70.864°W, 25 Jan 2012, Short, Arias, Gustafson (1, SEMC); Barinas, Ciudad Bolivia, approx 13 km SE, large Hacienda, 8.323°N, 70.470°W, 25 Jan 2012, 33





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Figures 33–34. *Bidessonotus* species, South American distributions.

Short, Arias, Gustafson (128, SEMC); Barinas, Ciudad Bolivia, approx 20 km S, small stream, 8.282°N, 70.397°W, 25 Jan 2012, Short, Arias, Gustafson (5, SEMC); Barinas, E Los Pasitos, 8.474°N, 70.536°W, 14 Jul 2009, Short, Camacho, Inciarte, Garcia, Gustafson, Shepard, Sites (11, SEMC); Bolivar, E Tumeremo, on road to Bochinche, 7.384°N, 61.325°W, 13 Jul 2010, Short, Arias, Tellez (7, SEMC); Cojedes, El Baul, 5 km S, large marsh, 8.900°N, 68.321°W, 21 Jan 2012, Short, Arias, Gustafson (13, SEMC); Cojedes, El Pao at Embalsa El Pao, next to main church, 9.636°N, 68.126°W, 21 Jan 2012, Short, Arias, Gustafson (3, SEMC); Delta Amacuro, Between Tucupita & Los Guires, 9.175°N, 61.910°W, 3 Feb 2010, Short & Garcia (7, SEMC); Delta Amacuro, between Tucupita & Temblador, small pond along road, 8.773°N, 62.238°W, 3 Feb 2010, Short, Garcia, Joly (3, SEMC); Delta Amacuro, Transect 3, 9.118°N, 61.959°W, 27 Aug 2009, R Cordero (1, SEMC); Delta Amacuro, Transect 3, 9.188°N, 61.883°W, 24 Aug 2009, R Cordero (2, SEMC); Guarico, between Palenque & Las Mercedes, 9.0631°N, 66.610°W, 4 Jul 2010, Short, Camacho, Tellez (9, SEMC); Guarico, 32 km SW Calabozo, 8.664°N, 67.552°W, 11 Feb 1969, PJ Spangler (85, USNM); Guarico, Hato Masaguaral, 40 km S of Calabozo, 8.566°N, 67.583°W, 5 Mar 1986, Spangler (628, USNM); Guarico, Hato Masaguaral, 44 km S of Calabozo, Gate Lagoon, 8.566°N, 67.583°W, 6 Mar 1986, Spangler (97, USNM); Guarico, Las Mercedes, approx 65 km S, 8.528°N, 66.376°W, 06 Jul 2010, Short, Arias, Camacho, Tellez (41, SEMC); Guarico, San Fernando, 7.942°N, 67.480°W, 12 Feb 1969, PJ Spangler (31, USNM); Guarico, Santa Rita, 2.6 km W, 8.121°N, 66.278°W, 6 Jul 2010, Short & Tellez (1, SEMC); Monagas, Maturin, S of, river crossing, 9.609°N, 63.138°W, 02 Feb 2010, Short & Garcia (33, SEMC); Monagas, Rio Azagua, 10.014°N, 63.142°W, 31 Jan 2010, Joly T, Louis J (23, MIZA); Monagas, S of Maturin, Morichal at road crossing, 9.273°N, 62.937°W, 2 Feb 2010, Short, Garcia, Joly (3, SEMC); Portuguesa, Guanare, N of, Rio Guanare, 9.041°N, 69.816°W, 19 Jan 2009, Garcia, Mauricio (6, MIZA); Sucre, El Pilar, approx 5 km SE, 10.523°N, 63.117°W, 29 Jan 2010, Short & Garcia (45, SEMC); Sucre, Finca Vuelta Larga, 10.501°N, 63.103°W, 29 Jan 2010, Short, Garcia, Joly (10, SEMC); Tachira, La Pedrera, 10 km E, Mata de Limon, small lagoon on finca, 7.502°N, 71.488°W, 26 Jan 2012, Short, Arias, Gustafson (17, SEMC); Trujillo, Agua Viva, NE, 9.629°N, 70.587°W, 29 Jan 2012, Short & Gustafson (1, SEMC); Trujillo, Granados, approx 3 km SW, 9.376°N, 70.818°W, 28 Jan 2012, Short, Arias, Gustafson (2, SEMC); Trujillo, La Cieba, approx 10 km E, by cemetery, 9.4750°N, 70.955°W, 28 Jan 2012, Short, Arias, Gustafson (2, SEMC); Zulia, Puente del Zulia, lagoon on finca, 8.551°N, 72.336°W, 27 Jan 2012, Short, Arias, Gustafson (3, SEMC).

Bidessonotus melanocephalus **Régimbart, 1895**

Figs 21, 34

Bidessonotus melanocephalus Régimbart, 1895: 332; J. Balfour-Browne 1947: 443; Young 1969: 2; 1990: 375; Biström 1988: 18; Nilsson 2016: 99.

Bidessus (*Bidessonotus*) *melanocephalus*, Zimmermann 1920: 62.

Bidessus melanocephalus, Blackwelder 1944: 76.

Diagnosis. Specimens of *B. melanocephalus* are darkly colored with the posterior surface of the head and the ventral surfaces dark brown. The prosternal process is lanceolate but not sulcate. The apical blade of the male median lobe is very broad with very well developed apicoventral and apicodorsal teeth and a broad tooth near the medial end of the proximal margin (Fig. 21a,d). The right lateral lobe has the apical segment apically broadly rounded and expanded along the ventral margin (Fig. 21b). The apical segment of the left lateral lobe is short, broad and curve and distinctly pointed along the dorsal margin (Fig. 21c).

Discussion. Young (1990) compared this species with *B. inconspicuus*. This is one of only a couple *Bidessonotus* species known from central and southern South America.

Distribution. Known from Brazil and Peru (Fig. 34, Young 1990).

Bidessonotus nepotinus J. Balfour-Browne, 1947

Fig. 31

Bidessonotus nepotinus J.Balfour-Browne, 1947: 442; Young 1969: 2; 1990: 364; Biström 1988: 18; Nilsson 2016: 99.

Diagnosis. Known only from a pair of females which are moderately darkly colored with three indistinct transverse maculae. The apex of the prosternal process is lanceolate. Given the absence of known males, a definitive diagnosis is difficult to establish.

Discussion. *Bidessonotus nepotinus* is known only from two female specimens (Balfour-Browne 1947; Young 1990). Balfour-Browne (1947) thought the species is close to or identical with *B. obtusatus*.

Distribution. *Bidessonotus nepotinus* is known only from Trinidad (Fig. 31).

Bidessonotus obtusatus Régimbart, 1895

Figs 1, 2, 22, 35

Bidessonotus obtusatus Régimbart, 1895: 336; J. Balfour-Browne 1947: 439; Young 1969: 2; 1990: 363; Biström 1988: 18; Nilsson 2016: 99.
Bidessus (*Bidessonotus*) *obtusatus*, Zimmermann 1920: 62.
Bidessus obtusatus, Blackwelder 1944: 76.

Diagnosis. Specimens of this species are rather darkly colored with variable light markings that are usually conspicuous. The anterior clypeal margin is weakly sulcate and medially rounded. The prosternal process is relatively broad, flat and apically narrowly rounded. The male median lobe is diagnostic with the apical blade broadly truncate on the ventral margin, broad dorsally with a prominent obliquely truncate apicodorsal projection and the proximal margin with a small, irregular medial tooth and more well developed dorsal tooth (Fig. 22a,d). The right lateral lobe has the apical segment as long as the basal segment and is elongate and parallel sided and apically narrowly rounded (Fig. 22b). The left lateral lobe is much broader than the right, apically broadly concave with a distinct lobe along the ventral margin (Fig. 22c).

Discussion. This is one of the commonest species in much of lowland South America with specimens collected especially from marshy lentic habitats and at lights. Young (1990) thought the species is related to *B. pollostus*, *B. rubellus*, *B. dubius* and *B. ploterus*.

Distribution. Specimens have been collected from throughout lowland South America (Fig. 35). Young (1990) reported seeing hundreds of specimens from Argentina, Brazil, Bolivia, French Guiana, Colombia, Ecuador, Paraguay, Peru, Suriname, and Venezuela. The species is seemingly not as common as others in northern South America, but is present in lowland areas of Venezuela east to French Guiana.

Bidessonotus otrerus Young, 1990

Figs 23, 32

Bidessonotus otrerus Young, 1990: 368; Nilsson 2016: 99.

Diagnosis. *Bidessonotus otrerus* is a brownish species with significant portions of the head and pronotum brown. The elytra are brown with weakly pale maculae. The prosternal process is narrow and slightly sulcate. The apical blade of the male median lobe is slender and dorsally narrowly rounded, the distal and proximal margins are irregularly undulate (Fig. 23a). The apex of the male median lobe is more obliquely contorted and twisted than it is in other species (Fig. 23a). The basal segment of the right lateral lobe is very large and broad and the apical segment is elongate and slender with the apex rounded (Fig. 23b). The left lateral lobe has the apical segment shorter than the right with the apex broadly and distinctly bilobed (Fig. 23c).

Discussion. Little is known of this species.

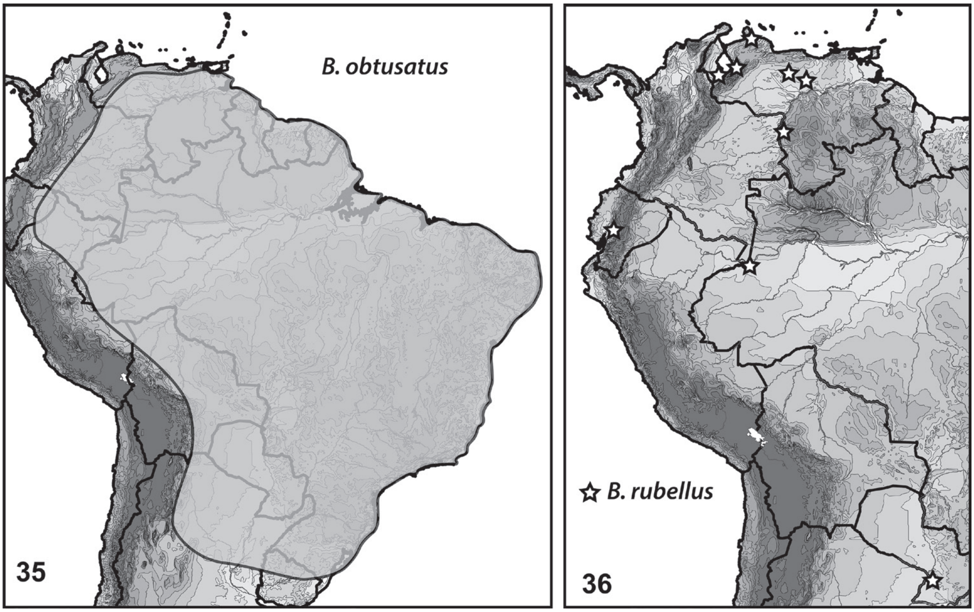
Distribution. Young (1990) reported the species from Colombia and Venezuela (Fig. 32). No new additional specimens were examined for this project.

Bidessonotus paludicolus Young, 1990

Figs 24, 30

Bidessonotus paludicolus Young, 1990: 372; Nilsson 2016: 99.

Diagnosis. Specimens are relatively darkly colored with the posterior surface of the head brown and the elytra evenly dark brown. The prosternal process is narrow and slightly sulcate. The male median lobe has the apical blade narrow ventrally and evenly and broadly expanded dorsally with the dorsal margin broadly truncate (Fig. 24a,d). The right lateral lobe has the apical segment very broad, relatively short and apically



Figures 35–36. *Bidessonotus* species, South American distributions.

broadly rounded (Fig. 24b). The left lateral lobe has the apical segment short, broad and apically very broadly rounded (Fig. 24c).

Discussion. Young (1990) regarded this species as similar to *B. mexicanus* from Mexico and Central America, but it is not well known.

Distribution. Young (1990) reported the species from Costa Rica and Mexico, but also from Venezuela (Guarico) (Fig. 30). No additional specimens were examined for this project.

Bidessonotus ploterus Young, 1990

Figs 25, 31

Bidessonotus ploterus Young, 1990; Nilsson 2016: 99.

Diagnosis. Specimens are relatively evenly brownish on the elytra with poorly-developed maculae. The prosternal process is lanceolate and slightly sulcate. This is a relatively small species (1.3-1.7 mm). The apical blade of the male median lobe is narrow with a relatively well developed anteroventral rounded prominence and the dorsal margin of the blade broadly truncate with a moderately distinctive medial tooth on the proximal margin (Fig. 25a,d). The right lateral lobe has the apical segment elongate, as long as the basal segment, with a prominent lobe on the ventral surface (Fig. 25b). The apical segment of the left lateral lobe is shorter and broader, apically obliquely truncate and apically expanded (Fig. 25c).

Discussion. Young (1990) regarded this species as similar to *B. obtusatus*.

Distribution. This species is known from Brazil (Mato Grosso) (Fig. 31, Young 1990). No additional specimens were examined for this project.

Bidessonotus rubellus **Young, 1990**

Figs 4, 26, 36

Bidessonotus rubellus Young, 1990: 366; Nilsson 2016: 99.

Diagnosis. Specimens are relatively darkly colored with the posterior surface of the head brown and the elytra dark reddish-brown with indistinct maculae. The prosternal process is moderately broad, apically rounded and not sulcate. The apical blade of the male median lobe is similar to that of *B. obtusatus* but is narrower, has the apicoventral region obiquely truncate and larger with the apicoproximal tooth more strongly developed (Fig. 26a). The right lateral lobe has the apical segment as long as the basal segment and is slender and only slightly expanded apically before narrowly rounded apex (Fig. 26b). The left lateral lobe has the apical segment broad and apically obliquely distinctly bilobed (Fig. 26c).

Discussion. *Bidessonotus rubellus* was thought to have genitalia similar to *B. obtusatus* by Young (1990), but inconclusively so. Specimens have been largely collected from lentic habitats and lights at night.

Distribution. *Bidessonotus rubellus* has been reported from Colombia, Ecuador, Panama, Paraguay and Venezuela (Fig. 36, Young 1990). Examined specimens include the following: **Venezuela:** Amazonas, Communidad Porvenir, just S of, 5.341°N, 67.755°W, 15 Jan 2009, Short & Garcia (1, SEMC); Falcon, Medanos de Coro, 11.436°N, 69.668°W, 09 Jul 2009, Short & Shepard (55, SEMC); Guarico, Las Mercedes, approx 65 km S, 8.528°N, 66.376°W, 09 Jan 2009, Short, Garcia, Camacho, Miller (6, SEMC); Trujillo, La Cieba, approx 10 km E, by cemetery, 9.475°N, 70.955°W, 28 Jan 2012, Short, Arias, Gustafson (34, SEMC); Zulia, Encontrados, approx 3 km SE, 9.033°N, 72.212°W, 27 Jan 2012, Short, Arias, Gustafson (16, SEMC).

Bidessonotus tibialis **Régimbart, 1895**

Figs 3, 27, 37

Bidessonotus tibialis Régimbart, 1895: 337; J. Balfour-Browne 1947: 447; Young 1969: 2; 1990: 357; Biström 1988: 18; Nilsson 2016: 99.

Bidessus (*Bidessonotus*) *tibialis*, Zimmermann 1920: 62.

Bidessus tibialis, Blackwelder 1944: 76.

Bidessonotus sobrinus J. Balfour-Browne, 1947: 445; Young 1969: 2; 1990: 358; Biström 1988: 18; Nilsson 2016: 99; **syn. n.**

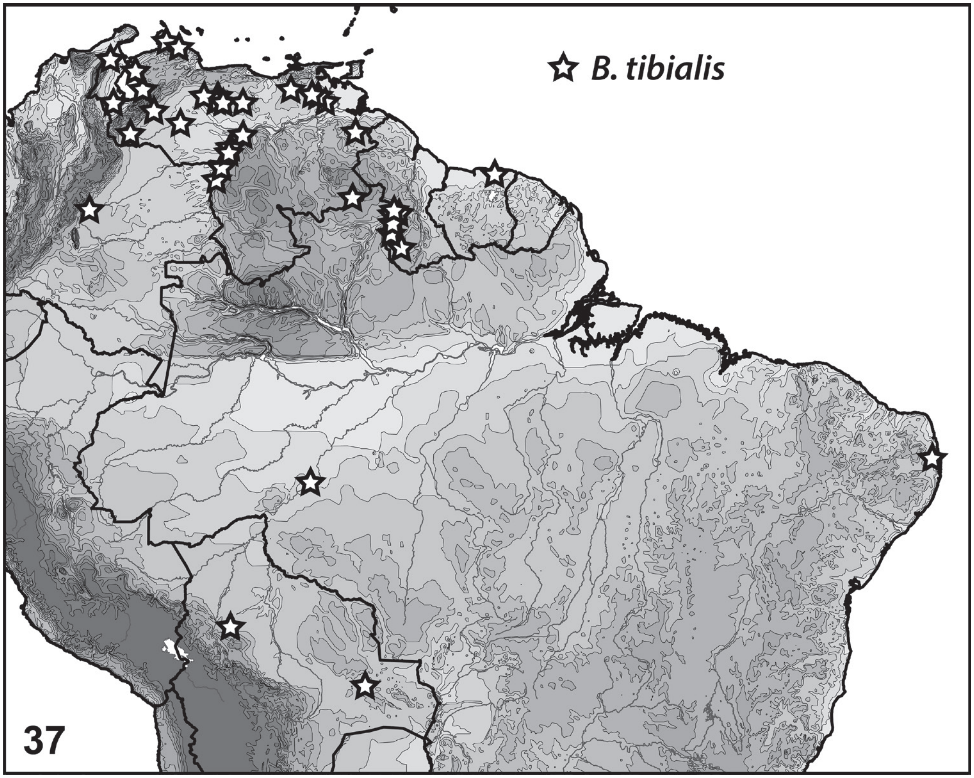


Figure 37. *Bidessonotus* species, South American distributions.

