

First record of the polychaete *Ficopomatus uschakovi* (Pillai, 1960) (Annelida, Serpulidae) in the Colombian Caribbean, South America

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Abstract

The genus *Ficopomatus* (Serpulidae) consists of sessile, tubicolous polychaete annelid worms that may colonize a diversity of substrata, and tolerate considerable variations in salinity. Thus, members of this genus, including *Ficopomatus uschakovi*, in some cases are exotic and maybe invasive. The purpose of our research was to collect and identify marine organisms associated with the submerged roots of mangrove trees in the Gulf of Urabá, Colombian Caribbean, South America. Within the Gulf, there is a well-developed forest of the Red Mangrove, *Rhizophora mangle*, along the margins of El Uno Bay. We sampled the roots of *R. mangle* from five stations of the bay, and we identified specimens of *F. uschakovi* from each of those stations. *Ficopomatus uschakovi* was found to be more abundant in regions of the bay that exhibit the lowest salinity. Based on a morphological comparison of the present specimens with the original species description, revised descriptions, and other records from the Indo-West Pacific, Mexican Pacific, and Venezuelan and Brazilian Caribbean, we suggest that *F. uschakovi* has a broader geographical distribution. Furthermore, because of this broad distribution, and the observed tolerance for low salinity in our study, we also suggest that *F. uschakovi* is a euryhaline species. It is also likely that *F. uschakovi* will be found in other localities in the Gulf of Urabá, and in other regions of the Colombian Caribbean. Thus, this record extends the distribution of the species to the Colombian Caribbean, giving the species a continuous distribution across the northern coast of South America.

Resumen

El género *Ficopomatus*, familia Serpulidae, está compuesto por gusanos poliquetos tubícolas y sésiles que pueden colonizar gran cantidad de sustratos y tolerar variaciones considerables de salinidad. Así, los miembros de éste género, incluyendo *Ficopomatus uschakovi*, en algunos casos pueden ser considerados exóticos y tal vez invasores. El propósito de nuestra investigación fue recolectar e identificar los organismos marinos asociados a raíces sumergidas de árboles de mangle rojo, *Rhizophora mangle*, en el golfo de Urabá, Caribe colombiano, Suramérica. Dentro del golfo de Urabá, existe un bosque bien desarrollado de *R. mangle*, a lo largo de las márgenes de la bahía El Uno. Se tomaron muestras de mangle rojo en cinco estaciones y se identificó a *F. uschakovi* para cada una de ellas. Esta especie exhibió mayor abundancia en zonas de la bahía con menor salinidad. Basados en la similitud morfológica que exhiben los ejemplares con la descripción original de la especie, descripciones revisadas e identificaciones reportadas en el oeste del Indopacífico, Pacífico mexicano y la zona Caribe de Venezuela y Brasil, sugerimos que *F. uschakovi* tiene una amplia distribución geográfica. Además, por esta amplia distribución y la tolerancia observada a bajas concentraciones salinas en nuestro estudio, sugerimos que *F. uschakovi* es una especie eurihalina. También es probable que *F. uschakovi* se pueda encontrar en otras localidades en el golfo de Urabá, y en otras regiones del Caribe colombiano. Este registro amplía la distribución de la especie al Caribe colombiano, lo cual demuestra una continuidad en la costa norte de Suramérica.

Keywords

Euryhaline, exotic species, polychaete, species distribution, taxonomy

Introduction

The family Serpulidae Rafinesque, 1815, includes a group of sedentary polychaetes that are easily recognizable by their calcareous tubes, with irregularly twisted or spiral growth, and by the complexity of their radiolar crown (Rouse and Pleijel 2001). However, other features, such as the shape of the operculum, the branchial crown, the form, type and position of chaetae along the collar, the thoracic membranes, as well as the thorax and abdomen, represent important taxonomic characters (Hove and Kupriyanova 2009). Some serpulids are solitary, but others such as *Hydroides* (Bastida-Zavala and Hove 2003), are gregarious, living in large groups or colonies that may cover the hard substrates of coral reefs, coastal lagoons, and the estuarine or brackish environments of tidal canals within mangrove forests (Bastida-Zavala and Salazar-Vallejo 2000). They are benthic, sessile organisms, and their tubes have been found attached to rocks, roots, wood, mollusc shells, dock structures, and boat hulls that facilitates their dispersal (Salgado-Barragán et al. 2004); few species have free tubes, unattached to any substratum, but living on a sandy bottom.

The genus *Ficopomatus* Southern, 1921 (subfamily Ficopomatinae Pillai, 1960) is characterized by having an opaque tube with or without keels, peristomes, and tabulae; a body that tapers in diameter from anterior to posterior; a conical or pear-shaped operculum inserted behind the left brachial lobe, uncovered or covered with either a chitinous, non-calcified endplate or with numerous chitinous spines in the distal tissue; the collar is non-lobed with “saw-edged” chaetae; the thorax may have free or

fused thoracic membranes; there are seven chaetigers with limbate notochaetae, and six uncinigerous tori having uncini with 6 to 12 teeth; the abdomen contains numerous segments with capillary-toothed chaetae (Day 1967, Hove and Weerdenburg 1978, Hove and Kupriyanova 2009). The genus comprises six species: *Ficopomatus enigmaticus* (Fauvel, 1923), *F. macrodon* Southern, 1921, *F. miamiensis* (Treadwell, 1934), *F. shenzzhensis* Li, Wang & Deng, 2012, *F. talehsapensis* Pillai, 2008 (Bastida-Zavala and García-Madrigal 2012) and *F. uschakovi* (Pillai, 1960). According to Pillai (2008), *F. uschakovi* should be included in *Neopomatus* Pillai, 1960 due to the presence of one pair of fused thoracic membranes; nevertheless, several authors do not accept this genus (Hove and Kupriyanova 2009, Bastida-Zavala and García-Madrigal 2012).

Ficopomatus uschakovi was described from Sri Lanka (Pillai 1960), and is widely distributed across the Indo-West Pacific (Hove and Weerdenburg 1978). It has been recorded in other regions, including the Mexican Pacific (Bastida-Zavala and García-Madrigal 2012), the Western Atlantic, in Paraíba, Brazil (de Assis et al. 2008), in Venezuela (Liñero-Arana and Díaz-Díaz 2012), and in the Eastern Atlantic, in the Gulf of Guinea (Hartmann-Schröder 1971). Therefore, *F. uschakovi* is thought to be an exotic, and possibly, an invasive species.

According to the World Wildlife Fund for Nature (2012), exotic and invasive species are those foreign species that have been naturally or artificially (accidentally or intentionally) introduced to a region where they did not exist before, and once there, are adapted to their new environment. Liñero-Arana and Díaz-Díaz (2012) mentioned that the presence of invasive species in a location outside their current distribution might result from five recognized causes: First, transfer by fouling communities (fouling) attached to the outside of boat hulls; second, introduction of species for culturing, or as bait for fishing; third, exchange of species through waterways; fourth, release of species related to the pet industry; and fifth, expulsion of organisms from the ballast waters of ships. In order to better understand the mechanisms by which a particular species may be found outside of its natural range, it is necessary to examine each of these five causes and their potential influence where such species are positively identified. Further, it is critically important to determine the presence of invasive species that may threaten or even lead to the extinction of native species by competition or loss of habitat (Castro-Díez et al. 2004).

This study provides the first record of *F. uschakovi* in the Gulf of Urabá, in a region that has been recently studied in the context of marine biodiversity. Additionally, our research provides a morphological comparison of *F. uschakovi* with a sympatric species, *F. miamiensis*, which may be competing for resources with the former, likely exotic, species within the Gulf.

Materials and methods

Study area. The Gulf of Urabá is located on the northern coast of Colombia adjacent to the Isthmus of Panama, and is part of the Nica-Colombian continental shelf

(Salazar-Vallejo 2000). The Gulf is part of the territory of Colombia's Department of Antioquia, and it is considered the second largest estuary of the Colombian Caribbean, representing 4291 km² of costal area, of which 650 km² are estuaries, dominated by mangrove forests (CORPOURABA 2003). According to Bernal et al. (2005), the Gulf of Urabá is a semi-enclosed body of water, approximately 80 km long and 25 km wide, with an average depth of 25 m, and maximum depth of 60 m. The Gulf receives fresh water from the Atrato River in the west, and other smaller rivers that empty into its southern end. The northern end of the Gulf is open to the Caribbean Sea, which interacts with river inflows to generate estuarine circulation patterns, including substantial freshwater surface layering. Within the Gulf, a relatively large number of bays and inlets have been formed as a result of the high levels of suspended sediments carried in from surrounding rivers, which in turn supports the establishment and growth of *Rhizophora mangle* (Red Mangrove), *Laguncularia racemosa* (White Mangrove), *Avicennia germinans* (Black Mangrove) and fern forests.