Diagnosis. Specimens have the elytra relatively uniformly-colored except in some specimens with darker and lighter markings, but poorly evident. The prosternal process is lanceolate and distinctly sulcate. The male genitalia are diagnostic with the apical blade moderately slender and distinctly and abruptly curved with the dorsal margin rounded and with a distinct anteroventral rounded prominence (Fig. 27a,d). The right lateral lobe has the apical segment very slender, as long as the basal segment and somewhat expanded apically (Fig. 27b). The right lateral lobe has the apical segment broader, apically obliquely truncate and somewhat expanded (Fig. 27c).

Discussion. This species and *B. sobrinus* are extremely similar, and Young (1990) thought they are probably the same species, a conclusion with which I agree. He did not formally synonymize the two, but they are regarded here as subjective synonyms (*B. tibialis* Régimbart, 1895 = *B. sobrinus* J. Balfour-Browne, 1947, syn. n.). Specimens have been collected mainly from a variety of habitats, both lentic and slow lotic.

Distribution. *Bidessonotus tibialis* is widespread in northern South America with records also from Bolivia, Brazil and Peru (Fig. 37) suggesting the species may be more widespread in the continent that current records indicate. Young (1990) reported this species from Brazil, Bolivia and Peru, and (as *B. sobrinus*) from Colombia, Panama, Suriname and Venezuela. Examined specimens include the following: **Bolivia:** Dpt

Sta Cruz, Prov Chiquitos, mud puddle in road, 1.8km SSW San Jose 17°40'51"S 60°44'33"W, 325m 27 Jun 1999, KB Miller (42, KBMC); Dpt St Cruz, Prov Chiquitos, 2.7km S San Jose, pool in stream, 17°52'20"S 60°44'26"W, 333m, 27 Jun 1999, KB Miller (9, KBMC); Dpt Sta Cruz, Prov Ichilo, 1.2km SSE Buena Vista, marsh, 19 Jun 1999, KB Miller (1, KBMC); Beni; 1.8k E San Borja, muddy pool, 14°52'02"W 66°43'45"W, 15 Jul 1998, KB Miller (1, KBMC). **Brazil:** Cuyaba, Aug (1, KBMC). **Colombia:** Meta, Villavicencio, 10 km S, 4.080°N, 73.684°W, 03 Mar 1969, PJ Spangler (8, USNM). **Guyana:** Pirara Ranch, Caskew Lake, 3.616°N, 59.666°W, 27 Apr 1995, Spangler & Perry (1, SEMC). Region 9, Along road to Parabara, creek crossing at Mushai Wao, 2.159°N, 59.292°W, 01 Nov 2013, Short, Isaacs, Salisbury (2, SEMC); Region 9, Farm pond on ranch, nr. Kusad Mts., 2.853°N, 59.922°W, 28 Oct 2013, AEZ Short (4, SEMC); Region 9, Karanambo, 3.749°N, 59.299°W, 02 Apr 1994, PJ Spangler (12, USNM); Region 9, Katu Wao River near ranch house, nr. Kusad Mts., 2.890°N, 59.850°W, 26 Oct 2013, Short, Isaacs, Salisbury (2, SEMC); Region 9, nr. Kusad Mts., large marshy area, 2.870°N, 59.916°W, 27 Oct 2013, Short, Isaacs, Salisbury (3, SEMC); Region 9, Pooled up creek, tributary of Katu Wao River, nr. Kusad Mts., 2.809°N, 59.865°W, 26 Oct 2013, Short, Isaacs, Salisbury (4, SEMC); Region 9, Ziida Karisihizi (Lake), nr. Kusad Mts., 2.829°N, 59.806°W, 25 Oct 2013, Short, Isaacs, Salisbury (1, SEMC); Region 9, Ziida Wao (Creek), nr. Kusad Mts., 2.828°N, 59.809°W, 25 Oct 2013, Short, Isaacs, Salisbury (32, SEMC); Pirara Ranch, Pirara River, 3.535°N, 59.675°W, 24 Apr 1995, Spangler & Perry (3, USNM). **Suriname:** Para, Paramaribo, 25 km S, 5.578°N, 55.192°W, 12 Jul 1969, PJ Spangler (5, USNM). **Venezuela:** Guarico, Calabozo, 32 km SW, 8.664°N, 67.552°W, 11 Feb 1969, PJ Spangler (4, USNM); Guarico, Hato Masaguaral, 8.566°N, 67.583°W, 06 Mar 1986, Spangler & Beaujon (1442, USNM). Amazonas, Communidad Porvenir, just S of, 5.341°N, 67.755°W, 15 jan 2009, Short & Miller (17, SEMC); Amazonas, Puerto Ayacucho, N, nr Iboruwa, "Tobogancito", 5.806°N, 67.438°W, 13 Jan 2009, KB Miller (3, SEMC); Anzoategui, Transect 1, 9.293°N, 64.223°W, 15 Aug 2009, R Cordero (1, SEMC); Apure, Mantecal, approx 10 km W, side road, 7.621°N, 69.061°W, 18 Jan 2009, Short, Camacho, Miller (15, SEMC); Barinas, Ciudad Bolivia, approx 13 km SE, large Hacienda, 8.323°N, 70.470°W, 25 Jan 2012, Short, Arias, Gustafson (11, SEMC); Bolivar, between Caicara & Los Pijiguaos, 7.3498°N, 66.298°W, 12 Jan 2009, Short, Camacho, Garcia, Joly, Miller (30, NMPC); Bolivar, Gran Sabana, 1 km E Pauji, tributary of Rio Pauji, 4.479°N, 61.581°W, 16 Jul 2010, Short, Arias, Tellez (4, SEMC); Bolivar, Los Pijiguaos, outcrop/morichal, 6.593°N, 66.820°W, 12 Jan 2009, Short & Miller (6, SEMC); Bolivar, Rio Caripito, 6.586°N, 67.029°W, 12 Jan 2009, Short & Miller (3, SEMC); Bolivar, Tumeremo, E, on road to Bochinche, 7.384°N, 61.325°W, 13 Jul 2010, Short, Arias, Tellez (14, SEMC); Cojedes, El Baul, 5 km S, large marsh, 8.900°N, 68.321°W, 21 Jan 2012, Short, Arias, Gustafson (4, SEMC); Falcon, Medanos de Coro, 11.436°N, 69.668°W, 09 Jul 2009, Short & Shepard (1, SEMC); Falcon, Tocopero, SE of, 11.448°N, 69.218°W, 10 Jul 2009, Short, Camacho, Inciarte, Garcia, Gustafson, Shepard, Sites (6, SEMC); Guarico, Calabozo, 32 km SW, 8.664°N, 67.552°W, 11 Feb 1969, PJ Spangler (12, USNM); Guarico, Las Mercedes, approx 65 km S, 8.528°N, 66.376°W, 09 Jan 2009, Short, Garcia, Camacho, Miller (30, SEMC); Monagas, Chaguaramas, 4 km S, 8.634°N, 62.765°W, 19 Jul 2010, Short, Arias, Tellez (2, SEMC); Monagas, Morichal Largo & Temblador, small pond between, 9.096°N, 62.726°W, 02 Feb 2010, Short, Garcia, Joly (10, SEMC); Monagas, S of Maturin, Morichal at road crossing, 9.273°N, 62.937°W, 02 Feb 2010, Short, Garcia, Joly (5, SEMC); Tachira, La Pedrera, 10 km E, Mata de Limon, small lagoon on finca, 7.502°N, 71.488°W, 26 Jan 2012, Short, Arias, Gustafson (4, SEMC); Trujillo, Granados, approx 3 km SW, 9.376°N, 70.818°W, 28 Jan 2012, Short, Arias, Gustafson (2, SEMC); Zulia, Puente del Zulia, lagoon on finca, 8.551°N, 72.336°W, 27 Jan 2012, Short, Arias, Gustafson (4, SEMC); Zulia, Quebrada Riencito, 10.860°N, 72.322°W, 30 Dec 2008, Short & Garcia (3, SEMC); Zulia, Sabana de Machango, 10.043°N, 71.007°W, 29 Jan 2012, Short, Arias, Gustafson (3, SEMC).

***Bidessonotus truncatus* J. Balfour-Browne, 1947**

Figs 28, 32

Bidessonotus truncatus J. Balfour-Browne, 1947: 440; Young 1969: 2; 1990: 376; Biström 1988: 18; Nilsson 2016: 99.

Diagnosis. Specimens of this species are darkly colored with the elytra nearly evenly dark brown. The prosternal process is relatively broad, flat, apically pointed, and weakly or not sulcate. The apical blade of the male median lobe is slender with the distal margin medially with an elongate spinous "horn" or process (Fig. 28a,d). The right lateral lobe has the apical segment relatively slender, medially more broadly expanded and as long as the basal segment (Fig. 28b). The left lateral lobe has the apical segment shorter, broadly obliquely concave apically and bilobed (Fig. 28c).

Discussion. Little has been reported about this species, but specimens were collected from both lentic and slow lotic habitats.

Distribution. Known from Bolivia, Brazil, Guayana, Paraguay, Peru, Suriname and Trinidad (Fig. 32, Young 1990). Examined specimens include the following: **Guyana:** Mayuruni Potaro, Takutu Mountains, 6.216°N, 59.049°W, 19 Dec 1983, Spangler, Faitoute, Ed W. (4, USNM). **Venezuela:** Amazonas, Communidad Porvenir, just S of, 5.341°N, 67.755°W, 15 Jan 2009, Short & Garcia (33, SEMC); Amazonas, Road between Puerto Ayacucho and Samariapo, 5.341°N, 67.755°W, 06 Jan 2006, Short, Andrew E (4, SEMC); Bolivar, Gran Sabana, between Kavanayen and Rt 10, 5.741°N, 61.515°W, 01 Aug 2008, Short, Andrew E (6, SEMC); Bolivar, Gran Sabana, N Santa Elena, Rio Guara at Rt 10, 4.622°N, 61.094°W, 17 Jul 2010, Short, Arias, Tellez (2, SEMC); Bolivar, Gran Sabana, N Santa Elena, River at Rt 10 crossing, 4.672°N, 61.068°W, 15 Jul 2010, Short, Camacho, Tellez (4, MIZA); Guarico, Hato Masaguaral, 8.566°N, 67.583°W, 06 Mar 1986, Spangler & Beaujon (8, USNM); Monagas, Morichal Largo & Temblador, small pond between, 9.096°N, 62.726°W, 02 Feb 2010, Short, Garcia, Joly (6, SEMC).

Bidessonotus vicinus J. Balfour-Browne, 1947

Figs 29, 31

Bidessonotus vicinus J. Balfour-Browne, 1947: 428; Young 1969: 2; 1990: 370; Biström 1988: 18; Nilsson 2016: 100.

Diagnosis. This is a relatively dark and weakly maculate species. The prosternal process is lanceolate, flat and apically pointed. The apical blade of the male median lobe is relatively simple, the anteroventral angle is moderately produced as a broad, curved, short process, the distal margin is broadly truncate to slightly undulate, and there are no other prominent spines, denticles or projections (Fig. 29a,d). The apical segment of the right lateral lobe is medially very broad, short and subtriangular (Fig. 29b). The left lateral lobe has the apical segment subquadrate and very broad (Fig. 19c).

Discussion. Although originally described from a female, Young (1990) clarified the identity of this species which is distributed in Central America and Venezuela.

Distribution. Young (1990) reported this species from Honduras, Panama and Venezuela (Fig. 31). No additional specimens were examined for this project.

Species in the Genus *Bidessonotus* Régimbart

Bidessonotus annae **sp. n.** – Venezuela
B. bicolor Guignot, 1957 – Brazil
B. browneanus J. Balfour-Browne, 1947 – Cuba, Dominican Republic, Jamaica, Puerto Rico
B. canis Miller, 1997 – Costa Rica
B. caraibus (Chevrolat, 1863) – Belize, Cuba
B. championi J. Balfour-Browne, 1947 – Costa Rica, Guatemala, Honduras, Nicaragua
B. dubius Young, 1990 – Brazil, French Guiana, Suriname, Venezuela
B. fallax J. Balfour-Browne, 1947 – Cuba
B. inconspicuus (LeConte, 1855) – Canada, USA (eastern states)
B. inigmaticus Young, 1990 – Mexico
B. josiahi **sp. n.** – Venezuela
B. longovalis (Blatchley, 1919) – USA (Alabama, Florida, Georgia)
B. melanocephalus Régimbart, 1895 – Brazil, Peru
B. mexicanus Régimbart, 1895 – Belize, Mexico, USA (Texas)
B. mobilis J. Balfour-Browne, 1947 – Belize, Guatemala, Mexico
B. morosus J. Balfour-Browne, 1947 – Mexico
B. nepotinus J. Balfour-Browne, 1947 – Trinidad
B. obtusatus Régimbart, 1895 – Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Paraguay, Peru, Suriname, Venezuela
B. otrerus Young, 1990 – Colombia, Venezuela
B. palecephalus **sp. n.** – Venezuela

B. paludicolus Young, 1990 – Costa Rica, Mexico, Venezuela
B. peregrinus J. Balfour-Browne, 1947 – Panama
B. pictus Young, 1990 – Costa Rica
B. ploterus Young, 1990 – Brazil
B. pollostus Young, 1990 – Belize
B. pulicarius (Aubé, 1838) – USA (Alabama, Florida, Georgia, Louisiana, Mississippi)
B. reductus **sp. n.** – Venezuela
B. regimbarti J. Balfour-Browne, 1947 – Mexico?
B. rhampherens Young, 1990 – Mexico
B. rubellus Young, 1990 – Colombia, Ecuador, Panama, Paraguay, Venezuela
B. septimus **sp. n.** – Venezuela
B. spinosus **sp. n.** – Venezuela
B. tibialis Régimbart, 1895 – Bolivia, Brazil, Peru (also Colombia, Panama, Suriname, Venezuela as *B. sobrinus*)
= *B. sobrinus* J. Balfour-Browne, 1947, **syn. n.**
B. truncatus J. Balfour-Browne, 1947 – Bolivia, Brazil, Guyana, Paraguay, Peru, Suriname, Trinidad
B. valdezi **sp. n.** – Guiana, Suriname
B. vicinus J. Balfour-Browne, 1947 – Honduras, Panama, Venezuela

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RESEARCH ARTICLE

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Sea snakes (Elapidae, Hydrophiinae) in their westernmost extent: an updated and illustrated checklist and key to the species in the Persian Gulf and Gulf of Oman

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Abstract

The Persian Gulf is known as the westernmost distribution limit for sea snakes, except for *Hydrophis platurus* (Linnaeus, 1766) that reaches southeastern Africa. Previous identification guides for sea snakes of the Persian Gulf and its adjacent waters in the Gulf of Oman were based on old data and confined mostly to written descriptions. Therefore, a series of field surveys were carried out in 2013 and 2014 through Iranian coastal waters of both gulfs to provide a comprehensive sampling of sea snakes in the area. This paper presents an illustrated and updated checklist and identification tool for sea snakes in the Persian Gulf and Gulf of Oman, which are based on new material and a review of the literature. This checklist includes ten species of marine hydrophiines, of which one, *Microcephalophis cantoris* (Günther, 1864), is a new record for the area. All specimens examined herein are deposited and available at the Zoological Museum of Shahid Bahonar University of Kerman, Kerman province, Iran.

Keywords

Indian Ocean, new record, reptiles, Serpentes, venomous, viviparous

Introduction

All true sea snakes of the subfamily Hydrophiinae share a common ancestor dating back to approximately six million years ago, although the majority of the extant lineages have diversified in the last three and half million years (Sanders et al. 2013). Now, more than 60 morphologically and ecologically diverse species of highly venomous marine hydrophiines live throughout tropical and subtropical coastal waters of the Indo-West Pacific region (Rasmussen et al. 2011b), with an exception, the Yellow-bellied Sea Snake, *Hydrophis platurus* (Linnaeus, 1766), that lives in both Indian and Pacific Oceans (Heatwole 1999). These sea snakes colonize various coastal habitats throughout their geographic range and play an important role in the food web of these coastal biomes by consuming various prey (Voris 1972).

The Persian Gulf is a semi-enclosed shallow marine environment (mean depth ca. 35 meters) lying in a subtropical and hyper-arid region in the northwestern Indian Ocean. This water body is considered a young sea (~15,000 years) with impoverished species biodiversity. Biota living in the Gulf must adapt to high temperatures and a hypersaline environment (Price 2002; Sheppard 1993; Sheppard et al. 2010). Sea surface temperature in the Gulf varies from 18 to 34°C throughout the year and salinity is more than 39 ppt in most areas (Sheppard et al. 2010).

Populations of sea snakes in the Persian Gulf are peculiar for two main reasons. First, because the Gulf is known as the westernmost extent of sea snakes (with the exception of *H. platurus*, which is also found in the east coast of Africa) (Heatwole 1999). Second, because the Persian Gulf can be considered as an excellent natural laboratory to study the adaptive responses of the rapidly evolving sea snakes to high salinities and fluctuating temperatures.

Nonetheless, our knowledge about the sea snake diversity in the Persian Gulf and its adjacent waters is based on older studies (e.g. Smith 1926; Volsøe 1939), documenting the occurrence of nine species of the subfamily Hydrophiinae in the area. Recently, taxonomy of the true sea snakes has been revised based on comprehensive molecular phylogenetic analyses (Sanders et al. 2013). After Sanders et al. (2013), sea snake species from the Persian Gulf and Gulf of Oman previously allocated to the genera *Enhydrina* Gray, 1849, *Lapemis* Gray, 1835 and *Pelamis* Daudin, 1803 are now all assigned to the single genus *Hydrophis* Latreille *in* Sonnini & Latreille, 1801; and the Small-headed Sea Snake previously known as *Hydrophis gracilis* (Shaw, 1802) is now assigned to the genus *Microcephalophis* Lesson, 1834. Furthermore, our new material examination confirmed the occurrence of a second species of Small-headed Sea Snake, namely *M. cantoris* (Günther, 1864), in the Gulf of Oman. Therefore, the checklists and identification keys for the sea snakes in the gulfs (e.g. Egan 2007; Gasperetti 1988; Leviton et al. 1992) must be revised and updated by examining new material and using updated taxonomic classification (e.g. Sanders et al. 2013). This paper aims at presenting an illustrated and up to date checklist for sea snakes in the Persian Gulf and Gulf of Oman, as well as easy to use identification keys to the genera and species recorded in both gulfs.