El Uno Bay is located near the southeastern end of the Gulf, to the north of the municipality of Turbo (Fig. 1A–C). The bay is approximately 1.8 km long, 0.89 km wide, with an average depth of 1.0 m, and extends in a north-south direction. According to the mangrove system by García-Padilla and Palacio (2008), and our observations during this research, El Uno Bay is subdivided into the following zones: Northern zone with *A. germinans* dominant in the inner region, and *R. mangle* in the outer region; northwestern fringe zone with well-developed *L. racemosa* trees and low numbers of *R. mangle* due to harvesting; eastern zone with *A. germinans* dominant in the inner region, and young and mature trees of *R. mangle* in the outer region; southwestern fringe zone with sparse overall development dominated by *R. mangle* and some *A. germinans* trees; and the southern zone with a semi-enclosed circulation system, receiving high and low tidal water exchange, and without mangrove trees.

Sampling. El Uno Bay was sampled at five stations during August 2009 (Fig. 1C). Sampling was conducted according to the following collection process: (i) selection of the submerged roots of *R. mangle* trees not reaching the substrate, when possible; (ii) cutting and removal of 1–5 roots from different trees at each station, (iii) fixation of roots in a solution of 10% formalin in sea water.

In the laboratory, sampled roots of *R. mangle* were processed as follows: (i) formalin was removed by multiple freshwater exchanges through a 250 µm sieve to retain organisms; (ii) invertebrate and algal specimens (macroalgae, cyanobacteria) were selected and removed from roots; (iii) invertebrate specimens were preserved in 70% ethanol; macroalgae were preserved in 4% formaldehyde; (iv) invertebrates were separated into higher-level taxa (e.g. phylum, class, family), and (v) polychaetes were identified to levels of family, genus and species. The polychaete specimens were deposited in the Colección de Invertebrados Marinos, Universidad de Antioquia (CIMUA).

Taxonomic analysis. Four polychaete families were identified (Nereididae, Sabeliidae, Serpulidae, Spionidae); however, only serpulids were considered for this research. For polychaete identification, we followed the dichotomous, taxonomic keys for genera prepared by Fauchald (1977), Bastida-Zavala and Salazar-Vallejo (2000) and Bastida-

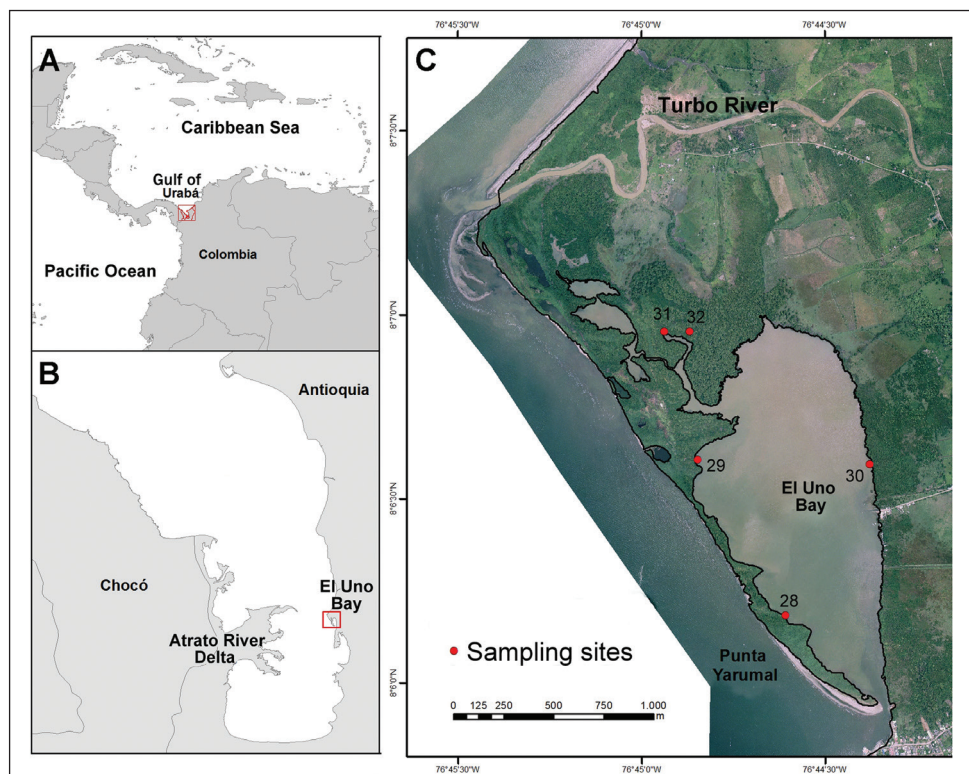


Figure 1. Study Area: **A** Colombia **B** Gulf of Urabá **C** El Uno Bay (Red points correspond to sampling sites).

Zavala (2009). For identification of the serpulid polychaete species, *F. uschakovi* and *F. miamiensis*, we followed taxonomic keys and/or descriptions from Hove and Weerdenburg (1978), Bastida-Zavala (2009) and Bastida-Zavala and García-Madrigal (2012).

Systematics

Family Serpulidae Rafinesque, 1815

Subfamily Ficopomatinae Pillai, 1960

Genus *Ficopomatus* Southern, 1921

***Ficopomatus uschakovi* (Pillai, 1960)**

http://species-id.net/wiki/Ficopomatus_uschakovi

Figure 2A–J

Neopomatus uschakovi Pillai, 1960: 28–32, fig. 10H, 11A–H, 12A–H, plate I, fig. 1, 2; Hartman 1965: 80; Pillai 1965: 172: 1971: 118–123, 127, fig. 9G, 10; Hartmann-Schröder 1971: 7–27. fig. 2, 3, 5, 7b-d, 11–14; Zibrowius 1973: 64.

Mercierella enigmatica, (not Fauvel 1923, Mesnil and Fauvel 1939): Hove and Weerdenburg 1978: 109–110, presented several examples of incorrect use of this name. *Neopomatus uschakovi* var. *lingayanensis*, Pillai 1965: 170–172, fig. 23A–I. *Neopomatus similis*, Pillai 1960: 32–33, fig. 12 I–M, plate II, fig. 1; Hartman 1965: 80. *Neopomatus similis* var. *rugosus*, Pillai 1960: 33–35, plate II, fig. 2; Hartman 1965: 80. *Ficopomatus uschakovi*, Hove and Weerdenburg 1978: 109–113, fig. 2a–d, 3a, f–k, 4j–n, r, x–z, 5d; Bastida-Zavala 2009: 530, fig. 1K; Bastida-Zavala and García-Madrigal 2012: 48–52, fig. 1A–E, 2A–I.

Type locality. Estuary of the Panadura River, Sri Lanka, Indian Ocean.

Material studied. CIMUA POLY SERP 0031B (1), Punta Yarumal (8°6'10"N, 76°44'36"W), El Uno Bay; Sta. 28, Root 3; August 8, 2009; col. C. Arteaga-Flórez. CIMUA POLY SERP 0032 (1), Punta Yarumal, (8°6'34"N, 76°44'22"W), El Uno Bay, Sta. 29, Root 5, August 8, 2009, col. C. Arteaga-Flórez. CIMUA POLY SERP 0033 (1), El Faro (8°6'36"N, 76°44'50"W), El Uno Bay; Sta. 30, Root 5; August 8, 2009; col. C. Arteaga-Flórez. CIMUA POLY SERP 0034 (5), Ciénaga de las Mujeres (8°6'55"N, 76°44'51"W), El Uno Bay; Sta. 31, Root 1; August 8, 2009, col. C. Arteaga-Flórez. CIMUA POLY SERP 0035 (12), Ciénaga de las Mujeres (8°6'56"N, 76°44'56"W), El Uno Bay; Sta. 32, Root 5; August 8, 2009; col. C. Arteaga-Flórez.