Materials and methods

The sea snakes examined herein were collected from the Iranian coastal waters of the Persian Gulf and Gulf of Oman (Figure 1). In this study, boundaries of both gulfs were assumed following International Hydrographic Organization (IHO). According to the descriptions of the organization, the Persian Gulf is separated from the Gulf of Oman by an imaginary line from Minab (27°00'N, 57°00'E) on the Iranian coast to Ras Qabr al-Hindi (26°20'N, 56°30'E) on the northeast tip of the Musandam Peninsula. Furthermore, the eastern limit of the Gulf of Oman is an imaginary line running from Ras Jiwani (25°01'N, 61°44'E) on the border of Pakistan and Iran to Ras al-Hadd (22°32'N, 59°47'E) in Oman (Figure 1).

Sea snakes were collected from by-catch of fishing trawlers in coastal waters of Bushehr Province in the western Persian Gulf, Jask and Ras-Meydani (Hormozgan Province) in the western Gulf of Oman and Beris and Pasa-Bandar (Sistan-O-Baluchestan Province) in the eastern Gulf of Oman in 2013 (Figure 1). Sea snakes were also collected from mangrove swamps of Jask (Hormozgan Province) in the western Gulf of Oman in 2013, and coastal waters of Larak Island (Hormozgan Province) in the eastern Persian Gulf in 2014 (Figure 1) using boat surveys.

A total of 14 characters was examined: each specimen was measured for total length (**TL**), snout-vent length (**SVL**), head length (**HL**), head width (**HW**), gap length (**GL**), snout to nostril length (**SNL**), nostril to eye length (**NEL**), neck diameter (**ND**) and greatest body diameter (**GBD**). Furthermore, number of supralabials (**NSL**), number of scale rows on the neck (**NSR**), number of scale rows on the body (**BSR**), number of ventrals (**NV**), and number of bands (**NB**) were also recorded for each specimen. SVL, HW, GL, SNL and NEL were measured following Ukuwela et al. (2012). HL was measured following Thorpe (1975). NSR and BSR were counted following Rasmussen (2001). NV was counted following Dowling (1951). After detailed morphological examination, a piece of trunk muscle was removed and preserved in ethanol 99% for future DNA analyses. All specimens were then preserved and fixed using the approved protocols (Leviton et al. 1992) and deposited in the Zoological Museum of Shahid Bahonar University of Kerman, Kerman Province, Iran (institutional code: ZMSBUK.HD).

Some external diagnostic characters (e.g. coloration patterns, number, size and shape of head shields, and body and ventral scales) were used to make updated and easy to use identification keys, which allow users to identify sea snakes in the field without the need of a binocular.

Morphological characters are presented using abbreviations (see above). Data of all measurements are in mm. Due to great interspecific and intraspecific variations in external characters of sea snakes (Rasmussen et al. 2011), diagnostic characters provided here are mostly applicable to the specimens from this area. Morphological data derived from previous literature dealing with sea snakes in the area are mentioned in brackets. Synonymies previously used for each species in the region are listed under each species. English common names presented herein are those suggested by the IUCN Red List of

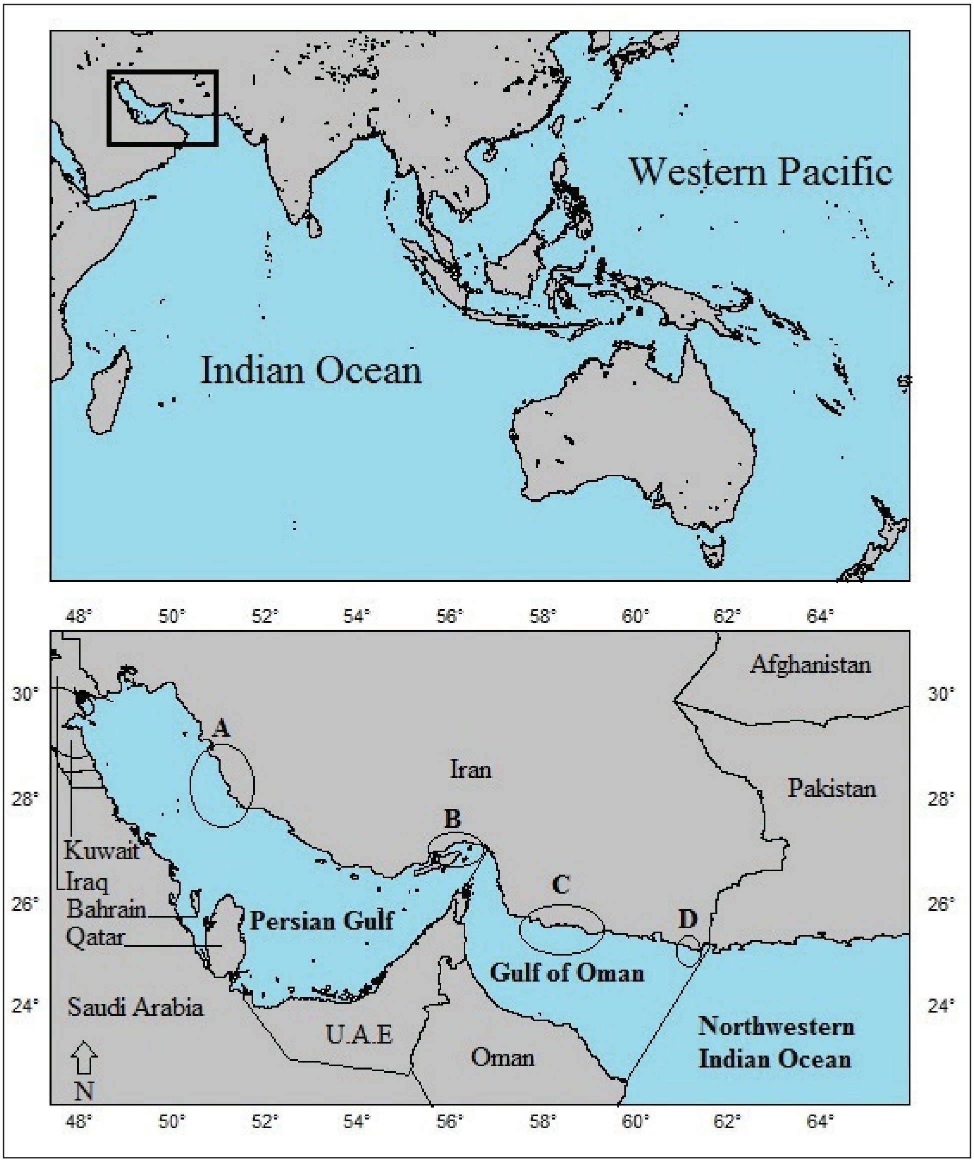

Figure 1. The upper map shows location of the Persian Gulf and Gulf of Oman in the Indo-West Pacific; the lower map shows study sites in the gulfs, including: **A** Bushehr Province **B** Qeshm Islands (Qeshm, Larak, Hormouz and Hengam Islands) **C** Jask and Ras-Meydani **D** Beris and Pasa-Bandar.

threatened species (IUCN 2016). Persian (Farsi) common names presented herein for the species in the genus *Hydrophis* are those suggested by Firouz (2005). For the two species in the genus *Microcephalophis*, English common names were directly translated into the Persian and presented herein as Persian common names.

Results

Key to the genera of the subfamily Hydrophiinae in the Persian Gulf and Gulf of Oman

1 Head extremely small; neck markedly slender; usually 5–6 supralabials; usually less than 25 scale rows on neck (Figures 23–26)................. ***Microcephalophis***

– Head and neck not as in 1; usually more than 6 supralabials; usually more than 25 scale rows on neck (Figures 5–22).................................. ***Hydrophis***

Key to the species of the genus *Hydrophis* in the Persian Gulf and Gulf of Oman

1 Tip of rostral decurved and pointed (beaked-shaped; Figures 2a and 3a); mental shield narrow and elongate (dagger-shaped), hidden in groove between chin shields (Figures 3a and 6c) (Figures 5–7) ...***Hydrophis schistosus***

– Tip of rostral curved and dentate (Figures 2b–d, 3b–h); mental shield short and triangulate (Figure 3b–h) **2**

2 Tip of rostral markedly tridentate (Figures 2b, 2c, 3b, 3c); ventrals on mid-body larger anteriorly than posteriorly, markedly distinguishable from adjacent scales (Figure 4a–b) **3**

– Tip of rostral markedly or slightly unidentate (Figures 2d, 3d-h); ventrals on mid-body almost of same size, slightly distinguishable or indistinguishable from adjacent scales (Figure 4c–f) **4**

3 Ventrals on anterior part of body markedly large, wide and rectangular in shape (Figure 4a), half width of body (Figures 8–9).....***Hydrophis viperinus***

– Ventrals on anterior part of body medium size, more or less hexagonal in shape (Figure 4b), less than half width of body (Figures 10–11)....***Hydrophis curtus***

4 Markedly sharp contrast in colors of dorsal and ventral portions of head and body, dark brown or black dorsally, yellow ventrally (Figure 13d); ventrals on mid-body more or less indistinguishable from adjacent scales (Figure 4f) (Figures 12–13) .... ***Hydrophis platurus***

– Not colored as in 4, usually banded body (Figures 15d, 17d–e, 19d, 20, 22); ventrals on mid-body slightly distinguishable from adjacent scales (Figure 4c–d)...**5**

5 Body bands narrower than light interspaces (Figure 15d) (Figures 14–15).... .... ***Hydrophis spiralis***

– Body bands as wide as or wider than light interspaces (Figures 17d–e, 19d, 20, 22)..**6**

6 Head slightly small; body elongate; body bands broader dorsally tapering to points in lateral sides (Figures 19d, 20, 22); usually less than 32 scale rows on neck **7**

– Head of medium size; body slightly stout; rhomboidal or rectangular dark body bands clearly distinct with light narrow interspaces (Figure 17); usually more than 34 scale rows on neck (Figures 16–17)..........***Hydrophis ornatus***

7 Scales on thickest part of body juxtaposed or feebly imbricate, more or less hexagonal or quadrangular in shape; total length rarely exceeding one meter in adults (Figures 21–22) .... ***Hydrophis lapemoides***

– Scales on thickest part of body more or less imbricate with bluntly pointed tips; total length more than one meter in adults (Figures 18–20) .... ***Hydrophis cyanocinctus***

Key to the species of the genus *Microcephalophis* in the Persian Gulf and Gulf of Oman

1 Less than 270 ventrals; prefrontal scale usually in contact with second supralabial (Figure 23) (Figures 23–24) .... ***Microcephalophis gracilis***

– More than 400 ventrals; prefrontal scale usually in contact with third supralabial (Figure 25) (Figures 25–26) .... ***Microcephalophis cantoris***

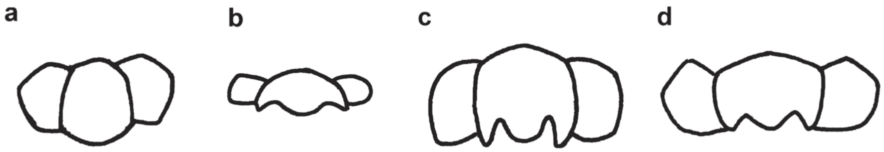

Figure 2. Various shapes of rostrals of sea snakes of the genus *Hydrophis* in the Persian Gulf and Gulf of Oman: **a** tip of rostral decurved and pointed (beaked-shaped) **b** and **c** tip of rostral tridentate **d** tip of rostral unidentate.

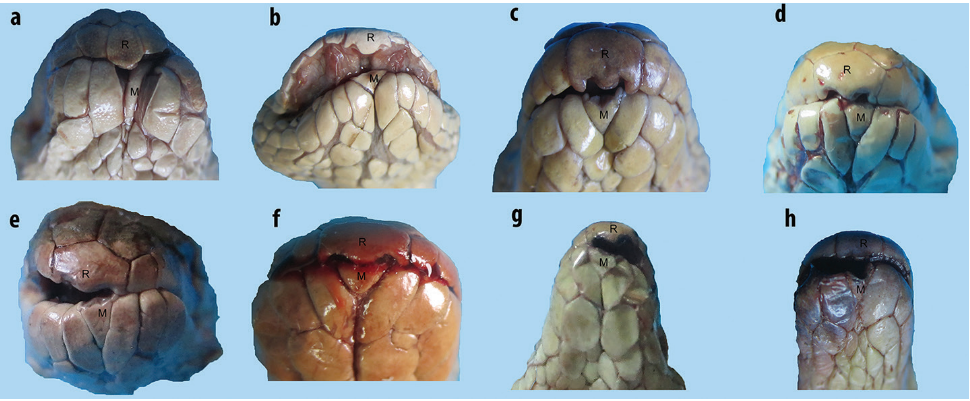

Figure 3. Rostrals and mentals of sea snakes of the genus *Hydrophis* in the Persian Gulf and Gulf of Oman: **a** tip of rostral decurved, pointed and beaked shaped, mental narrow, elongate and dagger-shaped (*Hydrophis schistosus*) **b** and **c** tip of rostral markedly tridentate, mental short and triangulate (*H. viperinus* and *H. curtus*, respectively) **d** tip of rostral markedly unidentate, mental short and triangulate (*H. ornatus*) **e–h** tip of rostral slightly unidentate, mental short and triangulate (*H. ornatus*, *H. spiralis*, *H. cyanocinctus* and *H. platurus*, respectively).

Taxonomic accounts

Family Elapidae Boie, 1827
Subfamily Hydrophiinae Fitzinger, 1843
Hydrophis Latreille *in* Sonnini & Latreille, 1801

Hydrophis schistosus Daudin, 1803

Common names: English – Beaked Sea Snake; Farsi – Mâr-e daryâï-ye nokdâr
Figures 3a, 4e, 5–7

Hydrophis schistosus Daudin, 1803: 386.
Enhydrina schistosa -Boulenger 1887: 408. -Boulenger 1896: 302. -Smith 1926: 39. -Volsøe 1939: 14. -Gasperetti 1988: 306. -Leviton et al. 1992: 120. -Carpenter et al. 1997: 246. -Firouz 1999: 191. -Latifi 2000: 336. -Baldwin and Gardner 2005: 248. -Firouz 2005: 209. -Soorae et al. 2010: 535. -Egan 2007: 143. -Safaei and Esmaili 2009: 45. -Rastegar-Pouyani et al. 2008: 20.
Hydrophis schistosus -Kamali 2013: 242. -Safaei-Mahroo et al. 2015: 282.

Material examined. Persian Gulf: 1 specimen, Larak Island [(ZMSBUK.HD.58), TL 971, SVL 857, HL 29.6, HW 12.6, GL 18.4, SNL 5.3, NEL 3.1, ND 52, GBD 100, NSL 7, NSR 47, BSR 57, NV 301], February 2014, collector: M. Ghavasi.

Gulf of Oman: 8 specimens, Jask and Ras-Meydani, depth 18–50m [(ZMSBUK.HD.14), TL 1147, SVL 1008, HL 29.4, HW 14.5, GL 20.8, SNL 5.3, NEL 3.7, ND 55, GBD 95, NSL 8, NSR 48, BSR 55, NV 315; (ZMSBUK.HD.21), TL 1180, SVL 1064, HL 31.2, HW 12.3, GL 22.4, SNL 5.4, NEL 3.4, ND 54, GBD 109, NSL 9, NSR 51, BSR 57, NV 303; (ZMSBUK.HD.25), juvenile, TL 508, SVL 451, HL 17.9, HW 7.7, GL 12, SNL 2.9, NEL 1.3, ND 26, GBD 39, NSL 8, NSR 51, BSR 59, NV 344; (ZMSBUK.HD.41), TL 1093, SVL 977, HL 30.5, ND 51, GBD 95, NSL 8, BSR 60; (ZMSBUK.HD.45), TL 1057, SVL 943, HL 31.3, HW 18, GL 20.5, SNL 4.4, NEL 3.9, ND 48, GBD 96, NSL 7, NSR 47, BSR 60, NV 323; (ZMSBUK.HD.50), TL 1172, SVL 1064, HL 36.7, HW 19.3, GL 23.7, SNL 5.5, NEL 4.6, ND 60, GBD 105, NSL 8, NSR 51, BSR 61, NV 316; (ZMSBUK.HD.51), TL 932, SVL 823, HL 28.4, HW 13.7, GL 17.7, SNL 5.6, NEL 3.4, ND 45, GBD 98, NSL 8, NSR 50, BSR 61, NV 325; (ZMSBUK.HD.52), TL 1230, SVL 1093, HL 35.2, HW 16.6, GL 23.5, SNL 4.8, NEL 4.4, ND 62, GBD 116, NSL 8, NSR 53, BSR 65, NV 340], October and November 2013, collector: M. Rezaie-Atagholipour; 3 specimens, Jask, mangrove swamps, depth 1–3m [(ZMSBUK.HD.27), TL 966, SVL 855, HL 28.3, HW12.3, GL 19.7, SNL 4.9, NEL 3.7, ND 44, GBD 90, NSL9, NSR 52, BSR 59, NV 327; (ZMSBUK.HD.29), TL 1080, SVL 947, HL 30.5, HW 18.1, GL 17, SNL 5.6, NEL 4.1, ND 50, GBD 80, NSL 9, NSR 40, BSR 58, NV 348; (ZMSBUK.HD.62), TL 1032, SVL 907, HL 28.5, HW 16, GL 20.1, SNL 5.2, NEL 4.5, ND 52, GBD 88, NSL 8, NSR 47, BSR 59, NV 327], December 2013, collector: M. Rezaie-Atagholipour; 2 specimens, Beris and

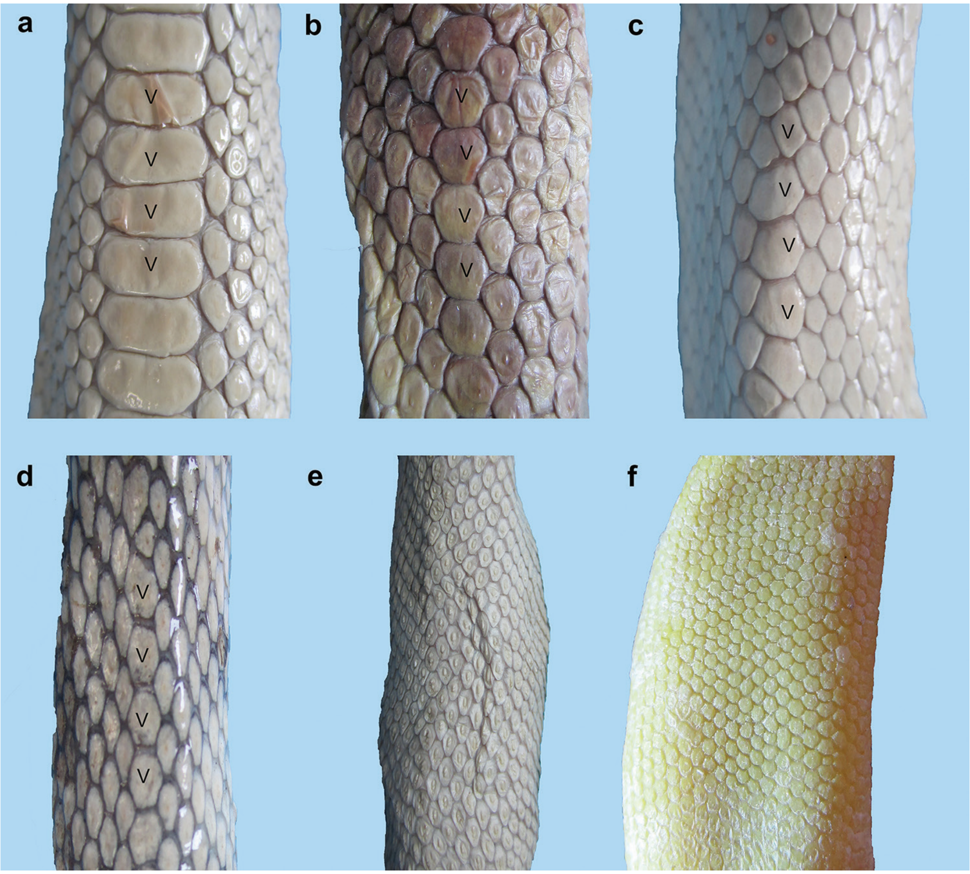

Figure 4. Various shapes of ventrals on the mid-body of sea snakes of the genus *Hydrophis* in the Persian Gulf and Gulf of Oman: **a** wide and enlarged, more or less rectangular in shape (*Hydrophis viperinus*) **b** medium size, distinguishable from the adjacent scales, more or less hexagonal in shape (*H. curtus*) **c** and **d** small and slightly distinguishable from adjacent scales (*H. ornatus* and *H. lapemoides*, respectively) **e** and **f** small and more or less indistinguishable from adjacent scales (*H. schistosus* and *H. platurus*, respectively).

Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.49), TL 1044, SVL 928, HL 30.8, HW 12.7, GL 19.3, SNL 5, NEL 3.7, ND 50, GBD 105, NSL 7, NSR 51, BSR 64, NV 302; (ZMSBUK.HD.53), TL 1095, SVL 955, HL 31.9, HW 14.7, GL 19.4, SNL 2.5, NEL 4.2, ND 50, GBD 95, NSL 8, NSR, BSR, NV, NB], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head of medium size; rostral beaked-shaped, elongate with decurved and pointed tip (Figures 2a, 3a); mental elongate, slender and dagger-shaped, hidden in the groove between chin shields (Figures 3a, 6c); body slightly elongate, not markedly slender anteriorly (Figure 6e–f); 301–348 ventrals [340–354 (Volsøe 1939)], small and more or less indistinguishable from adjacent scales at mid-body (Figure 4e); 40–55 scale rows on neck and 53–65 on body [47–52 and 56–60 (Volsøe 1939)].

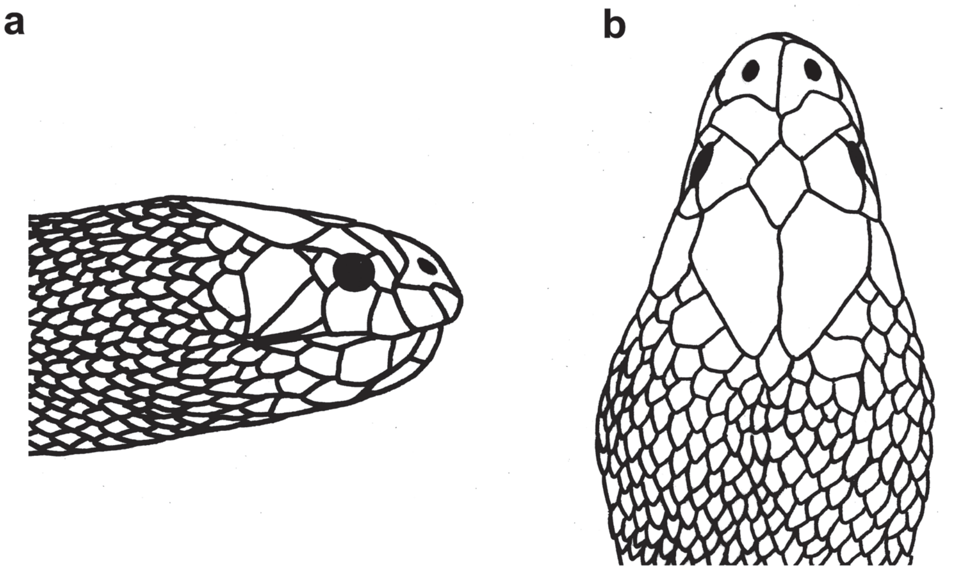

Figure 5. Head of *Hydrophis schistosus*: **a** lateral view **b** dorsal view.

Coloration. Gray or dark olive dorsally, whitish ventrally; body rings developed in juveniles but paler or absent in adults (Figure 6e); exceptionally black dorsally (Figure 6f).

Size. Mean TL 1036 mm, maximum 1230 mm (n = 14) [n = 3, maximum TL 1350 mm (Volsøe 1939)]

General distribution. Indo- West Pacific, from the Persian Gulf to Australia (David and Ineich 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. *Hydrophis schistosus* is distinct from other species in the Persian Gulf and Gulf of Oman due to its beaked-shaped rostral and dagger-shaped mental. Results of our field surveys showed that the species is more abundant in the Gulf of Oman rather than in the Persian Gulf. This is supported by other studies as eight specimens have been hitherto examined from the Gulf of Oman (Boulenger 1887, 1896; Smith 1926; Volsøe 1939) versus three specimens from the Persian Gulf (Corkill 1932; Smith 1926; present study). Furthermore, during two months boat surveys in Hara (mangrove) Biosphere Reserve in the eastern Persian Gulf, only two specimens of the species were found (Rezaie-Atagholipour et al. 2012). Nonetheless, two specimens collected by Rezaie-Atagholipour et al. (2012) and the only specimen collected in this study were from Strait of Hormoz in the boundary of the two gulfs. Therefore these three specimens may be vagrant, and can not be strictly allocated to a particular population in the Persian Gulf. Concerning the two remaining specimens reported from the Gulf by Corkill (1932) and Smith (1926), no exact locality was mentioned. In conclusion, populations of *H. schistosus* in the Persian Gulf seem likely to be in low abundance. On the other hand, results of this study showed that the species is one of the most abundant sea snakes in the Gulf of Oman. In total,

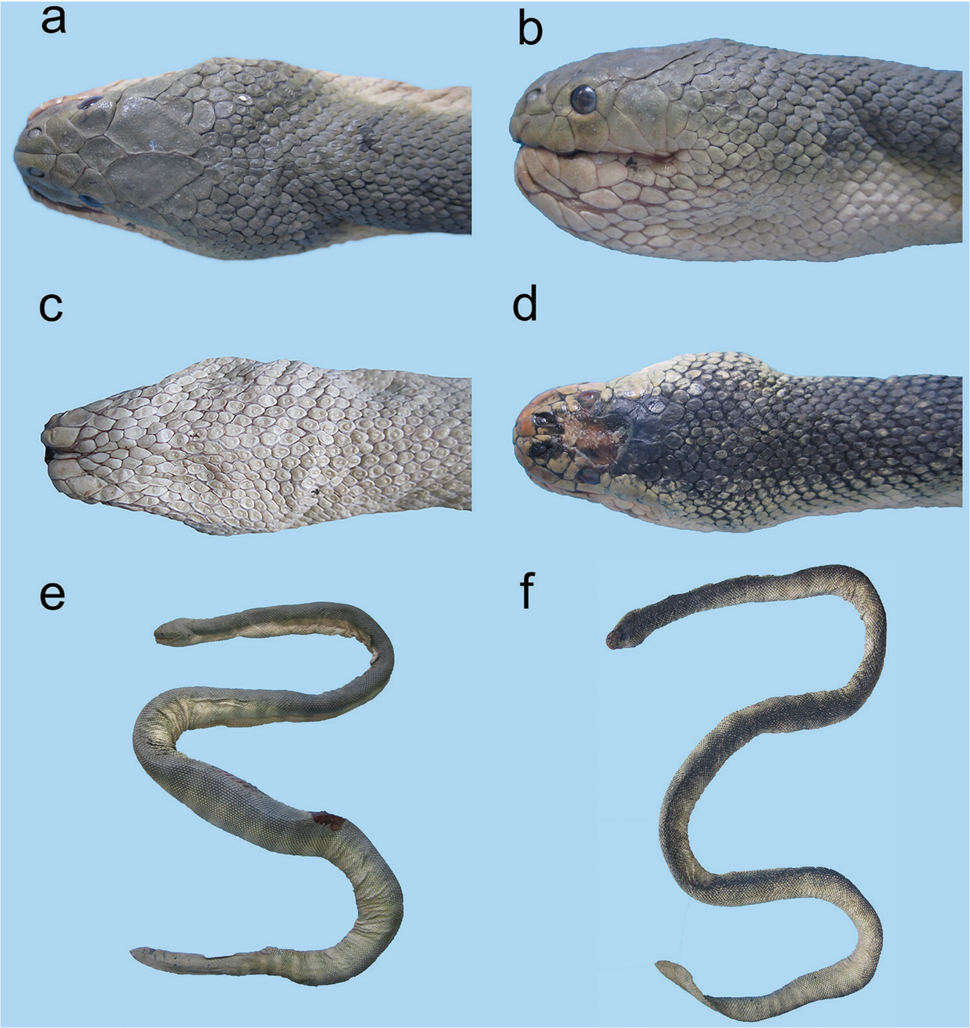

Figure 6. *Hydrophis schistosus*: **a** dorsal view **b** lateral view, and **c** ventral view of head **d** dorsal view of head of a black specimen **e** typical body color **f** black dorsally.

26% of all specimens examined here were *H. schistosus*, all but one collected from the Gulf of Oman. Approximately 71% (261 of 367 specimens) of sea snakes that Safaei and Esmaili (2009) collected from coastal waters of Hormozgan Province (eastern Persian Gulf and western Gulf of Oman) were *H. schistosus*. They mentioned that most of these specimens were collected from Gulf of Oman. They failed however to report the exact proportions. Mating behavior of the species was sighted during a boat survey through coastal waters of Jask (western Gulf of Oman) in December 2013, the two animals having been seen intertwined and floating on the surface (Figure 7). *Hydrophis schistosus* is an aggressive sea snake. This snake is prey-specific, mostly consuming spiny catfishes (Glodek and Voris 1982; Voris and Moffett 1981).

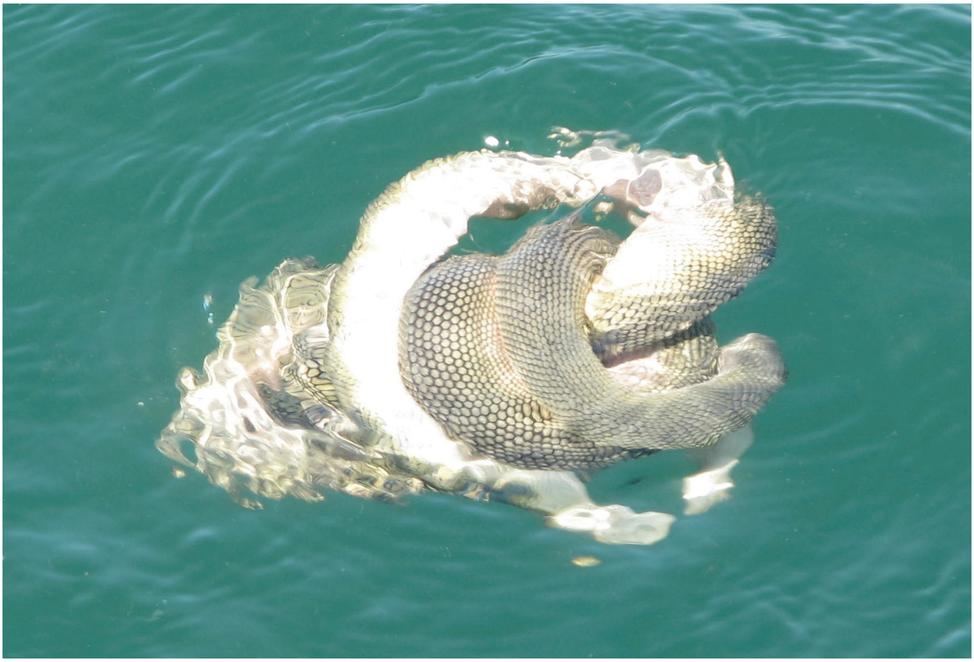

Figure 7. Mating behavior of *Hydrophis schistosus*: two individuals intertwined each other and floating on the surface in the coastal waters of Jask (western Gulf of Oman), December 2013.

Recent morphological and molecular evidence revealed that this species consists of two convergent lineages through its geographical distribution range. Now, the Australian lineage is elevated to species status and provisionally referred as to *H. zweifeli* (see Ukuwela et al. 2013).

*Hydrophis viperinus (*Schmidt, 1852)

Common names: English – Viperine Sea Snake; Farsi – Mâr-e daryâï-ye af' ïshekl
Figures 3b, 4a, 8–9

Thalassophis viperina Schmidt, 1852: 79.
Thalassophis viperina -Smith 1926: 35. -Volsøe 1939: 10.
Hydrophis jayakari -Boulenger 1887: 408.
Hydrophis plumbea -Murray 1887: 34.
Distira viperina -Boulenger 1896: 298.
Praescutata viperina -Corkill and Cochrane 1965: 494. -Joger 1984: 31. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 325. -Leviton et al. 1992: 127. -Carpenter et al. 1997: 249. Firouz 1999: 192. -Baldwin and Gardner 2005: 251. -Firouz 2005: 210. -Egan 2007: 166. -Rastegar-Pouyani et al. 2008: 20. -Soorae et al. 2010: 535.
Hydrophis viperinus -Kamali 2013: 244. -Safaei-Mahroo et al. 2015: 282.

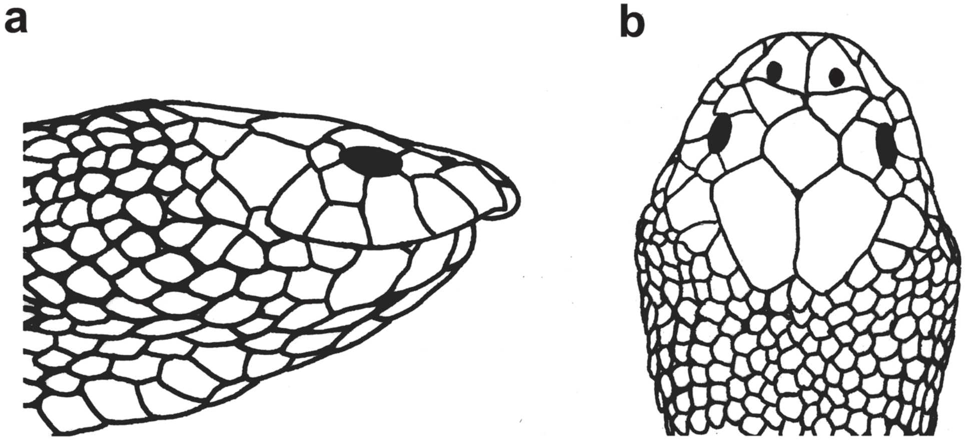

Figure 8. Head of *Hydrophis viperinus*: **a** lateral view **b** dorsal view.

Material examined. Gulf of Oman: 2 specimens, Beris and Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.20), TL 737, SVL 656, HL 19.1, HW 12.6, GL 14.8, SNL 3, NEL 3, ND 35, GBD 67, NSL 8, NSR 29, BSR 47, NV 250; (ZMSBUK.HD.43), TL 740, SVL 657, HL 18.9, HW 14.9, GL 13.3, SNL 3.9, NEL 2.8, ND 38, GBD 68, NSL 7, NSR 30, BSR 43, NV 265], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head large, short and depressed (Figures 8–9); tip of rostral curved and markedly tridentate (Figures 2b, 3b); usually 7–8 supralabials, none in contact with prefrontal (Figure 8); 250–265 large ventrals [245–291 (Volsøe 1939)], markedly distinguishable from adjacent scales (Figure 4a), larger anteriorly than posteriorly; ventrals on anterior part of body wide and enlarged, half width of body, more or less rectangular in shape; 29–38 scale rows on neck, 39–47 on body [27–31 and 40–43 (Volsøe 1939)].