Description. Complete specimen: Irregularly curved calcareous tubes, forming agregations. Thorax colour, brown; tori colour dark brown; abdomen colour beige; dark brown medial line along the dorsum. Length, 5.0 mm; width, 0.6 mm, with 7 thoracic chaetigers and 33 abdominal chaetigers. Branchial crown colour beige, divided into two groups of radioles: six radioles on right side, and seven radioles on left side; each radiole with six transverse bands in a ring-like arrangement with wide dark brown color pattern; most basal ring wider and darker than the rest; ventral base of branchial crown black. Inter-radiolar membrane absent. Operculum spherical with radial symmetry (Fig. 2B, C, E, F), and with a sub-convex distal plate; four rows of transparent spines directed outward, with spines of the interior row approximately one-half the length of spines in the other rows; peduncle colour, beige with dark brown groove. Eyes absent. Collar with entire margin; thoracic membranes fused along the dorsum; six thoracic neuropodial tori. Chaetae from collar serrated, with one longitudinal line of teeth from the base to the apex (Fig. 2I, J), thorax with capillary chaetae (Fig. 2H), and abdomen with geniculate chaetae, proximal half serrated (Fig. 2G), and distal half smooth. Thoracic uncini saw-shaped with 6–7 teeth (Fig. 2K). Rounded pygidium with a midline incision.

Variations. The specimens vary in length from 3 mm to 7.5 mm, in width from 0.5 mm to 0.8 mm. The number of chaetigers varies from 36 to 45. The number of transparent rows of spines from the operculum varies from 1 to 4. The number of transversal rings in the crown varies from 4 to 6.

Remarks. *Ficopomatus uschakovi* was present in samples from the opening of El Uno Bay, in sympatry with *F. miamiensis*, although *F. uschakovi* was more abundant inside of El Uno Bay. Of these two serpulid species, only *F. uschakovi* was found within the

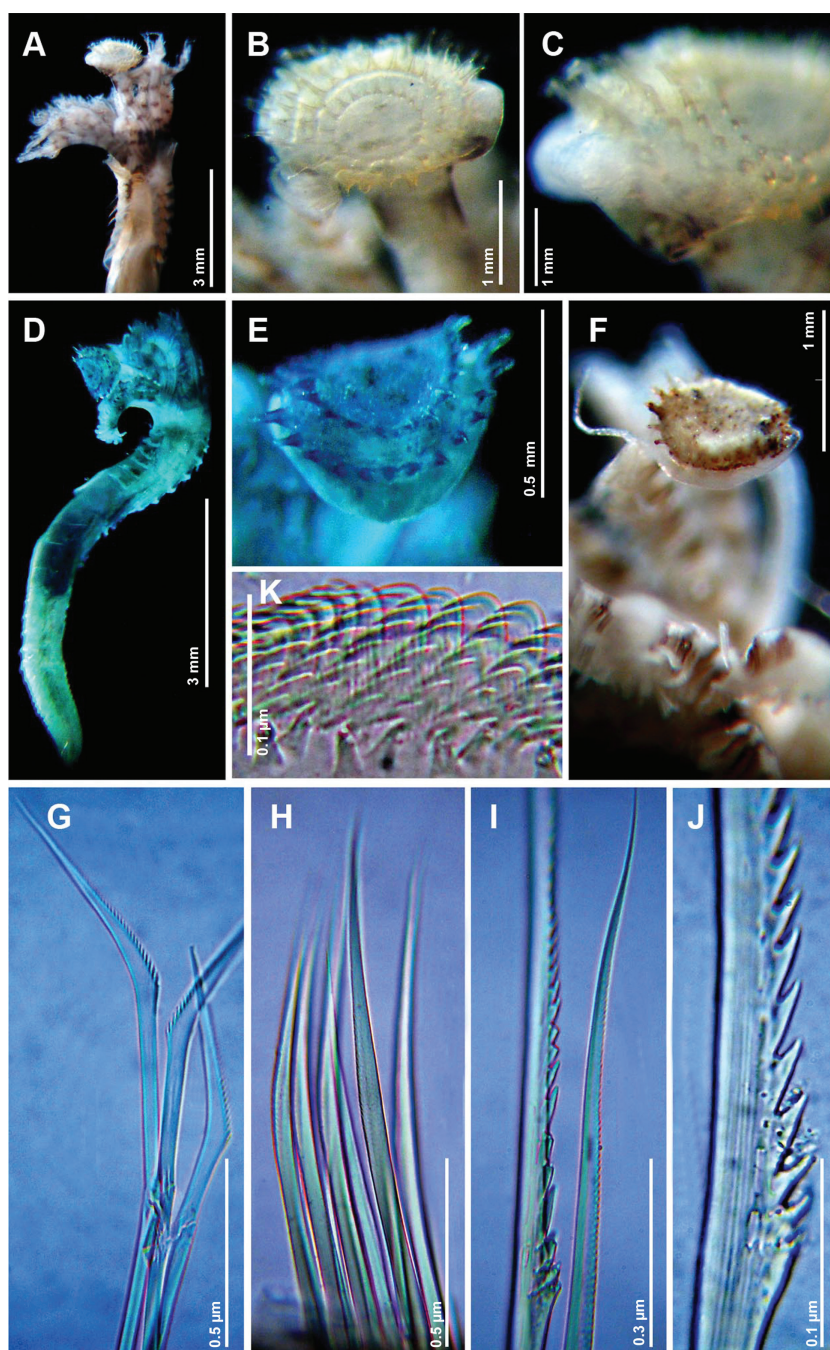


Figure 2. *Ficopomatus uschakovi* (Pillai, 1960). Specimen SERP 0031B: **A** Antero-dorsal view **B** Operculum in anterior view **C** Operculum in lateral view **G** Geniculate chaetae from the abdomen **H** Limbate chaetae from chaetiger 3 **I** Toothed and limbate chaetae from collar **J** Toothed chaetae, detail **K** Uncini from chaetiger 3. Specimen SERP 0033 in methyl green: **D** Complete specimen in dorsal view **E** Operculum in lateral view. Specimen 1 SERP 0034: **F** Operculum in lateral view.

inner bay, which may indicate that this species has replaced *F. miamiensis* in that region. Morphologically, *F. uschakovi* differs from *F. miamiensis* by the presence of a spherical operculum with 1–4 transparent spines in a radial arrangement, and dorsal fusion of the thoracic membranes. These characters represent important diagnostic features for recognizing *F. uschakovi*, according to Hove and Weerdenburg (1978). Of the remaining taxonomic characters, the presence of seven thoracic chaetigers, and toothed collar chaetae, are generic characters. Distinctively, *F. uschakovi* builds calcareous tubes with longitudinal keels, and well-formed rings, whereas *F. miamiensis* builds smoother calcareous tubes that exhibit only very diffuse growth rings (Hove and Weerdenburg 1978).

Hove and Weerdenburg (1978) comment that *F. uschakovi* has been commonly misidentified as *F. enigmaticus*, because both species are able to live in brackish water. However, Hartmann-Schröder (1971) and Pillai (1971) clarified this confusion, emphasizing on the geographical separation of these species; *Ficopomatus enigmaticus* occurs in subtropical regions of Europe, while *F. uschakovi*, originally recorded in the Indo-West Pacific region, was recently found in the Caribbean Sea and the Tropical Eastern Pacific. Nevertheless, according to Hove and Weerdenburg (1978), the most important features for splitting these two species are in terms of the morphology. While *F. uschakovi* has an operculum with a sub-convex distal plate, *F. enigmaticus* has a concave distal plate. Also, *F. enigmaticus* sometimes has, dorsally, incomplete and irregular rows of spines, and may have one to three short radial accessories spines, while *F. uschakovi* lack accessory spines and has complete and regular rows of spines in the operculum.

According to Hove and Weerdenburg (1978), *F. uschakovi* has a distribution in the southern hemisphere, from India, through the Indian Ocean, to the Philippines and northern Australia. However, it has been recorded also from the Caribbean region, in Venezuela (Liñero-Arana and Díaz-Díaz 2012) and north-eastern Brazil (de Assis et al. 2008); and from the tropical Eastern Pacific, in Mexico (Bastida-Zavala and García-Madrigal 2012).

We consider *F. uschakovi* as an exotic species in the Colombian Caribbean. It is likely that this species may have been transported to the Gulf of Urabá from the Indo-Pacific attached to hulls of ships crossing from the Pacific Ocean to Caribbean Sea through Panama Canal, or from the Eastern coast of Africa to the Caribbean. Once in the Gulf, the species migrated to El Uno Bay, which is very close to the place where the ships are charged, aided by the tidal currents. Also, in support that *F. uschakovi* is an exotic species: during 2009 the species was found only in El Uno Bay, southern Gulf of Urabá; but, during 2012, this species was found also to the north of El Uno Bay, where it was not found before. This means that the distribution of the species has spread along the eastern coast of the Gulf in a South-North direction. This study provides the first record of *F. uschakovi* in Colombia. However, many localities of the northern Colombian Caribbean lack information on the distribution of *F. uschakovi*, which limits our understanding of its distribution in the southern Caribbean. Further distributional data will be presented in a forthcoming paper on the biogeography of the species.

Finally, specimens of *F. uschakovi* were found on mangrove roots in association with specimens of other species belonging to the families Nereididae (*Neanthes succinea*,

Table 1. Physical-chemical conditions found in El Uno Bay, during the sampling period. Abbreviations: O₂ oxygen; T Temperature; TDS dissolved solids; Sal Salinity; Cond Conductivity.

Locality	Site	Station	[O ₂] (mg/L)	O ₂ (%)	T (°C)	pH	TDS (ppt)	Sal (ppt)	Cond. (mS)	Specific cond. (mS)
El Uno Bay	Punta Yarumal	28	4,18	61	30,4	7,13	> 2000	9,2	17,41	13,88
El Uno Bay	Punta Yarumal	29	5,16	66,6	29,8	7,22	> 2000	9	16,87	15,48
El Uno Bay	El Faro	30	4,33	69,7	28,6	7,53	> 2000	9,2	14,85	15,57
El Uno Bay	Ciénaga de las Mujeres	31	2,12	31,2	27,5	7,3	> 2000	0,4	0,16	0,09
El Uno Bay	Ciénaga de las Mujeres	32	0,55	7,6	26,4	7,35	> 2000	1,3	13,54	11,72

Stenoninereis tecolutlensis and *Namalycastis* sp. 1), Sabellidae (*Demonax lacunosus*), and Spionidae (*Boccardiella* sp.). Future research should include formal descriptions of these other species, and an assessment of their respective distribution patterns. Physical-chemical conditions found within the Bay during the sampling period are provided in Table 1.

Distribution. Indian Ocean from the Eastern coast of Africa to Australia; Eastern Pacific in Southern Mexico; Western Atlantic, in the Colombian, Venezuelan and Brazilian Caribbean coasts. Eastern Atlantic, in the Gulf of Guinea.

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References

- Assis JE de, Alonso C, Christoffersen ML (2008) First record of *Ficopomatus uschakovi* (Pillai, 1960) Serpulidae (Polychaeta: Annelida) for the Western Atlantic. *Revista Nordestina de Biología* 19 (1): 51–58.
- Bastida-Zavala JR (2009) Serpulidae Rafinesque, 1815. 43: 521–554, In: de León-González JA, Bastida-Zavala JR, Carrera-Parra LF, García-Garza ME, Peña-Rivera A, Salazar-Vallejo

- SI, Solís-Weiss V (Eds) Poliquetos (Annelida: Polychaeta) de México y América tropical. Universidad Autónoma de Nuevo León, Monterrey, México, 737 pp.
- Bastida-Zavala JR, Salazar-Vallejo SI (2000) Serpúlidos (Polychaeta: Serpulidae) del Caribe noroccidental con claves para la región del Gran Caribe: *Salmacina*, *Ficopomatus*, *Pomatoceros*, *Pomatostegus*, *Protula*, *Pseudovermilia*, *Spirobranchus* y *Vermilipsis*. Revista de Biología Tropical 48(4): 807–840.
- Bastida-Zavala JR, Hove HA (2003) Revision of *Hydroides* Gunnerus, 1768 (Polychaeta: Serpulidae) from the eastern pacific region and hawaii. Bulletin Zoological Museum University of Amsterdam 56(4): 67–110.
- Bastida-Zavala JR, García-Madrigal S (2012) First record in the Tropical Eastern Pacific of the exotic species *Ficopomatus uschakovi* (Polychaeta, Serpulidae). Zookeys 238: 45–55. doi: 10.3897/zookeys.238.3970
- Bernal G, Toro M, Montoya-Jaramillo LJ, Garizábal-Carmona CE (2005) Estudio de la dispersión de los sedimentos del río Atrato y sus impactos sobre la problemática ambiental costera del Golfo de Urabá. Gestión y Ambiente 8: 123–135.
- Castro-Diez P, Valladares F, Alonso A (2004) La creciente amenaza de las invasiones biológicas. Ecosistemas 13(3): 61–68.
- CORPOURABA (2003) Caracterización y zonificación de los manglares del Golfo de Urabá-Departamento de Antioquia. Proyecto Zonificación y Ordenamiento de los manglares de Urabá. Convenio 201671 FONADE-Corporación para el Desarrollo Sostenible del Urabá, Apartadó, 80 pp.
- Day JH (1967) A Monograph on the Polychaeta of Southern Africa. Bulletin of the British Museum of Natural History Publication 656: 1–878.
- Fauchald K (1977) The polychaete worms, definitions and keys to the Orders, Families and Genera. Natural History Museum of Los Angeles Country, Los Angeles, 146 pp.
- Fauvel P (1923) Un nouveau serpulien d'eau saumâtre *Mercierella* n.g., *enigmatica* n.sp. Bulletin de la Société Zoologique de France 47: 424–430.
- García-Padilla JM, Palacio J (2008) Macroinvertebrados asociados a las raíces sumergidas del Mangle Rojo (*Rhizophora mangle*) en las bahías Turbo y El Uno, Golfo de Urabá (Caribe colombiano). Gestión y Ambiente 11(3): 55–66.
- Hartman O (1965) Catalogue of the Polychaetous Annelids of the World. Supplement 1960–5 and Index. Allan Hancock Foundation Occasional Papers 23 (Supp.): 1–197.
- Hartmann-Schröder G (1971) Annelida, Borstenwürmer, Polychaeta. Tierwelt Deutschlands 58: 1–594.
- Hove HA ten, Weerdenburg JCA (1978) A generic revision of the brackish-water serpulid *Ficopomatus* Southern 1921 (Polychaeta: Serpulinae), including *Mierciella* Fauvel 1923 *Sphaeropomatus* Treadwell 1934, *Mercierellopsis* Rioja 1945 and *Neopomatus* Pillai 1960. Biological Bulletin 154(1): 96–120. doi: 10.2307/1540777
- Hove HA ten, Kupriyanova EK (2009) Taxonomy of Serpulidae (Annelida, Polychaeta): The state of affairs. Zootaxa 2036: 1–126.
- Liñero-Arana I, Díaz-Díaz O (2012) Presencia del poliqueto exótico *Ficopomatus uschakovi* (Polychaeta: Serpulidae) en Venezuela: Descripción y comentarios sobre distribución. Revista Interciencia 37(3): 234–237.

- Mesnil F, Fauvel P (1939) Polychetes sedentaires de l'Expédition des Siboga. Maldanidae, Cirratullidae, Capitellidae, Sabellidae et Serpulidae. Siboga Expedition 24(2): 1–42.
- Pillai TG (1960) Some marine and brackish-water serpulid Polychaeta from Ceylon, including new genera and species. Ceylon Journal of Sciences, Biological Sciences 3: 1–40.
- Pillai TG (1965) Annelida Polychaeta from the Philippines and Indonesia. Ceylon Journal of Science, Biological Sciences 4: 110–177.
- Pillai TG (1971) Studies on a collection of marine and brackish-water polychaete annelids of the family Serpulidae from Ceylon. Ceylon Journal of Sciences, Biological Sciences 9: 88–130.
- Pillai TG (2008) *Ficopomatus talehsapensis*, a new brackish-water species (Polychaeta: Serpulidae: Ficopomatinae) from Thailand, with discussions on the relationships of taxa constituting the subfamily, opercular insertion as a taxonomic character and their taxonomy, a key to its taxa, and zoogeography. Zootaxa 1967: 36–52.
- Rouse GW, Pleijel F (2001) Polychaetes. Oxford University Press, London, 354 pp.
- Salazar-Vallejo SI (2000) Biogeografía marina del Gran Caribe. Interciencia 25(1): 7–12.
- Salgado-Barragán J, Méndez N, Toledano-Granados A (2004) *Ficopomatus miamiensis* (Polychaeta: Serpulidae) and *Styela canopus* (Ascidiacea: Styelidae), non-native species in Urías estuary, SE Gulf of California, Mexico. Cahiers de Biologie Marine 45: 167–173.
- World Wildlife Fund for Nature (2012) Introducción de especies exóticas. http://www.wwf.es/que_hacemos/especies/problemas/introduccion_de_especies_exoticas/ [accessed on November 26th, 2012]
- Zibrowius H (1973) Serpulidae (Annelida Polychaeta) des côtes Ouest de l'Afrique et des archipels voisins. Annales Musee Royal de l'Afrique Centrale, Belgique, series 8, Sciences Zoologiques 208: 1–93.