Coloration. Dark gray dorsally, dirty white ventrally; with or without pale body bands broadest dorsally; tip of tail usually black (Figure 9d).

Size. Maximum TL 740 mm (n = 2); [n = 8, mean TL 662 mm, maximum TL 780 mm (Volsøe 1939)].

General distribution. Indian Ocean, from the Persian Gulf to Malay Archipelago (David and Ineich 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. *Hydrophis viperinus* is distinct from other sea snakes in the Persian Gulf and Gulf of Oman by having markedly rectangular-shaped and enlarged ventrals on the anterior part of the body. Smith (1926) and Wall (1921) mentioned that the Persian Gulf is the westernmost distribution limit of *H. viperinus*. Volsøe (1939) had doubts about it: "their only exact records from the Persian Gulf are however from Muscat, which is situated about 400 km outside the Strait of Hormoz". We agree with Volsøe (1939) as the two specimens we examined in this study and the specimens examined in other studies in the area (e.g. Boulenger 1887; Volsøe 1939) have all been

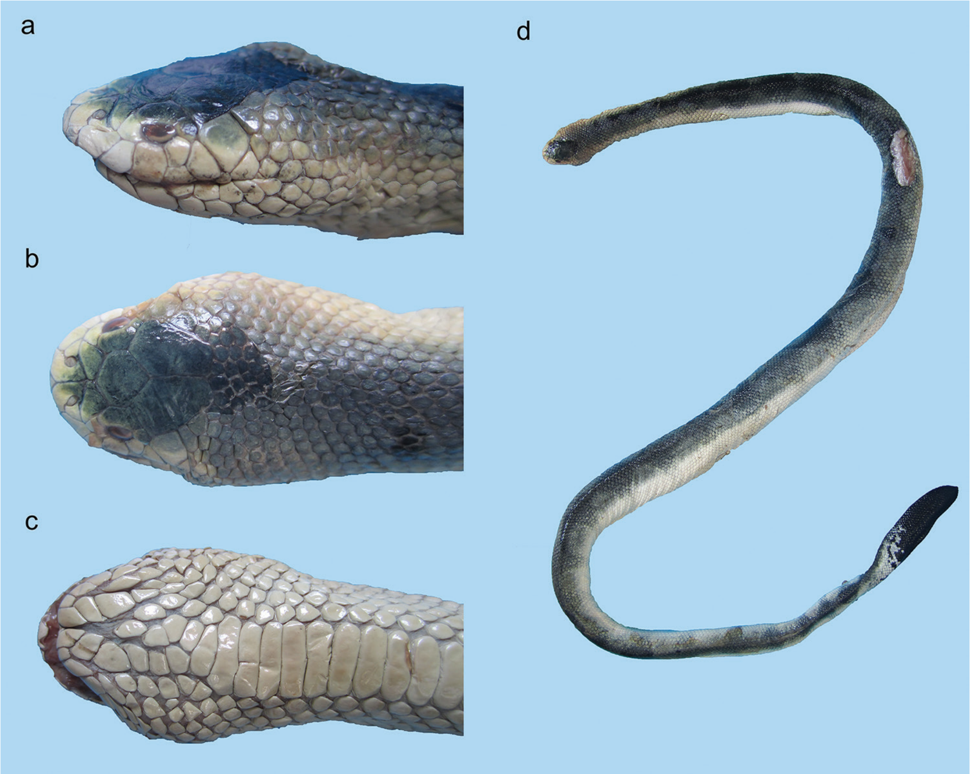

Figure 9. *Hydrophis viperinus*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** body.

collected from the Gulf of Oman. We did not find any specimen of *H. viperinus* in Iranian coastal waters of the Persian Gulf during our field surveys. Therefore, population of *H. viperinus* in the Persian Gulf, if present, seems likely to be in low abundance.

Hydrophis curtus **(Shaw, 1802)**

Common names: English – Shaw's Sea Snake, Short Sea Snake, Spine-bellied Sea Snake; Farsi – Mâr-e daryâï-ye kutâh
Figures 3c, 4b, 10–11

Hydrus curtus Shaw, 1802: 562.
Enhydris curtus -Werner 1895: 19.
Lapemis curtus -Smith 1926: 112. -Kennedy 1937: 748. -Volsøe 1939: 21. -Corkill and Cochrane 1965: 495. -Joger 1984: 29. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 317. -Leviton et al. 1992: 125. -Carpenter et al. 1997: 248. -Firouz 1999: 192. -Baldwin and Gardner 2005: 250. -Firouz 2005: 210. -Soorae et al. 2006: 109. -Rastegar-Pouyani et al. 2008: 20. -Safaei and Esmaili 2009: 45. -Soorae et al. 2010: 535. -Kordi and Shabanipour 2012: 71. -Rezaie-

Atagholipour 2012: 494. - Sereshk and Bakhtiari 2014: 116. -Sereshk and Bakhtiari 2015: 15781.
Hydrophis curtus -Kamali 2013: 237. -Safaei-Mahroo et al. 2015: 282.

Material examined. Persian Gulf: 8 specimens, Bushehr Province [(ZMSBUK.HD.1), TL 915, SVL 831, HL 32.9, HW 24.9, GL 22.9, SNL 7.9, NEL 4.8, ND 74, GBD 130, NSL 8, NSR 32, BSR 39, NV 158, NB 39; (ZMSBUK.HD.2), TL 900, SVL 805, HL 34, HW 20.5, GL 23, SNL 7.3, NEL 5.4, ND 80, GBD 130, NSL 8, NSR 29, BSR 37, NV 187, NB 45; (ZMSBUK.HD.5), TL 835, SVL 755, HL 31.5, HW 16.8, GL 26, SNL 7.1, NEL 4.6, ND 62, GBD 95, NSL 8, NSR 30, BSR 39, NV 165, NB 47; (ZMSBUK.HD.11), TL 852, SVL 751, HL 30.3, HW 16.8, GL 22.2, SNL 5.8, NEL 4.5, ND 72, GBD 107, NSL 9, NSR 28, BSR 33, NV 147, NB 50; (ZMSBUK.HD.15), TL 1008, SVL 910, HL 34.2, HW 19.2, GL 23.9, SNL 6.6, NEL 5, ND 80, GBD 125, NSL 8, NSR 31, BSR 39, NV 185, NB 55; (ZMSBUK.HD.17), TL 869, SVL 781, HL 28.7, HW 15.8, GL 20.7, SNL 6, NEL 4.3, ND 61, GBD 75, NSL 7, NSR 24, BSR 36, NV 153, NB 48; (ZMSBUK.HD.47), TL 797, SVL 716, HL 30.5, HW 16.9, GL 19.7, SNL 5.6, NEL 4.6, ND 50, GBD 62, NSL 8, NSR 30, BSR 37, NV 158, NB 45; (ZMSBUK.HD.48), TL 716, SVL 642, HL 28.4, HW 14.8, GL 18.4, SNL 4.3, NEL 4.2, ND 55, GBD 85, NSL 8, NSR 33, BSR 43, NV 199, NB 46], September 2013, collector: M. Rezaie-Atagholipour; 1 specimen, Larak Island [(ZMSBUK.HD.61), TL 783, SVL 700, HL 28.5, HW 15.3, GL 20.3, SNL 5, NEL 4.7, ND 62, GBD 95, NSL 8, NSR 32, BSR 42, NV 200, NB 51], February 2014, collector: M. Ghavasi.

Gulf of Oman: 6 specimens, Beris and Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.8), TL 855, SVL 772, HL 34.1, HW 21.6, GL 21.5, SNL 5.43, NEL 4.91, ND 70, GBD 93, NSL 7, NSR 28, BSR 34, NV 158; (ZMSBUK.HD.18), TL 960, SVL 865, HL 34, HW 16.5, GL 25, SNL 5.8, NEL 5.7, ND 72, GBD 115, NSL 7, NSR 32, BSR 37, NV 157; (ZMSBUK.HD.19), TL 825, SVL 753, HL 28.9, HW 18.1, GL 19.2, SNL 4.8, NEL 4.5, ND 58, GBD 100, NSL 8, NSR 33, BSR 40, NV201, NB 47; (ZMSBUK.HD.44), TL 1015, SVL 925, HL 40.9, HW 27.7, GL 25.6, SNL 6.6, NEL 5.3, ND 73, GBD 99, NSL 8, NSR 34, BSR 43, NV 197, NB 49; (ZMSBUK.HD.57), TL 745, SVL 674, HL 29.7, HW 17.6, GL 20.3, SNL 3.9, NEL 3.6, ND 57, GBD 85, NSL 7, NSR 33, BSR 38, NV 185, NB 50; (ZMSBUK.HD.60), TL 965, SVL 872, HL 32.7, HW 18.1, GL 23.4, SNL 5.6, NEL 5.5, ND 65, GBD 117, NSL 8, NSR31, BSR 39, NV 174, NB 51], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head large (Figure11); tip of rostral markedly tridentate (Figures 2c, 3c); parietals divided into small shields (Figures 10b, 11d–f); 7–9 supralabials, second contacts with prefrontal (Figure 10), third and fourth or only fourth touch eye; body short and stout (Figure 11j–l); 147–201 medium size ventrals, distinguishable from the adjacent scales (Figure 4b), larger anteriorly than posteriorly; ventrals on anterior part of body more or less hexagonal in shape, less than half width of body; 28–38 scale rows on neck and 32–43 on body [27–31 and 32–38 (Volsøe 1939)].

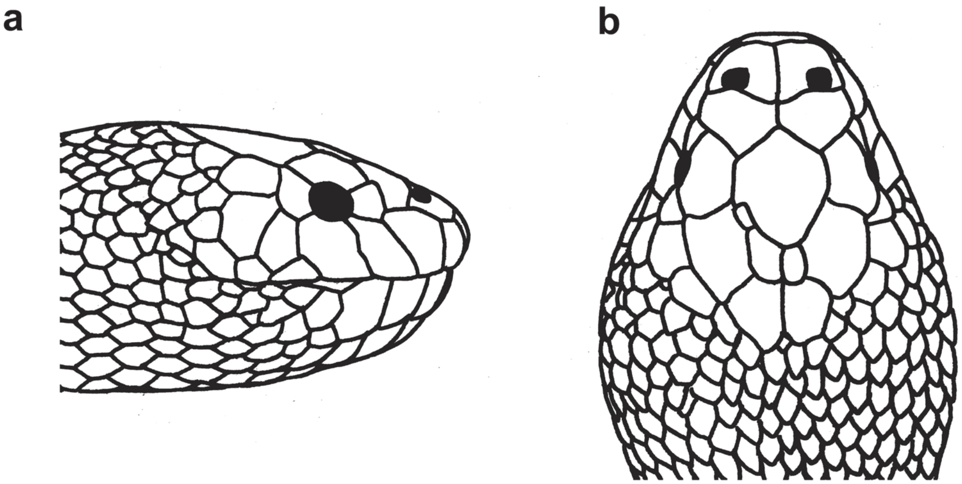

Figure 10. Head of *Hydrophis curtus*: **a** lateral view **b** dorsal view.

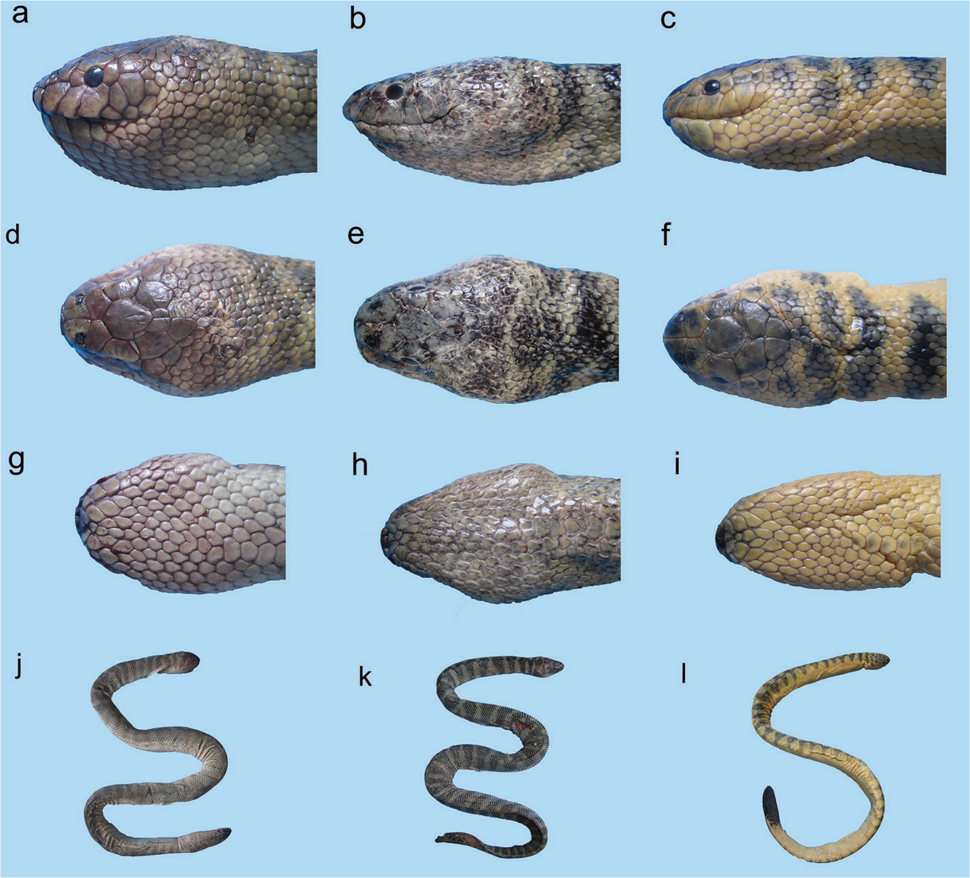

Figure 11. *Hydrophis curtus*: **a, b, c** lateral view **d, e, f** dorsal view **g, h, i** ventral view of head; and **j, k, l** body of a typical gray specimen, a rare black specimen and a rare yellow specimen, respectively.

Coloration. Three color patterns observed in this study: 1- usually gray dorsally, gray-whitish ventrally with pale gray dorsal bands (Figures 11a, d, g, j); 2- rarely yellowish body with blackish dorsal bands (Figure 11c, f, i, l); 3- rarely black-grayish body with black dorsal bands (Figure 11b, e, h, k); 39–55 dorsal bands in all three types usually fused laterally, zigzag in form; tip of tail usually black.

Size. Mean TL 716 mm, maximum 1015 mm (n = 15); [n = 12, mean TL 606 mm, maximum TL 860 mm (Volsøe 1939)].

General distribution. Indo- West Pacific, from the Persian Gulf to Australia (David and Ineich 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. In the Persian Gulf and Gulf of Oman, *H. curtus* may be roughly confused with *H. ornatus* at a glance. *Hydrophis curtus* however can be quickly distinguished from *H. ornatus* by having parietals divided into small shields and laterally fused dorsal bands, zigzag in form, versus clearly distinguishable dorsal bands in *H. ornatus*. Volsøe (1939) mentioned that *H. curtus* is one of the most abundant sea snakes in the Iranian coastal waters of the eastern Persian Gulf. Our results show that it is abundant in the western part of the Iranian Persian Gulf (Bushehr Province) as well. *Hydrophis curtus* is a diet generalist, known to prey on fish belonging to 33 families, cuttlefish and amphipods (Rezaie-Atagholipour 2012).

Hydrophis platurus (Linnaeus, 1766)

Common names: English – Pelagic Sea Snake, Yellow-bellied Sea Snake; Farsi – Mâr-e daryâï-ye shekam zard
Figures 3h, 4f, 12, 13

Anguis platura Linnaeus, 1766: 391.
Hydrus platurus -Werner 1895: 18. -Boulenger 1897: 468.
Pelamis platurus -Volsøe 1939: 23. -Corkill and Cochrane 1965: 495. -Leviton and Anderson 1967: 188. -Gallagher 1971: 31. -Eissa and El-Assy 1975: 129. -Joger 1984: 30. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 323. -Leviton et al. 1992: 126. -Carpenter et al. 1997: 248. -Firouz 1999: 192. -Latifi 2000: 347. -Baldwin and Gardner 2005: 251. -Firouz 2005: 210. -Soorae et al. 2006: 109. -Egan 2007: 163. -Rastegar-Pouyani et al. 2008: 20. -Safaei and Esmaili 2009: 45. -Soorae et al. 2010: 535.
Hydrophis platurus -Kamali 2013: 241. -Safaei-Mahroo et al. 2015: 282.