***Brachymyrmex* species with tumuliform metathoracic spiracles: description of three new species and discussion of dimorphism in the genus (Hymenoptera, Formicidae)**

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Abstract

Brachymyrmex is a taxonomically challenging ant genus that is badly in need of review. Most species are very small and soft bodied and current descriptions regularly lack clarity making species identification a daunting task. Furthermore, the monophyly of *Brachymyrmex* has not been established and the relationships among its species and with closely related genera are poorly understood. Most species of *Brachymyrmex* are monomorphic, but two dimorphic species have been assigned to the genus before. Here, we redescribe these dimorphic taxa, *B. pilipes* and *B. micromegas*, and describe three new monomorphic species, *B. brasiliensis* **sp. n.**, *B. delabiei* **sp. n.** and *B. feitosa* **sp. n.** All five species occur in Brazil and have tumuliform metathoracic spiracles, which are lacking in other *Brachymyrmex* species. We discuss dimorphism and its evolution in the genus and provide a distribution map, illustrations and a species identification key based on workers.

Keywords

Brazil, Formicinae, ants, new species, *Brachymyrmex*, dimorphism

Introduction

The cosmopolitan ant subfamily Formicinae contains 11 tribes, 60 genera and over 3,000 species, and has been shown to be monophyletic (Shattuck 1992, Johnson et al. 2003, Brady et al. 2000, 2006, Moreau et al. 2006), however, classification within the subfamily is not fully resolved and many genera are in need of thorough review. One of these genera is *Brachymyrmex* Mayr, 1868 which, following the classification proposed by Bolton (2003) belongs to the tribe Plagiolepidini.

Brachymyrmex is a genus of minute ants that at first glance exhibit little morphological variation. Currently only the 9-segmented antennae and lack of antennal club have been proposed to diagnose workers of the genus (Bolton 2003). The combination of small size, soft metasoma, and the simple morphology makes observations and interpretation of morphological characters difficult. These difficulties impede taxonomic revisions and even led Creighton (1950) to call *Brachymyrmex* a “miserable little genus”. Nevertheless, 57 described species, subspecies, and varieties are currently assigned to *Brachymyrmex* (Bolton, 2013). The genus has a mainly Neotropical distribution, ranging from the United States to Argentina and Chile, including the Caribbean islands (Kempf 1972, Brandão 1991, Bolton 1995, 2003), but some species have been introduced to Japan (M. Yoshimura, pers. comm.), and Madagascar (Dejean et al. 2010).

The first complete taxonomic revision of *Brachymyrmex* was published by Santschi (1923) and included 27 species and 15 subspecies and varieties. In this revision, Santschi (1923) recognized two subgenera: 1) *Brachymyrmex sensu stricto* (including most of the species) and 2) *Brysha* Santschi, 1923 (four species: *Brachymyrmex* (*Brysha*) *pilipes* Mayr, 1887; *B. (B.) micromegas* Emery in Santschi 1923; *B. (B.) antennatus* Santschi, 1929 and *B. (B.) gaucho* Santschi, 1917). *Brachymyrmex sensu stricto* contains species that have hairy legs, antennae without erect hairs and the second segment of the antennal funiculus much shorter than the first (= third antennal segment much shorter than the second). *Brysha* species have legs and antennae with erect hairs and the second segment of the antennal funiculus is as long as or longer than the first. Unlike other species in the genus, two of the species of the subgenus *Brysha*, *B. pilipes* and *B. micromegas*, have dimorphic workers. Ambiguity remains regarding the status of *Brysha*. Brown (1973) provisionally synonymized it under *Brachymyrmex* and Bolton (1995, 2013) accepted this synonymy in his catalogues without substantiating the decision. We tentatively follow these latter authors, but phylogenetic work is required to settle the issue.

Here, as part of a larger taxonomic revision of the genus, we identify and revise the species of *Brachymyrmex* that have tumuliform metathoracic spiracles (= spiracles that are fully dorsal and highly elevated on the meso-metanotum in lateral view). This group contains the two dimorphic *Brachymyrmex* species mentioned above, which we redescribe here. Although tumuliform metathoracic spiracles are not present in any previously known monomorphic *Brachymyrmex* species, we found them present in three new, monomorphic species of the genus, which we describe here. All species with tumuliform metathoracic spiracles occur in Brazil. Hence, the *Brachymyrmex* species of this country may provide new insights into the evolution of dimorphism. We discuss dimorphism in *Brachymyrmex* and the status of the genus.

Material and methods

Material and repositories

We studied the *Brachymyrmex* material of the following institutions which includes all relevant types and additional specimens; collection acronyms follow Ward (1989).

CASC	California Academy of Sciences, San Francisco, California, USA
CPDC	Laboratório de Mirmecologia do Centro de Pesquisas do Cacau, Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC), Itabuna, Bahia, Brazil
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, USA
MCSN	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHNV	Naturhistorisches Museum, Wien, Austria
UFUC	Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil
USNM	Department of Entomology, National Museum of Natural History Smithsonian Institution, Washington DC, USA

Images

Photographs of the ants including dorsal, lateral and full-face views of workers and queens were taken at the MCZC with an imaging system that consisted of a Leica MZ16 stereo microscope, a Leica DCF 420 digital camera, and the Auto-Montage Professional software Leica Application Suite 3.7 and Helicon Focus 5.1; and at the USNM with an imaging system that consisted of a Leica Z16APO microscope and a JVC KY-F75U digital camera with a Leica Motor-focus System attached to an IBM IntelM Pro computer, on which composite images were assembled using Auto-Montage Pro Version 5.03.0018 BETA (Synoptics Ltd.). Scanning electron micrographs were taken with a LaB6 electron source. Images were processed with Adobe Photoshop CS. The distribution map was created using the software ArcGIS v10.1 (Esri, Redlands, CA).

Measurements

Measurements were made using an Advanced Optical Microscope at 120 × magnification and a Leica Z16 APO microscope with a fiber optic ring lamp at 80 × magnification. All measurements are in mm.

*Head Length*₁ (HL₁). The maximum length of the head capsule excluding the mandibles; measured in full-face view, as a straight line from the mid-point of the anterior clypeal margin to the mid-point of the posterior (= vertexal) margin of the head (for major workers the posterior margin is defined by a virtual line between the posterior apices of the head).

*Head Length*₂ (HL₂). Distance from posterior margin of the frontal triangle (see Bolton 1994, p. 192) to vertexal margin in full-face view.

*Head Length*₃ (HL₃). Measurement of the gena in lateral view; this measurement equals the distance from the anterior margin of the eye to the posterior edge of clypeus, perpendicular to this edge.

Head Width (HW). The maximum width of the head behind the eyes, measured in full-face view.

Scape Length (SL). The maximum length of the scape, excluding the basal constriction that occurs just distal to the condylar bulb.

Eye Length (EL). Maximum diameter of the compound eye.

Weber's Length (WL). The diagonal length of the mesosoma, in profile, from the anterior-most point of the pronotum to the posterior-most basal angle of the metapleuron (this measurement excludes the cervical neck of the pronotum).

Pronotum Length (PnL). Length from anterior edge to posterior edge of pronotum in dorsal view along the midline (this measurement excludes the cervical neck of the pronotum).

Pronotum Width (PnW). Width viewed dorsally, measured from side to side.

Mesonotum Length (ML). Length viewed dorsally, measured from anterior edge of mesonotum to mesometanotal suture, with both in the same plane of focus.

Mesonotum Width (MW). Width viewed dorsally, measured from side to side.

Indices

Cephalic Index (CI). $(HW/HL_1) \times 100$.

Scape Index (SI₁). $(SL/HW) \times 100$.

*Scape Index*₁ (SI₂). $(SL/HL_2) \times 100$.

Ocular Index (OI). $(EL/HW) \times 100$.

Morphological terminology follows Bolton (1994); terminology for hair inclination follows Kugler (1994).

Results

Redescription of dimorphic species

Brachymyrmex micromegas Emery

http://species-id.net/wiki/Brachymyrmex_micromegas

Figs 1–6, 28

Brachymyrmex (*Brysha*) *micromegas* Emery, in Santschi 1923: 675, figs 30, 32 (w)
BRAZIL (MCSN, MZSP) [examined].

Lectotype (here designated). 1 minor worker, **Brazil**, São Paulo, Ipiranga (MCSN) [USNM ENT 00757222]. **Paralectotypes.** 4 major workers, 1 minor worker, **Brazil**,



Figure 1–6. *Brachymyrmex micromegas* Emery (Lectotype) **1** Major worker, head in full-face view **2** Major worker, body in lateral view **3** Major worker, body in dorsal view **4** Minor worker, head in full-face view **5** Minor worker, body in lateral view **6** Minor worker in dorsal view.

São Paulo, São Paulo city, Ipiranga (MCSN) [USNM ENT 00757222], (MZSP) [USNM ENT 00757824 – 00757827].

Additional material examined. 1 minor worker, **Brazil**, São Paulo, Agudos, 05 Nov 1967, col. W. Kempf (MZSP) [USNM ENT 00757830]; 1 minor worker, **Brazil**, São Paulo, Anhembi, Faz B. Rico, 14 Feb 1969, cols. W. Kempf, J.C. Magalhães, L.T.F.M. Kulman (MZSP) [USNM ENT 00757834].

Diagnosis. This species can be differentiated from most other *Brachymyrmex* species by the following: presence of tumuliform metathoracic spiracles; worker caste dimorphic; toruli touching the posterior clypeal margin, but never surpassing it (best observed in anterodorsal oblique view); and clypeus with a row of long thick hairs near the anterior margin (see Fig. 15). These traits are shared with *B. pilipes*, but *B. micro-megas* differs from *B. pilipes* by smooth and shiny body, with very fine longitudinal striations restricted to the metapleura; the body color is usually light brown (Fig. 1).

Minor worker. *Lectotype measurements* (mm) (n=1) HL₁ 0.78; HL₂ 0.49; HL₃ 0.29; HW 0.70; SL 0.72; EL 0.21; WL 0.98; PnL 0.29; PnW 0.53; ML 0.23; MW 0.53; *Indices* CI 90; SI₁ 102.77; SI₂ 148; OI 30.55.

Paralectotype measurements (mm) HL₁ 0.78; HL₂ 0.49; HL₃ 0.29; HW 0.70; SL 0.72; EL 0.21; WL 0.98; PnL 0.29; PnW 0.53; ML 0.23; MW 0.53; *Indices* CI 90; SI₁ 102.77; SI₂ 148; OI 30.55.

Additional material examined measurements (mm) (n=2) HL₁ 0.83 – 0.94; HL₂ 0.25 – 0.33; HW 0.77 – 0.86; SL 0.74 – 0.80; EL 0.16 – 0.19; WL 1.0 – 1.10; PnL 0.29 – 0.33; PnW 0.53 – 0.59; ML 0.23 – 0.27; MW 0.25 – 0.33; *Indices* CI 92 – 94; SI₁ 92 – 97; SI₂ 71 – 76; OI 21 – 22.

Description. Head longer than wide, sub-rectangular. Posterior cephalic border slightly concave. Clypeus large, with rounded anterior margin. Toruli touching the posterior clypeal margin but never surpassing it (best observed in anterodorsal oblique view). Scapes long, surpassing the posterior margin of the head. Ocelli present. Eyes well developed, situated posterior to mid line of head, with 14–15 ommatidia at maximum diameter. Promesonotum in profile conspicuously convex, higher than propodeum. Mesonotum inclined, strongly convex, in profile and separated from pronotum (Fig. 5).

Metanotal groove deep, wide. Metathoracic spiracles fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view (Fig. 5). Propodeal spiracle near to declivity of propodeum. Petiolar scale not inclined forward.

Body smooth and shiny, except for the metapleura, which have very fine, longitudinal striations. Most of mandibular surface smooth and shiny (best observed in anterodorsal oblique view). Entire body, including antennae, legs and palps with conspicuous erect and sub-erect pilosity. Clypeus with a row of many long thick hairs near the anterior margin, the rest of the clypeal surface with many shorter hairs. Gaster smooth and shiny without scattered long erect hairs and without dense pubescence. Body usually light brown, gaster often darker.

Major worker. *Paralectotype measurements* (mm) (n=3). HL₁ 1.66 – 1.88; HL₂ 1.17; HL₃ 0.57 – 0.63; HW 1.66 – 1.83; SL 1.12 – 1.23; EL 0.25 – 0.28; WL 1.66 – 1.8; PnL 0.49 – 0.73; PnW 1.05 – 1.13; ML 0.55 – 0.63; MW 0.63 – 0.75; *Indices* CI 95 – 100; SI₁ 61.6 – 74.12; SI₂ 105; OI 15.1 – 15.7.

Description. Head strongly cordate, broader at eye level (Fig. 1). Clypeus large, with anterior margin rounded. Toruli touching the posterior clypeal margin but never surpassing it. Scapes surpassing the posterior margin of the head. Ocelli present. Eyes well developed, situated posterior to the midline of the head. Promesonotum in profile strongly convex, higher than the propodeum.

Metanotal groove deep. Metathoracic spiracles fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view (Fig. 2). Propodeal spiracle near to declivity of propodeum. Petiole scale not inclined forward, rounded.

Body smooth and shiny, except for the metapleura, which has very fine, longitudinal striations. The entire body, including antennae, legs and palps with conspicuous, erect and sub-erect pilosity. Clypeus with a row of many long thick hairs near anterior margin, the rest of the clypeal surface shiny and with many shorter hairs. Body light brown.

Queen and male. Unknown.

Distribution. Brazil: São Paulo State.

Remarks. Because the specimens were poorly mounted, not all measurements could be taken on all ants. The type-series was collected near the locality where the Independência Park arboretum is now located, just beside the MZSP building in Ipiranga, São Paulo, Brazil. Despite recent field trips to the locality, none specimens have been collected (R.M. Feitosa, pers. comm.).

Brachymyrmex pilipes Mayr

http://species-id.net/wiki/Brachymyrmex_pilipes

Figs 7–16, 28

Brachymyrmex pilipes Mayr, 1887: 524 (q.m.) BRAZIL (NHMV) [examined]. Santschi 1929: 310 (w.). BRAZIL (NHMB) [examined]. Combination in *Brachymyrmex* (*Brysha*): Santschi 1923: 674.

Lectotype (here designated). 1 queen, *Paralectotypes* 1 queen, 1 male, **Brazil**, Santa Catharina (NHMV).

Additional material examined. 6 minor workers, **Brazil**, Paraná, Rio Azul, 1000 m, Oct. 1959, col. F. Plaumann (MZSP) [USNM ENT 00757822, USNM ENT 00757823]; 2 major workers, 2 minor workers, 1 queen, **Brazil**, Paraná, Rio Negro (NHMB); 3 minor workers, **Brazil**, Santa Catharina, Chapecó, Dic. 1957, col. F. Plaumann leg. (MZSP) [USNM ENT 00757821]; 6 minor workers, **Brazil**, Santa Catharina, Nova Teutonia, 27°11'S, 52°23'W, 300–500 m, Jul. 1958, col. F. Plaumann (MZSP) [USNM ENT 00757829, USNM ENT 00757831, USNM ENT 00757832]; 1 minor worker, **Brazil**, Rio de Janeiro, Nova Friburgo, Fazenda Barreto, 22°9'40.4712"S, 42°31'27.4866"W, 1068 m, 11–12 Jun 2011, col. T.M.S. Mesquita (UFUC) [USNM ENT 00757824]; 1 minor worker, **Brazil**, São Paulo, Ubatuba, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, 23°19'S 45°06'W, 870–1000 m, 22 Apr 2005, col. M. Uehara (MZSP) [USNM ENT 00757823].

Diagnosis. This species can be differentiated from most of the *Brachymyrmex* by the following: presence of tumuliform metathoracic spiracles; worker caste dimorphic; toruli touching the posterior clypeal margin, but never surpassing it (best observed in anterodorsal oblique view); and long thick hairs in a row near anterior clypeal margin (Fig. 15). These traits are shared with *B. micromegas*, but *B. pilipes* differs by the fine,

longitudinal striations on most of the mesosoma (Fig. 16), and the gaster color often is darker than the body color.

Minor worker. *Measurements* (mm) (n=8) HL₁ 0.62 – 1.21; HL₂ 0.50 – 0.74; HL₃ 0.33 – 0.39; HW 0.60 – 1.07; SL 0.57 – 1.17; EL 0.12 – 0.22; WL 0.97 – 1.42; PnL 0.40 – 0.55; PnW 0.64 – 0.76; ML 0.20 – 0.33; MW 0.33 – 0.37; *Indices* CI 88 – 97; SI₁ 95 – 109; SI₂ 114 – 158; OI 18 – 20.