Material examined. Gulf of Oman: 1 specimen, Jask and Ras-Meydani , depth 18–50m [(ZMSBUK.HD.26), TL 401, SVL 352, HL 25, HW 10.1, GL 17.7, SNL 3.4, NEL 4.7, ND 34, GBD 38, NSL 10, NSR 39, BSR 46], October and November 2013, collector: M. Rezaie-Atagholipour; 2 specimens, Beris and Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.12), TL 611, SVL 551, HL 34.5, HW 13, GL 22.2, SNL 4.7, NEL 6, ND 27, GBD 63, NSL 9, NV 333; (ZMSBUK.HD.23), TL 690, SVL

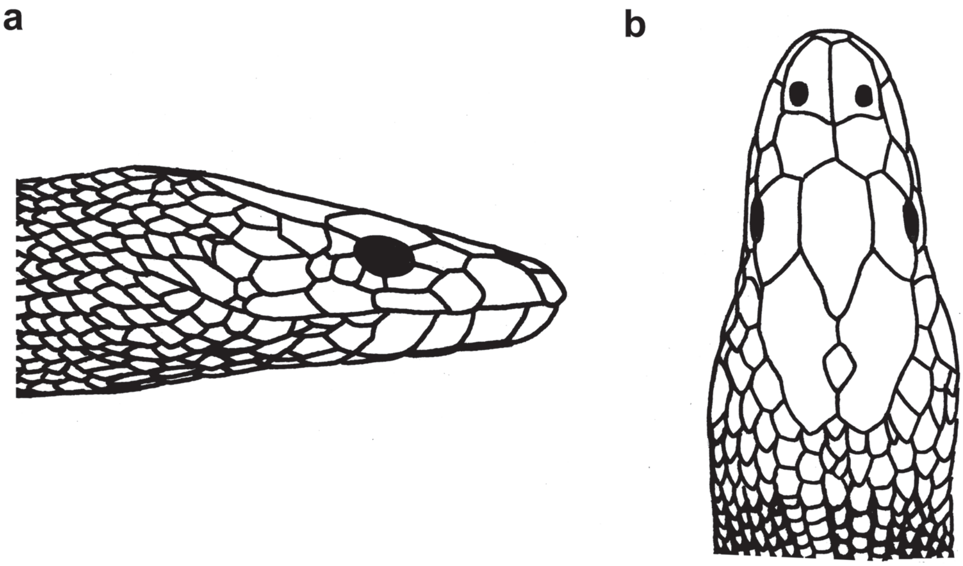

Figure 12. Head of *Hydrophis platurus*: **a** lateral view **b** dorsal view.

618, HL 35.8, HW 17.9, GL 29.7, SNL 5, NEL 6.8, ND 52, GBD 72, NSL 9, NSR 56, BSR 58, NV 330], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head narrow; snout elongate (Figures 12–13); 9–10 supralabials, second touches prefrontal scale, four and fifth separated from eye by suboculars or contact eye (Figures 12a, 13a); body short, not stout (Figure 13d); 330–333 small ventral scales [265–367 (Volsøe 1939)], more or less indistinguishable from adjacent scales at mid-body (Figure 4f).

Coloration. This species has a unique color pattern making it distinguishable from other sea snakes; dorsal half of head and body black, dark green or dark brown, ventral half of head and body yellow, a markedly sharp contrast between dorsal and ventral portions; tail yellow in ventral portion, spotted or barred in dorsal portion (Figure 13d); sometimes with pale dorsal color.

Size. Mean TL 567 mm, maximum 690 mm (n = 3); [n = 5, mean TL 449 mm, maximum 565 mm (Volsøe 1939)].

General distribution. Indo-Pacific, from east and south of Africa to the west coast of Americas (Heatwole 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. *Hydrophis platurus* is distinguishable from other species in the region by having a unique color pattern (see above). *Hydrophis platurus* has been known as the only planktonic tetrapod, spending a considerable portion of its life floating at the depth of 20–50 m, but preying on fish at the sea surface by float-and-wait feeding strategy, passively drifting with surface and subsurface marine currents. It has consequently the widest distribution of all squamatan reptiles (Cook and Brischoux 2014; Hecht et al. 1974; Sheehy III et al. 2012). None of the specimens collected in this project were

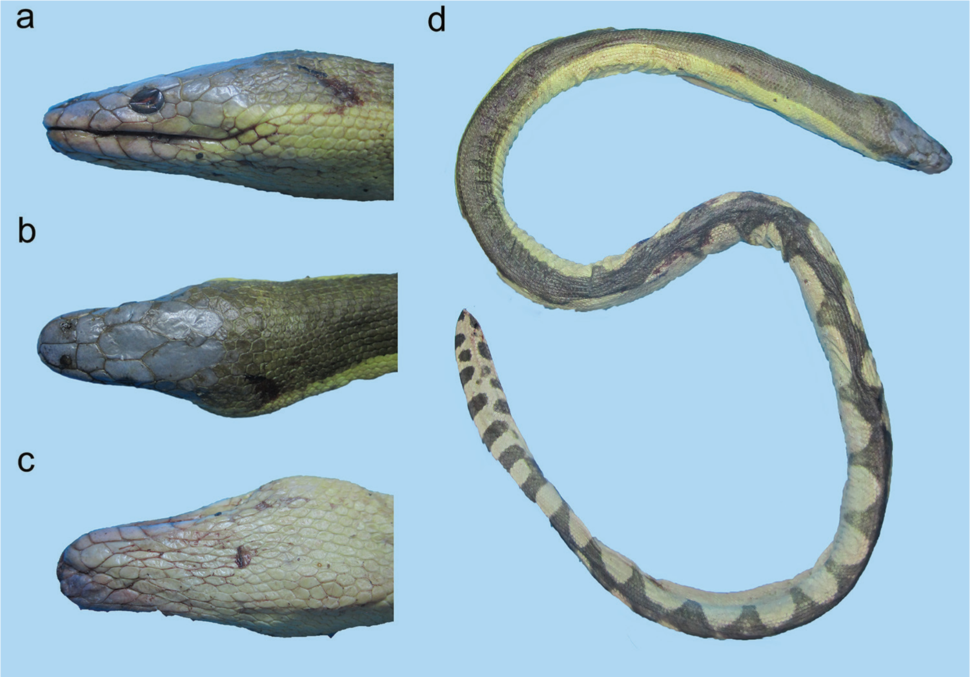

Figure 13. *Hydrophis platurus*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** body.

from the Persian Gulf, although there are records from the Persian Gulf (e.g. Eissa and El-Assy 1975; Gallagher 1971; Soorae et al. 2006; Volsøe 1939; Werner 1895).

Hydrophis spiralis **(Shaw, 1802)**

Common names: English – Yellow Sea Snake; Farsi – Mâr-e daryâï-ye zard
Figures 3f, 14–15

Hydrus spiralis Shaw, 1802: 564.
Hydrus temporalis -Blanford 1881: 680.
Hydrus robusta -Boulenger 1887: 408.
Hydrophis spiralis -Smith 1926: 48. -Volsøe 1939: 15. -Haas 1961: 21. -Leviton et al. 1992: 124. -Carpenter et al. 1997: 247. -Firouz 1999: 192. -Latifi 2000: 343. -Baldwin and Gardner 2005: 250. -Rastegar-Pouyani et al. 2008: 20. -Safaei and Esmaili 2009: 45. -Kamali 2013: 243. -Safaei-Mahroo et al. 2015: 282.
Hydrophis spiralis spiralis -Corkill and Cochrane 1965: 495. -Joger 1984: 34. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 315. -Firouz 2005: 209. -Egan 2007: 154. -Soorae et al. 2010: 535.

Material examined. Gulf of Oman: 1 specimen, Jask, depth 1–3m [(ZMSBUK.HD.55), TL 1925, SVL 1775, HL 44.3, HW 20.6, GL 28, SNL 7.5, NEL 5.8, ND

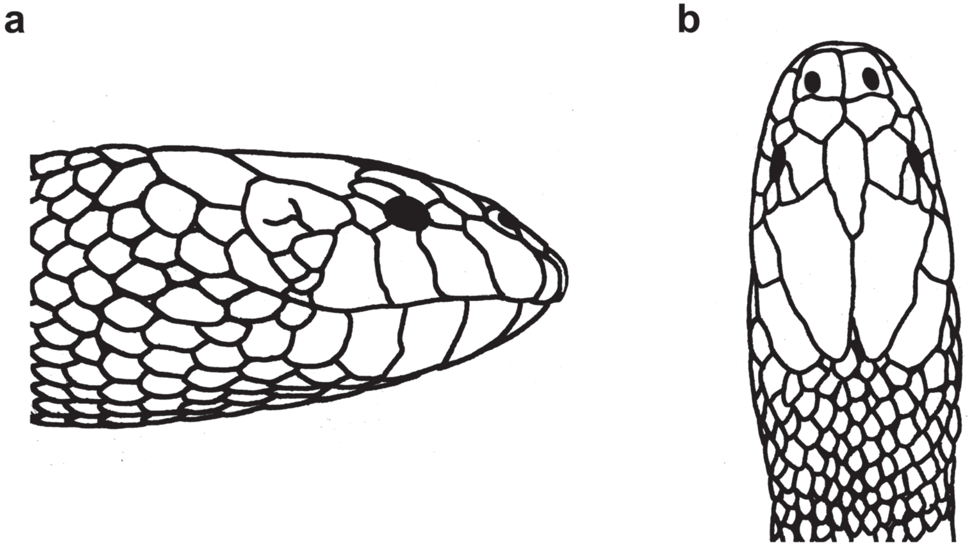

Figure 14. Head of *Hydrophis spiralis*: **a** lateral view **b** dorsal view.

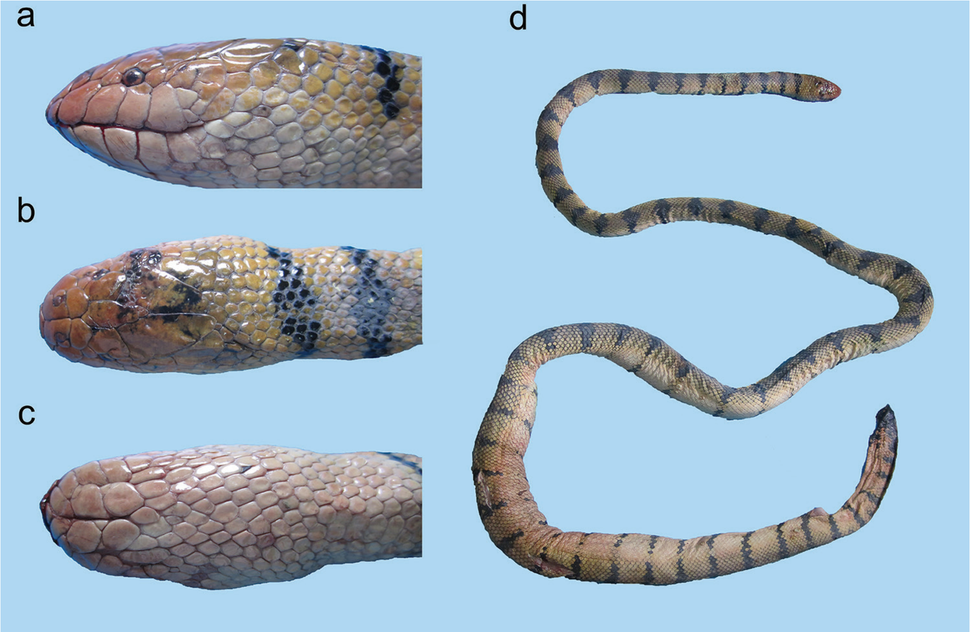

Figure 15. *Hydrophis spiralis*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** body.

67, GBD 90, NSL 7, NSR 30, BSR 38, NV 387, NB 61], December 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head of medium size (Figure 15); second supralabial touches prefrontal scale (Figure 14); body markedly elongate, not slender anteriorly (Figure 15d);

387 ventrals [363–385 (Volsøe 1939)], slightly distinguishable from adjacent scales; [27–31 scale rows on neck, 34–38 on body (n = 4, Volsøe 1939; n = 1, present study)].

Coloration. Yellowish body with 61 [30–60 more or less (Gasperetti 1988)] narrow black rings, narrower than yellowish interspaces; head yellowish as body (Figure 15); [a black ventral line sometimes present, head blackish with a horseshoe-shaped mark above in young individuals (Gasperetti 1988)].

Size. TL 1925mm (n = 1); [n = 4, mean TL 1587 mm; maximum TL 1984 mm (Volsøe 1939)].

General distribution. Indian Ocean, from the Persian Gulf to Malay Archipelago (David and Ineich 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. *Hydrophis spiralis* is distinguishable from other species in the area by its yellow body and narrow black rings (narrower than yellow interspaces). This species is the longest among all marine hydrophiines (Heatwole 1999). We could catch only one specimen of *H. spiralis*, which was collected from Jask in the western Gulf of Oman. Other authors however recorded the species from the Persian Gulf (e.g. Blanford 1881; Haas 1961; Volsøe 1939).

***Hydrophis ornatus* (Gray, 1842)**

Common names: English – Ornate Reef Sea Snake, Ornate Sea Snake; Farsi – Mâr-e daryâï-ye ârâsteh
Figures 3d, 3e, 4c, 16–17

Aturia ornata Gray, 1842: 61.
Hydrophis elliotti -Boulenger 1887: 408.
Distira ornata -Werner 1895: 19. -Boulenger 1896: 290.
Hydrophis ornatus ornatus -Smith 1926: 81. -Corkill and Cochrane 1965: 494. -Joger 1984: 34. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 315. -Firouz 2005: 209.
Hydrophis ornatus -Volsøe 1939: 18. -Leviton et al. 1992: 123. -Carpenter et al. 1997: 247. -Firouz 1999: 192. -Latifi 2000: 342. -Baldwin and Gardner 2005: 249. -Egan 2007: 151. -Rastegar-Pouyani et al. 2008: 20. -Safaei and Esmaili 2009: 45. -Soorae et al. 2010: 535. -Kamali 2013: 240. -Safaei-Mahroo et al. 2015: 282.

Material examined. Persian Gulf: 3 specimens, Bushehr Province [(ZMSBUK.HD.10), TL 813, SVL 722, HL 26, HW 16.7, GL 18.8, SNL 4.9, NEL 3.9, ND 53, GBD 80, NSL 7, NSR 35, BSR 42, NB 41; (ZMSBUK.HD.13), TL 879, SVL 791, HL 28.1, HW 15, GL 12.5, SNL 4.2, NEL 4, ND 55, GBD 89, NSL 7, NSR 40, BSR 44, NV 302, NB 46; (ZMSBUK.HD.16), TL 1200, SVL 1072, HL 36.6, HW 23.7, GL 27.6, SNL 6, NEL 5.2, ND 74, GBD 157, NSL 7, NSR 41, BSR 50, NV 306, NB 53], September 2013, collector: M. Rezaie-Atagholipour.

Gulf of Oman: 3 specimens, Beris and Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.3), TL 1015, SVL 908, HL 32.9, HW 30, GL 21.9, SNL 6.9, NEL 5.2, ND 68,

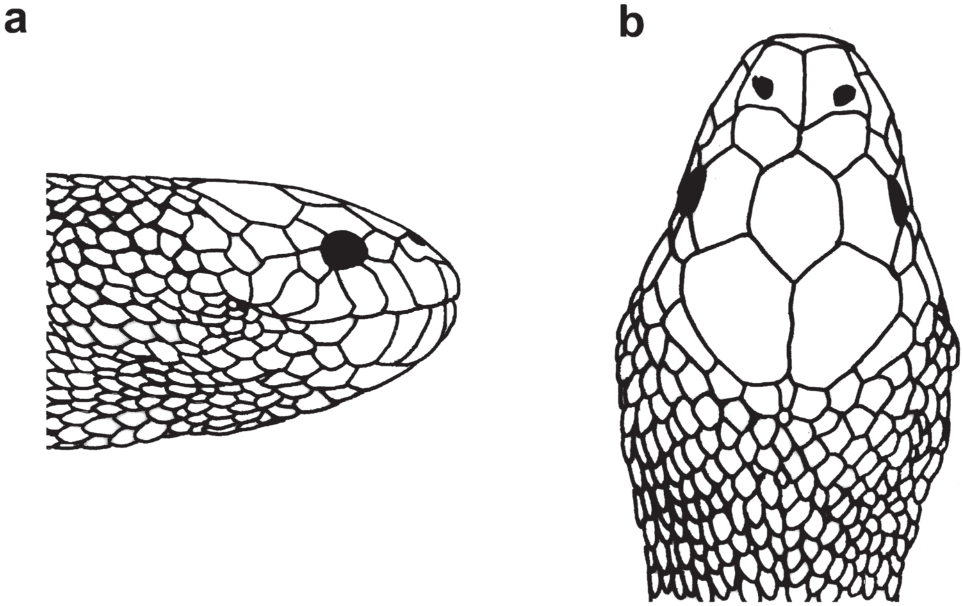

Figure 16. Head of *Hydrophis ornatus*: **a** lateral view **b** dorsal view.

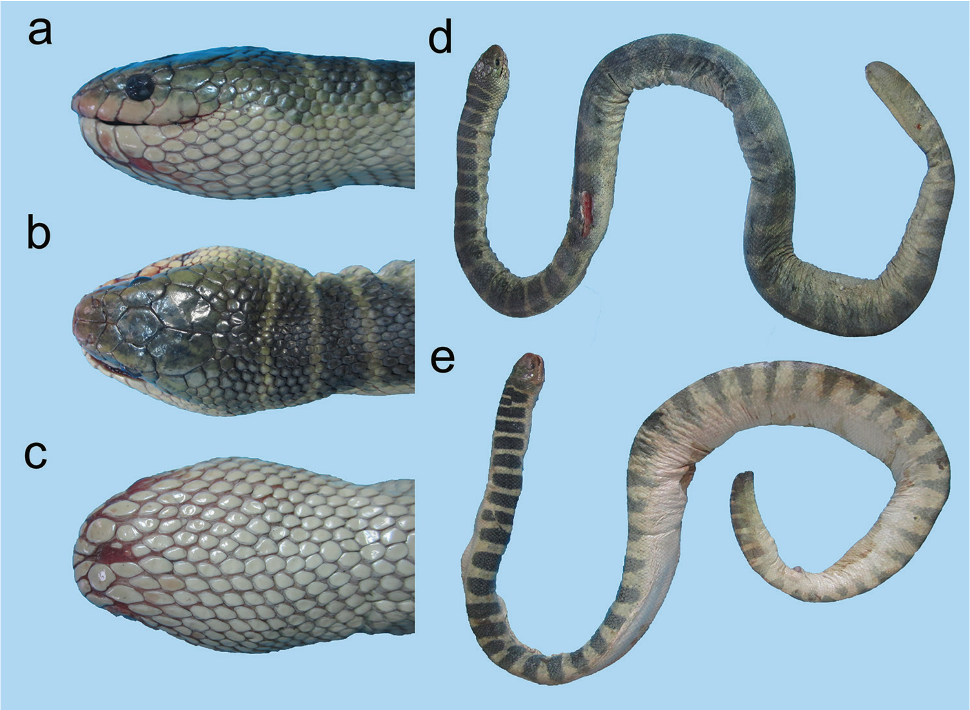

Figure 17. *Hydrophis ornatus*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** gray body **e** dirty white body.