Description. Head slightly longer than wide, almost squared, slightly narrowing anteriorly. Posterior cephalic border slightly concave. Clypeus large, with rounded anterior margin. Toruli touching the posterior clypeal margin, but never surpassing it (best observed in anterodorsal oblique view) (Fig. 15). Scapes long, surpassing the posterior margin of the head. Ocelli present. Eyes well developed, located at the midline of the head, with 10–11 ommatidia at their maximum diameter. Mesonotum conspicuously convex. Metanotal groove deep and wide. Metathoracic spiracles fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view (Fig. 8). Propodeum strongly convex, unarmed. Propodeal spiracle near to posteriopropodeal margin. Petiole scale rounded and not inclined forward.

Head and gaster smooth and shiny. Mesosoma with very fine, dense longitudinal and oblique striations. Most of mandibular surface with longitudinal rugulae (best observed in anterodorsal oblique view). Entire body, including antennae, legs, and palps with conspicuous erect and suberect pilosity that are larger on dorsum. Long thick hairs in a row near to the anterior clypeal margin. Most of clypeal surface with many erect hairs, which are shorter than the thick hairs. Body light brown, gaster dark brown, hairs lighter.

Major worker. *Measurements* (mm) (n=2) HL₁ 1.44 – 1.46; HL₂ 0.92 – 0.94; HL₃ 0.37 – 0.39; HW 1.35; SL 1.17; EL 0.20 – 0.21; WL 1.60 – 1.83; PnL 0.59; PnW 0.88; ML 0.39; MW 0.49. *Indices* CI 92; SI₁ 104.34; SI₂ 58 – 68; OI 17.39.

Description. Head bigger than that of the minor worker, squared with posterior corners angulate and posterior cephalic border slightly concave. Clypeus large, with rounded anterior margin. Toruli touching the posterior clypeal margin, never surpassing it. Scapes long, surpassing the posterior margin of the head. Ocelli present. Eyes well developed, located at mid line of head, with 11 ommatidia at their maximum diameter.

Mesonotum conspicuously convex. Metanotal groove present. Metathoracic spiracles fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view (Fig. 11). Propodeum strongly convex, unarmed. Propodeal spiracle near posteriopropodeal margin. Petiolar scale rounded and inclined forward.

Head and gaster smooth and shiny. Mesosoma with very fine, dense longitudinal and oblique striations. Entire body, including antennae, legs, and palps with conspicuous erect and suberect pilosity that is longer on the dorsum. Long hairs in a row near anterior clypeal margin. Most of clypeal surface with abundant erect hairs, which are shorter than the thick hairs. Body light brown, gaster dark brown, hairs lighter colored.

Queen. *Lectotype measurement* (mm) (n=1) HL₁ 1.61; HL₂ 0.42; HW 1.88; SL 1.54; EL 0.47; WL 4.04; PnL 2.21; PnW 2.19; ML 0.97; MW 1.59. *Indices* CI 116.17; SI₁ 82.27; OI 25.31.

Description. Same as worker except for standard queen modifications and the following: abundant erect hairs and dense pubescence on entire body. There is a row

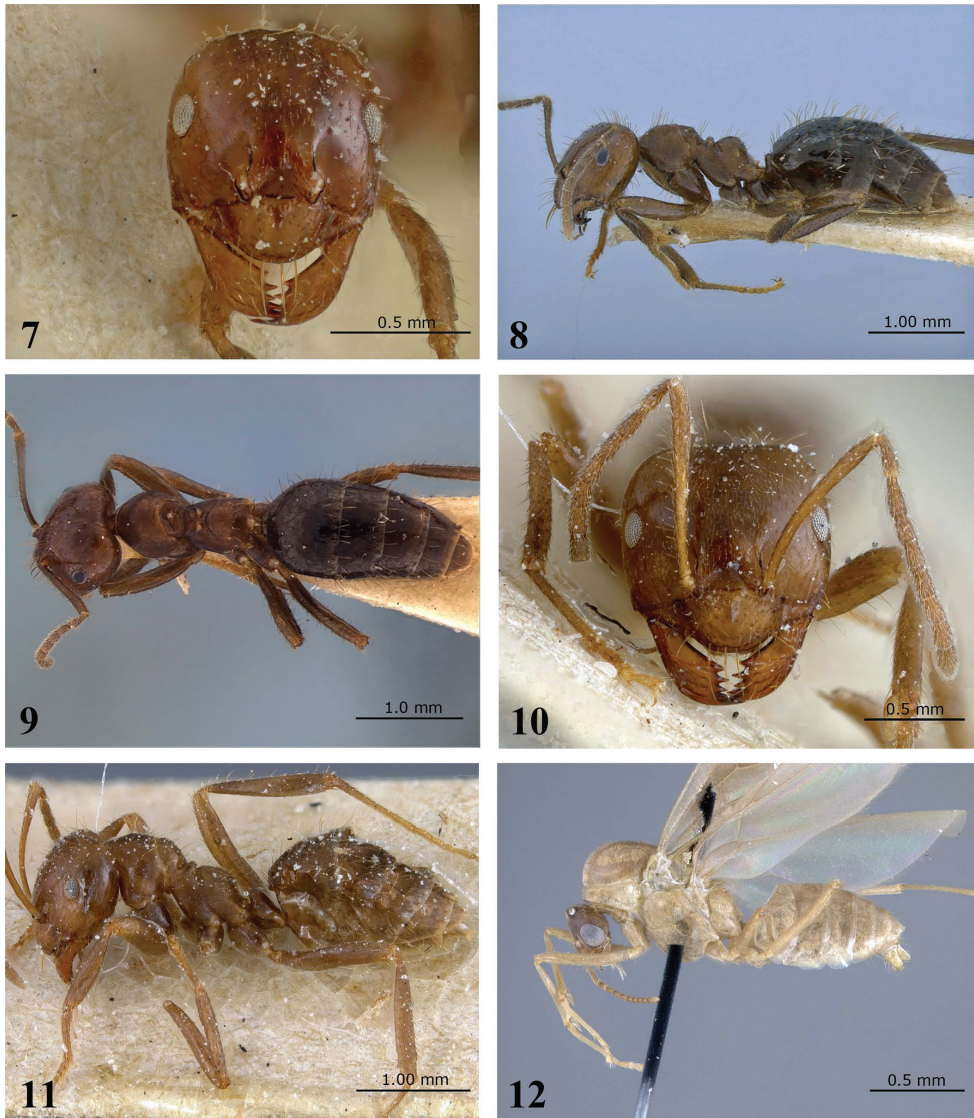


Figure 7–12. *Brachymyrmex pilipes* Mayr **7** Minor worker, head in full-face view **8** Minor worker, body in lateral view **9** Minor worker, body in dorsal view **10** Major worker, head in full-face view **11** Major worker, body in lateral view **12** Male, body in lateral view.

of thick hairs near the anterior margin of clypeus, similar to the workers and abundant pubescence on the body (Fig. 13). Body dark brown.

Male. *Paralectotype measurements* (mm) (n=1) HL 0.31; EL 0.16; WL 0.88.

Description. Scapes surpassing the posterior margin of the head, few erect hairs, and sparse pubescence on the body; some sparse long hairs on the tibiae. Head brown, mesosoma and gaster yellow. Penis valves longer than parameres *in situ*.

Distribution. Brazil: states of Paraná, Santa Catharina, São Paulo and Rio de Janeiro.