GBD 110, NSL 8, NSR 37, BSR 42, NV 251, NB 51; (ZMSBUK.HD.7), TL 985, SVL 800, HL 32.6, HW 19.5, GL 23, SNL 6.5, NEL 5.2, ND 65, GBD 97, NSL 7, NSR 38, BSR 48, NV 260, NB 51; (ZMSBUK.HD.59), TL 1035, HL 33.9, HW 20.1, GL 24.1, SNL 5, NEL 5.3, ND 65, GBD 140, NSL 8, NSR 34, BSR 48, NV 286, NB 49], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head of medium size (Figure 17); 7–8 supralabials, second usually in contact with prefrontal, third and fourth, or third, fourth and fifth touch eye (Figure 16); body slightly stout, not markedly elongate (Figure 17d–e); 251–306 ventrals, slightly distinguishable from adjacent scales (Figure 4c); 34–43 scale rows on neck and 40–50 on body.

Coloration. Body dirty white (Figure 17e) to grayish (Figure 17d) with 41–53 rhomboidal or rectangular black or dark olive bands along body and tail, clearly distinguishable from each other (Figure 17 d-e).

Size. Mean TL 988mm, maximum 1200 mm (n = 6); [n = 1, TL 885 mm(Volsøe 1939)].

General distribution. Indo-West Pacific, from the Persian Gulf to Australia (David and Ineich 1999; Smith 1926).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. In the Persian Gulf and Gulf of Oman, *H. ornatus* may be roughly misidentified with *H. curtus* (for more details see remarks of *H. curtus*).

Hydrophis cyanocinctus **Daudin, 1803**

Common names: English – Annulated Sea Snake, Bluebanded Sea Snake; Farsi – Mâr-e daryâï-ye halqehdâr
Figures 3g, 18–20

Hydrophis cyanocinctus Daudin, 1803: 383.
Hydrophis cyanocinctus -Smith 1926: 56. -Schmidt 1939: 87. -Volsøe 1939: 17. -Laurent 1948: 9. -Haas 1957: 87. -Haas 1961: 21. -Corkill and Cochrane 1965: 494. -Leviton and Anderson 1967: 188. -Gallagher 1971: 31. -Eissa and El-Assy 1975: 129. -Joger 1984: 33. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 310. -Leviton et al. 1992: 121. -Carpenter et al. 1997: 246. -Firouz 1999: 192. -Latifi 2000: 338. -Baldwin and Gardner 2005: 248. -Firouz 2005: 209. -Egan 2007: 145. -Rastegar-Pouyani et al. 2008: 20. -Safaei and Esmaili 2009: 45. -Soorae et al. 2010: 535. -Calvete et al. 2012: 4091. -Rezaie-Atagholipour et al. 2012: 53. -Rezaie-Atagholipour et al. 2012b: 416. -Kamali 2013: 238. Rezaie-Atagholipour et al. 2013: 328. -Safaei-Mahroo et al. 2015: 282. -Sereshk and Bakhtiari 2015: 15781. -Khorjestan et al. 2016: 45.
Hydrophis cyanocincta -Boulenger 1887: 408.
Distira cyanocincta -Werner 1895: 19. -Boulenger 1896: 294.

Material examined. Persian Gulf: 1 specimen, Bushehr Province [(ZMSBUK.HD.9), TL 1185, SVL 1075, HL 23.9, HW 12.5, GL 13.4, SNL 4, NEL 3.6, ND 44,

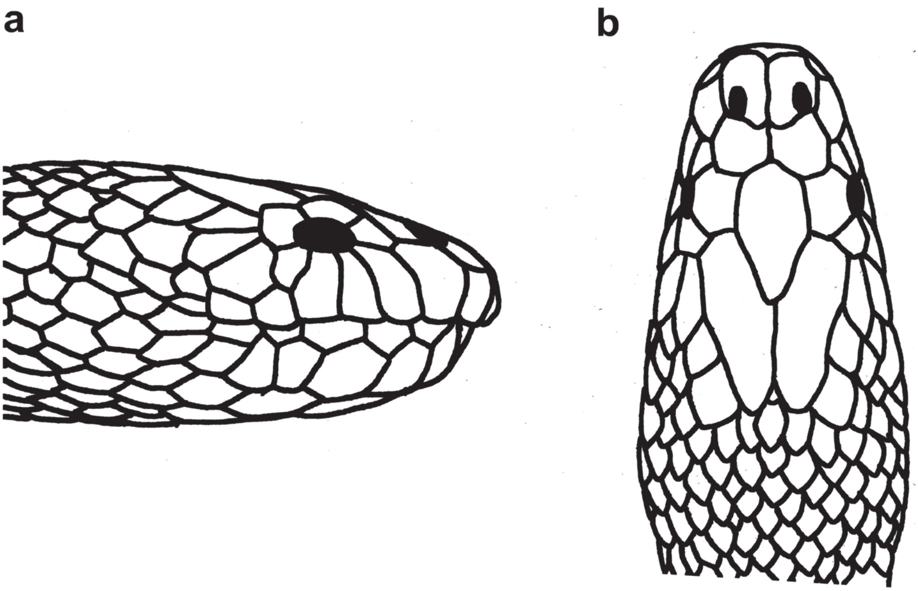

Figure 18. Head of *Hydrophis cyanocinctus*: **a** lateral view **b** dorsal view.

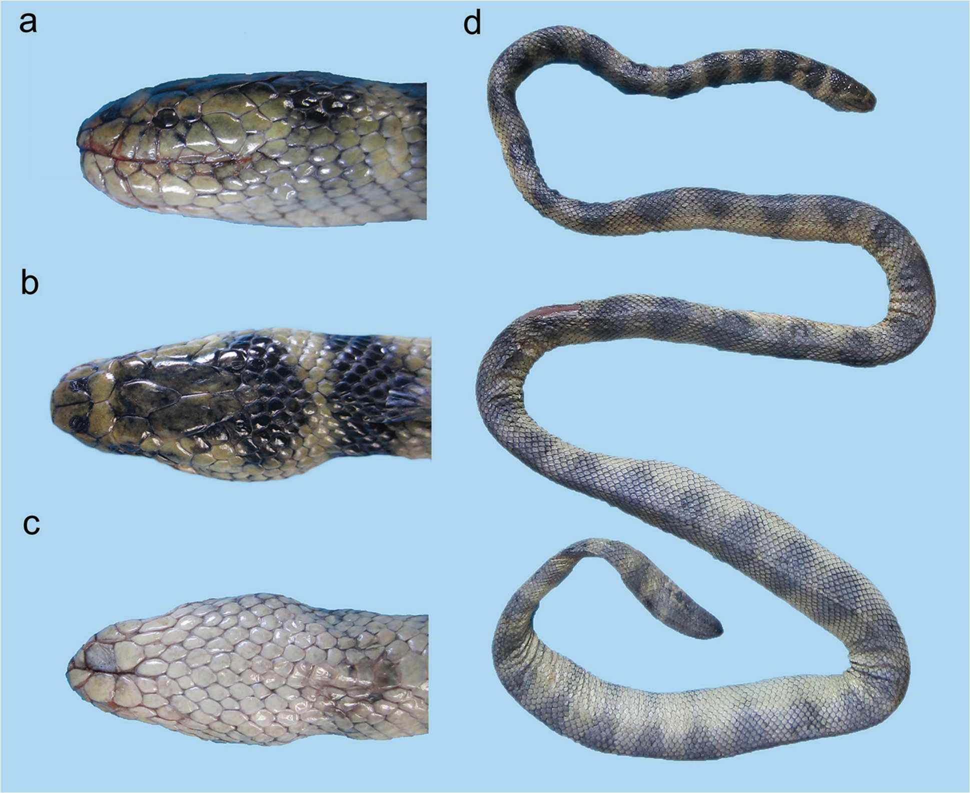

Figure 19. *Hydrophis cyanocinctus*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** body.

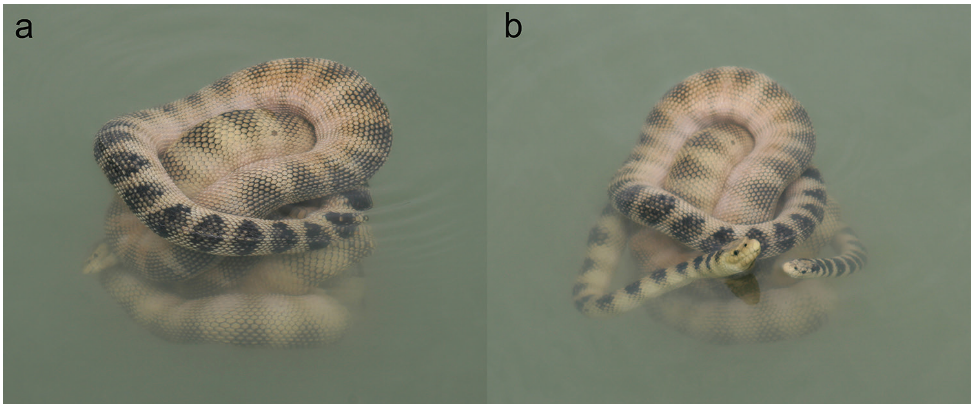

Figure 20. Two *Hydrophis cyanocinctus* intertwined each other and floating on the surface in a mangrove channel in Jask (western Gulf of Oman).

GBD 67, NSL 8, NSR 28, BSR 41, NV 359, NB 54], September 2013, collector: M. Rezaie-Atagholipour.

Gulf of Oman: 3 specimens, Beris and Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.4), TL 1275, SVL 1160, HL 25.3, HW 10.7, GL 13.3, SNL 5, NEL 4.4, ND 38, GBD 82, NSL 8, NSR 29, BSR 39, NV 332, NB 56; (ZMSBUK.HD.6), TL 1447, SVL 1332, HL 27.3, HW 16.8, GL 17.9, SNL 4.6, NEL 3.2, ND 24, GBD 105, NSL 8, NSR 29, BSR 40, NV 339, NB 53; (ZMSBUK.HD.56), TL 1065, SVL 463, HL 14.8, HW 10.5, GL 13.9, SNL 3.7, NEL 2.5, ND 38, GBD 67, NSL 8, NSR 25, BSR 39, NV 300, NB 51], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head slightly small (Figure 19); 7–8 supralabials, second in contact with prefrontal (Figure 18), third, fourth and fifth [or third and fourth, or fourth and fifth (Gasperetti 1988)] touch eye; body elongate but not markedly slender anteriorly (Figure 19d); 300–359 ventrals [345–372 (Volsøe 1939)], slightly distinguishable from adjacent scales at mid-body; body scales on thickest part of the body with round or bluntly pointed tips, slightly or distinctly imbricate; 25–31 scale rows on neck, 39–41 on body [28–31 and 38–44 (Volsøe 1939)].

Coloration. Body dark olive, grayish, or dirty white, dorsally darker and ventrally paler; 51–56 [44–54 (Volsøe 1939)] black rings broader dorsally, or broader bands tapering to points on laterals, on body and tail (Figure 19d); head black in juveniles, usually with a yellow horseshoe-shaped mark above (Figure 19b); adults with head sometimes of same color as body without the horseshoe-shaped mark (Figure 20b).

Size. Mean TL 1243 mm, maximum 1447 mm (n = 4); [n = 7, mean TL 1195 mm, maximum TL 1495 mm (Volsøe 1939)].

General distribution. Indo-West Pacific, from the Persian Gulf to Japan (David and Ineich 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. In the Persian Gulf and Gulf of Oman, juveniles of *Hydrophis cyanocinctus* (smaller than one meter) are morphologically close to *H. lapemoides*. In this case, focusing on the shape of scales in the thickest part of the body (with rounded or bluntly pointed tips versus more or less hexagonal or quadrangular in shape in *H. lapemoides*) is helpful (see diagnostic features for both species). But adults exceed one meter, which is very rare in *H. lapemoides*. Wall (1921) mentioned that *H. cyanocinctus* is probably the most abundant species in the region. Volsøe (1939) however mentioned that in the Persian Gulf it is equaled or even surpassed by *H. lapemoides* and *H. curtus*. Gasperetti (1988) mentioned that both *H. cyanocinctus* and *H. lapemoides* are the most abundant sea snakes in both gulfs. Rezaie-Atagholipour et al. (2012) mentioned that *H. cyanocinctus* is the most abundant sea snake in Hara Biosphere Reserve (the largest mangrove stand in the northwestern Indian Ocean) of the Persian Gulf. Intertwining of two *H. cyanocinctus* is sometimes observed in the mangrove channels of the same ecosystem and other mangrove stands in the area (Figure 20; for more details see Rezaie-Atagholipour et al. 2012). Rezaie-Atagholipour et al. (2013) studied feeding habits of the same population in the biosphere reserve and found that main prey items for *H. cyanocinctus* in this protected area are the mudskippers (Gobiidae, Oxudercinae). The venom proteomes were also investigated for the same population of *H. cyanocinctus* in the Hara Biosphere Reserve of the Persian Gulf (Calvete et al. 2012; Khorjestan et al. 2016).

***Hydrophis lapemoides* (Gray, 1849)**

Common names: English – Persian Gulf Sea Snake; Farsi – Mâr-e daryâï-ye khalij-e fârs
Figures 4d, 21–22

Aturia lapemoides Gray, 1849: 46.
Distira lapemidoides -Werner 1895: 20. -Boulenger 1896: 297.
Hydrophis lapemoides -Smith 1926: 86. -Kennedy 1937: 748. -Volsøe 1939: 19. -Corkill and Cochrane 1965: 494. -Joger 1984: 33. -Leviton and Aldrich 1984: XXIV. -Gasperetti 1988: 312. -Leviton et al. 1992: 123. -Rasmussen 1993: 97. -Carpenter et al. 1997: 247. -Firouz 1999: 192. -Latifi 2000: 340. -Baldwin and Gardner 2005: 249. -Firouz 2005: 209. -Soorae et al. 2006: 109. -Egan 2007: 148. -Rastegar-Pouyani et al. 2008: 20. -Safaei and Esmaili 2009: 45. -Soorae et al. 2010: 535. -Safaei-Mahroo et al. 2015: 282.
Chitulia lapemoides -Kamali 2013: 236.

Material examined. Gulf of Oman: 1 specimen, Jask and Ras-Meydani, depth 18–50m [(ZMSBUK.HD.40), TL 775, SVL 702, HL 19, HW 9.2, GL 11.7, SNL 3.4, NEL 2.4, ND 30, GBD 65, NSL 7, NSR 30, BSR 43, NB 45], October and November 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head slightly small (Figure 22); [8 supralabials, second in contact with prefrontal, third and fourth or third, fourth and fifth touch eye (Gasperetti 1988)] (Figure 21); body elongate but not markedly slender anteriorly (Figure 22); [290–404 ventrals (Volsøe 1939)], slightly distinguishable from adjacent scales (Figure 4d); body

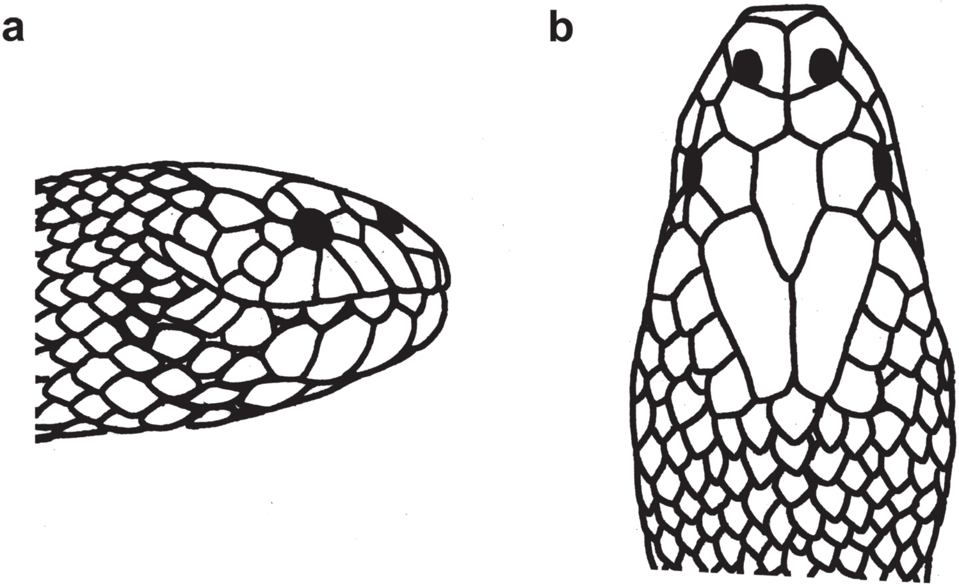

Figure 21. Head of *Hydrophis lapemoides*: **a** lateral view **b** dorsal view.

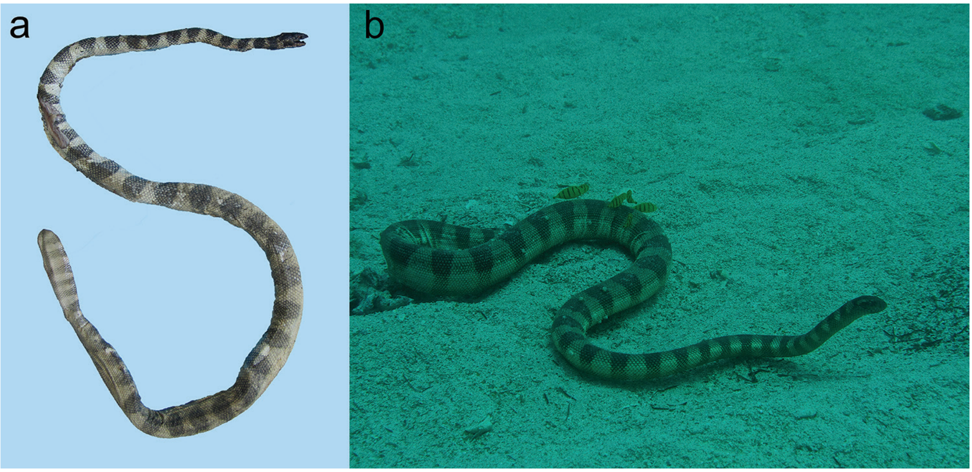

Figure 22. *Hydrophis lapemoides*: **a** body of a specimen examined in this study **b** living individual in coastal waters of Abu Dhabi, UAE, eastern Persian Gulf, depth 10 m, June 2015 (photographed by Rima W. Jabado).

scales in thickest part of body more or less quadrangular or hexagonal in shape and juxtaposed; [29–31 scale rows on neck, 41–46 on body (Volsøe 1939)].

Coloration. Body olive-whitish, dirty white, darker dorsally and paler ventrally; [41–55 (Volsøe 1939)] black rings broader dorsally, or broader bands tapering to points on the sides, on the body and tail (Figure 22a); head black in juveniles, usually with a yellow horseshoe-shaped mark above; adults with head sometimes of same color as body without the horseshoe-shaped mark.

Size. TL 775 mm (n = 1); [n = 8, mean TL 781 mm, maximum TL 895 mm (Volsøe 1939)].

General distribution. Indian Ocean, from the Persian Gulf to Malay Archipelago (Minton 1966; Rasmussen 1987).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. *Hydrophis lapemoides* may be easily misidentified with juveniles *H. cyanocinctus* in the Persian Gulf and Gulf of Oman (for more details see remarks on *H. cyanocinctus*). Rasmussen (1993) suggested that *H. lapemoides* is very abundant in the Persian Gulf. Gasperetti (1988) mentioned that *H. lapemoides* along with *H. cyanocinctus* are the most abundant sea snakes in both gulfs. We however could catch only one specimen during our field surveys, which was collected from Jask in the western Gulf of Oman.

Microcephalophis Lesson, 1834

Microcephalophis gracilis (Shaw, 1802)

Common names: English – Graceful Small-headed Sea Snake, Slender Sea Snake; Farsi – Mâr-e daryâï-ye sarkuchak-e barâzandeh
Figures 23–24

Hydrus gracilis Shaw, 1802: 560.
Microcephalophis gracilis gracilis -Smith 1926: 121. -Kennedy 1937: 748. -Volsøe 1939: 25. -Corkill and Cochrane 1965: 494. -Joger 1984: 35. -Gasperetti 1988: 320.
Microcephalophis gracilis -Corkill 1932: 51. -Carpenter et al. 1997: 248. -Baldwin and Gardner 2005: 251. -Egan 2007: 160. -Safaei and Esmaili 2009: 45.
Hydrophis gracilis gracilis -Leviton and Aldrich 1984: XXIV. -Firouz 2005: 209.
Hydrophis gracilis -Leviton et al. 1992: 122. -Firouz 1999: 192. -Latifi 2000: 339. -Rastegar-Pouyani et al. 2008: 20. -Soorae et al. 2010: 535. -Kamali 2013: 239. -Safaei-Mahroo et al. 2015: 282.

Material examined. Gulf of Oman: 11 specimens, Beris and Pasa-Bandar, depth 20–40m [(ZMSBUK.HD.31), TL 968, SVL 878, HL 13.1, HW 5.3, GL 7.7, SNL 3.1, NEL 1.1, ND 24, GBD 66, NSL 5, NSR 19, BSR 33, NV 237, NB 21; (ZMSBUK.HD.32), TL 830, SVL 757, HL 116, HW 4.4, GL 7, SNL 2.7, NEL 1.2, ND 19, GBD 66, NSL 6, NSR 18, BSR 31, NV 269, NB 43; (ZMSBUK.HD.33), TL 978, SVL 893, HL 13.1, HW 5.9, GL 7.8, SNL 3.4, NEL 1.9, ND 20, GBD 54, NSL 6, NSR 15, BSR 29, NV245, NB 59; (ZMSBUK.HD.34), TL 900, SVL 821, HL 12.3, HW 5.2, GL 7.9, SNL 2.8, NEL 1.4, ND 23, GBD 67, NSL 6, NSR 18, BSR 29, NV 253, NB 55; (ZMSBUK.HD.35), TL 893, SVL 821, HL 12.1, HW 6.3, GL 9, SNL 3, NEL 1.8, ND 20, GBD 55, NSL 6, NSR 17, BSR 31, NV 223, NB 20; (ZMSBUK.

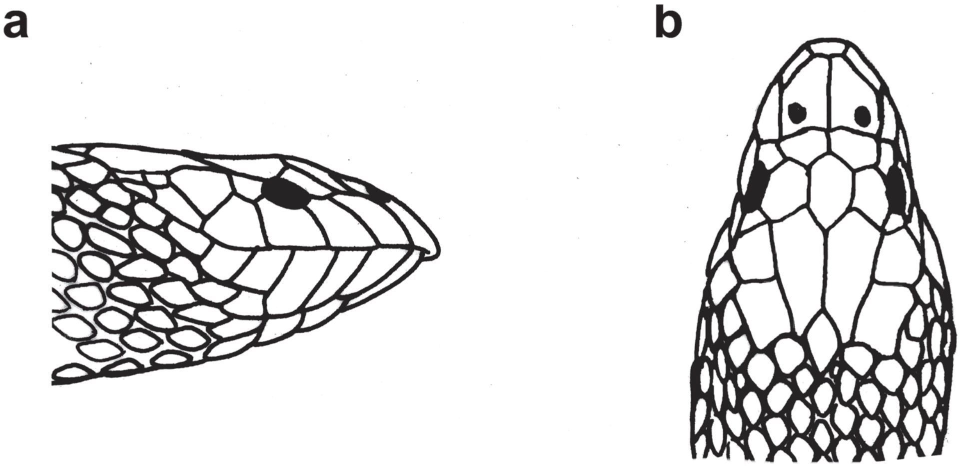

Figure 23. Head of *Microcephalophis gracilis*: **a** lateral view **b** dorsal view.

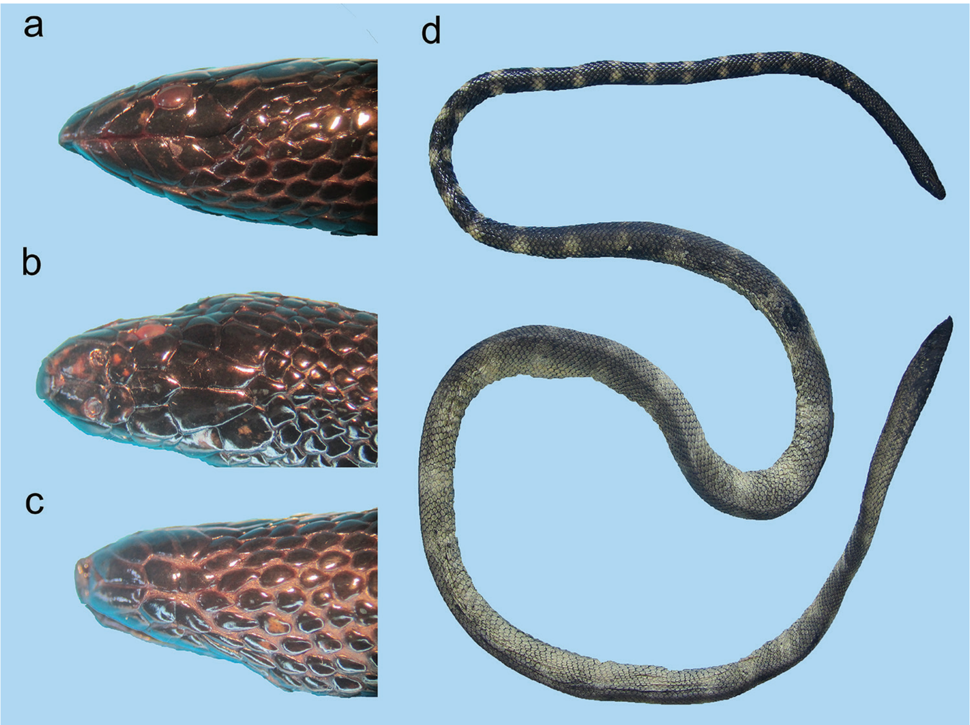

Figure 24. *Microcephalophis gracilis*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** body.

HD.36), TL 900, SVL 820, HL 12.2, HW 5.1, GL 9, SNL 3.6, NEL 1.7, ND 22, GBD 58, NSL 6, NSR 18, BSR 31, NV 231, NB 51; (ZMSBUK.HD.37), TL 957, SVL 870, HL 12.5, HW 5.7, GL 8.5, SNL 3.5, NEL 1.4, ND 20, GBD 50, NSL 6, NSR 19, BSR 32, NV 264, NB 46; (ZMSBUK.HD.38), TL860, SVL 787, HL 12.3, HW 5.4, GL 7.7, SNL 3, NEL 1.5, ND 20, GBD 60, NSL 6, NSR 19, BSR 29, NV

229, NB 27; (ZMSBUK.HD.39), TL 935, SVL 847, HL 12.8, HW 5.7, GL 8, SNL 3.4, NEL 2.2, ND 22, GBD 78, NSL 6, NSR 19, BSR 30, NV 229, NB 41; (ZMSBUK.HD.46), TL 827, SVL 752, HL 12.7, HW 5.6, GL 9, SNL 3.4, NEL 1.5, ND 18, GBD 62, NSL 6, NSR 19, BSR 30, NV 242, NB 48; (ZMSBUK.HD.54), TL 922, SVL 837, HL 13.2, HW 5.9, GL 8.9, SNL 3.2, NEL 1.4, ND 20, GBD 67, NSL 6, NSR 19, BSR 31, NV 246, NB 53], August 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head extremely small (Figure 24); 5–6 supralabials, second usually in contact with prefrontal, third and fourth touch eye (Figure 23a); neck markedly slender; body elongate, markedly slender anteriorly (Figure 24d); 15–20 scale rows on neck, 20–33 on body [18–19 and 31 (Volsøe 1939)]; 223–269 ventrals [232–269 (Volsøe 1939)].

Coloration. Gray to dark gray dorsally, gray-whitish ventrally, darker anteriorly than posteriorly; 20–59 black bands broader dorsally; bands on necks and anterior part of body are black and merge each other only ventrally or ventrally and dorsally (Figure 24d); bands on the posterior part of the body are paler, or sometimes absent.

Size. Mean TL 906 mm, maximum 978 mm (n = 11); [n = 9, mean TL 865.5 mm, maximum TL 1030 mm (Volsøe 1939)].

General distribution. Indo- West Pacific, from the Persian Gulf to Australia (David and Ineich 1999).

IUCN Red List Category. Least concern (IUCN 2016).

Remarks. *Microcephalophis gracilis* and the other Small-headed Sea Snake, *M. cantoris*, recorded here for the first time in the area (see below), are easily distinguishable from other species in the region by having an extremely small head and slender neck. However, these two species may be confused with each other at a glance. *Microcephalophis gracilis* is distinguishable from *M. cantoris* by having less number of ventrals (223–269 versus 404–468 in *M cantoris*). All material examined in this study was collected from eastern Gulf of Oman. Volsøe (1939) however recorded material from the western Gulf of Oman and western Persian Gulf.

Microcephalophis cantoris (Günther, 1864)

Common names: English – Gunther's Sea Snake; Farsi – Mâr-e daryâï-ye gunder
Figures 25–26

Hydrophis cantoris Günther, 1864: 374.

Material examined. Gulf of Oman: 1 specimen, Jask and Ras-Meydani, depth 18–50m [(ZMSBUK.HD.), TL 1124, SVL 992, HL 33.5, HW 12.3, GL 20.2, SNL 5.1, NEL 4.4, ND 51, GBD 101, NSL 6, NSR 24, BSR 41, NV 446], October and November 2013, collector: M. Rezaie-Atagholipour.

Diagnosis. Head extremely small and pointed (Figure 26); third supralabial usually in contact with prefrontal (Figure 25a); body elongate, markedly slender anteriorly; neck markedly slender (Figure 26d); 24 scale rows on neck [23–25 (rarely 21) (Leviton et al. 2003)] and 41 on body; 446 ventrals [404–468 (Leviton et al. 2003)].

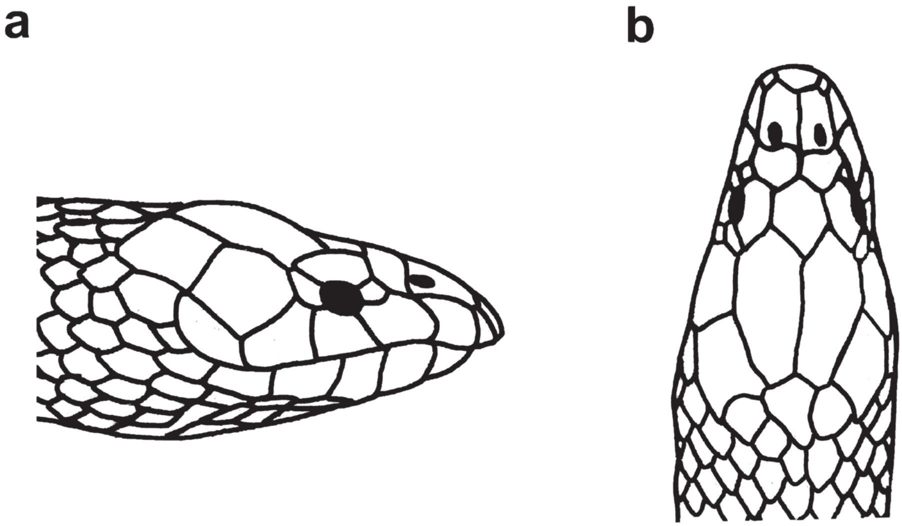

Figure 25. Head of *Microcephalophis cantoris*: **a** lateral view **b** dorsal view.

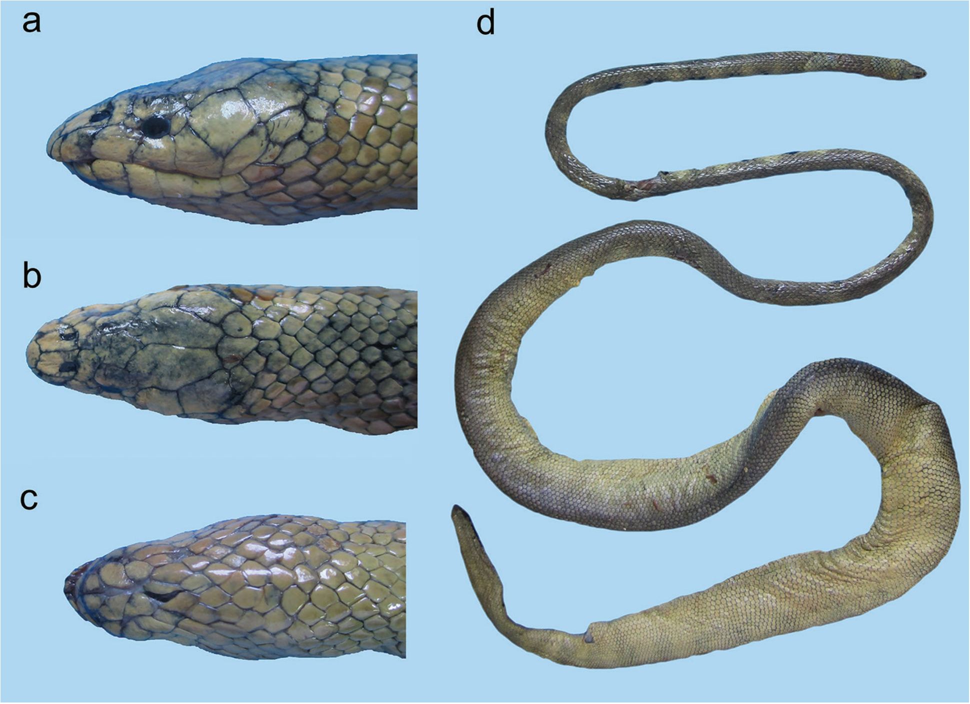

Figure 26. *Microcephalophis cantoris*: **a** lateral view **b** dorsal view, and **c** ventral view of head **d** body.

Coloration. Head yellowish; neck and body dark olive dorsally, yellowish ventrally; dorsal portion of body uniform in color and not banded; neck with the rings paler dorsally and black ventrally (Figure 26d); [Dark greenish olive dorsally, yellowish ventrally;

ventrals blackish; dorsal portion of body uniform in color and not banded; slender part of body with 20–28 blackish bands merging dorsally and ventrally (Günther 1864)].

Size. TL 1124 mm (n = 1) [1450 mm in males and 1880 mm in females (Leviton et al. 2003)]

General distribution. Indian Ocean, from the Gulf of Oman to Malay Archipelago.

IUCN Red List Category. Data deficient (IUCN 2016).

Remarks. It is the first record of *M. cantoris* in this area. By this record, westernmost extent of *M. cantoris* expands from Pakistan to the Gulf of Oman. Safaei and Esmaili (2009) recorded four specimens of this species from the same area localities (Jask), but they have presented neither morphological data nor descriptions of the specimens. Furthermore, their specimens were not deposited in any public museum or collection and we couldn't find them for further morphological examination. Regarding the single specimen examined herein, the shape of the fangs was found to be unique: elongated fangs markedly protruding outside the lower jaw when mouth is closed. This unusual characteristic could be age-dependent or likely a specific character which was overlooked by other authors. Further studies on this specimen are much recommended.

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