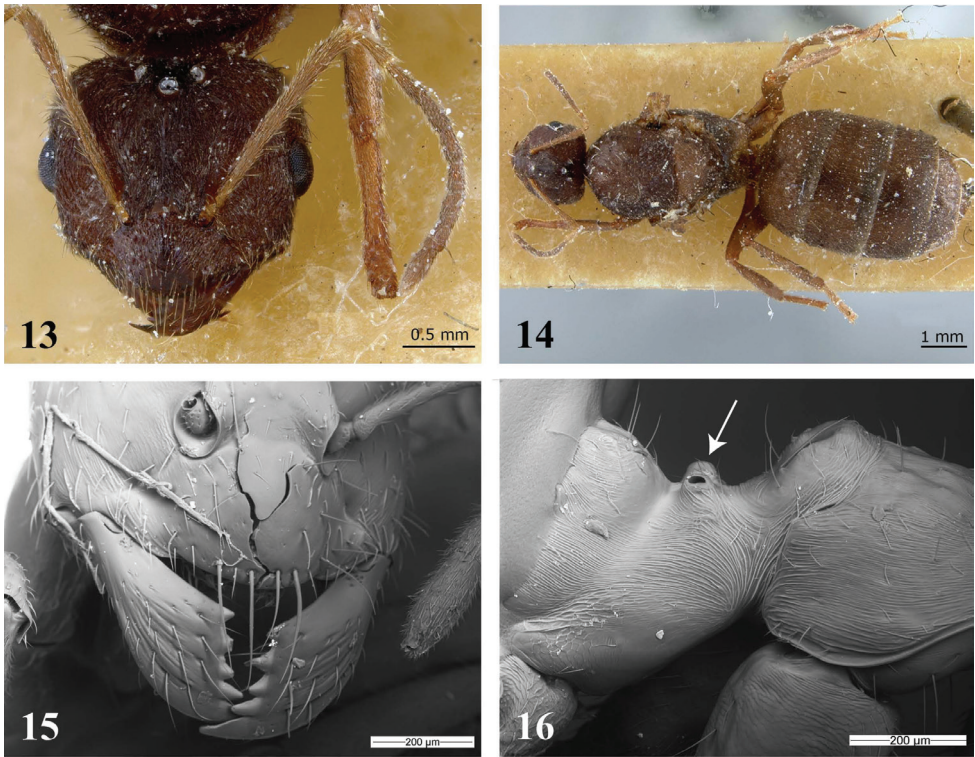


Figure 13–16. *Brachymyrmex pilipes* Mayr. **13** Queen (Lectotype), head in full-face view **14** Queen (Lectotype), body in dorsal view **15** Minor worker, clypeus **16** Minor worker, mesosoma in right lateral view.

Remarks. The specimen from São Paulo at Ubatuba, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia [USNM ENT 00757823] was collected in an area of relatively well-preserved mature forest with some remnants of primary forest where selective logging took place until 1970 (Magrini et al. 2011). Habitat information is lacking for the other specimens.

Description of new monomorphic species

Brachymyrmex brasiliensis sp. n.

<http://zoobank.org/84634C4B-8171-4A8A-B851-E9296D863F3B>

http://species-id.net/wiki/Brachymyrmex_brasiliensis

Figs 19–21, 28

Holotype worker (MZSP) [USNM 00757748] and **Paratype worker** (UFUC) [USNM ENT 00757833]: **Brazil**, Rio de Janeiro, Nova Friburgo, Fazenda Barreto, 22°9'40.4712"S, 42°31'27.4866"W, 1068 m, 11–12 Jun 2011, col. T.M.S. Mesquita.

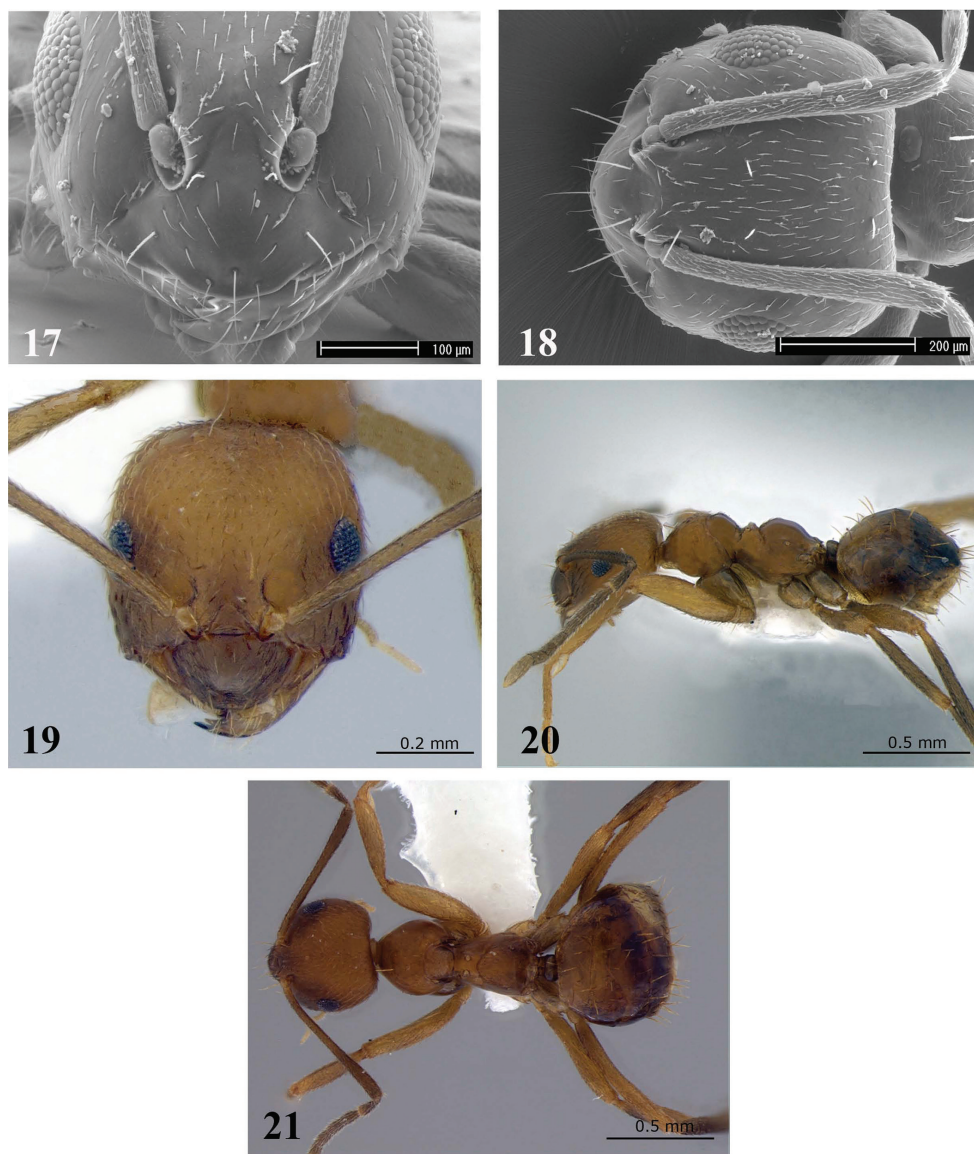


Figure 17–21. **17** Frontal view of the clypeus of a *Brachymyrmex* monomorphic specimen showing the distribution of hairs: one central hair near to the anterior margin; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli **18** Head of the same specimen in semidorsal view (SEM pictures, were taken by J. Cillis, T. Delsinne and M. Leponce (RBINS)). *Brachymyrmex brasiliensis* sp. n. (Holotype) **19** Worker, head in full-face view **20** Worker, body in lateral view **21** Worker, body in dorsal view.

Additional material examined. 1 worker, **Brazil**, Goiás, Anápolis, 12 Feb 1958, col. W. Kempf (MZSP) [USNM ENT 00757820].

Diagnosis. This species differs from most other *Brachymyrmex* species by the presence of tumuliform metathoracic spiracles, and clypeus with five long, erect hairs ar-

ranged as follows: one central hair near to the anterior margin, usually conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli (see Fig. 17–18). Unique features for *B. brasiliensis* are the smooth and shiny gaster and, opaque head and mesosoma.

Worker. *Holotype measurements* (mm) HL₁ 0.59; HL₂ 0.36; HL₃ 0.15; HW 0.53; SL 0.67; EL 0.11; WL 0.71; PnL 0.24; PnW 0.36; ML 0.15; MW 0.18; *Indices* CI 90; SI₁ 127; SI₂ 187.5; OI 25.

Paratype measurements (mm) HL₁ 0.59; HL₂ 0.36; HL₃ 0.15; HW 0.53; SL 0.67; EL 0.11; WL 0.71; PnL 0.24; PnW 0.36; ML 0.15; MW 0.18; *Indices* CI 90; SI₁ 127; SI₂ 187.5; OI 25.

Additional material examined (mm) HL₁ 0.61; HL₂ 0.40; HL₃ 0.15; HW 0.53; SL 0.68; EL 0.13; WL 0.73; PnL 0.24; PnW 0.36; ML 0.15; MW 0.18; *Indices* CI 89; SI₁ 129; SI₂ 187.5; OI 25.

Description. Head slightly longer than wide. Posterior cephalic border slightly convex, sides slightly convex. Anterior clypeal margin rounded. Toruli touching the posterior clypeal margin but never surpassing it (best observed in anterodorsal oblique view; see Fig. 17). Scapes long, surpassing the posterior margin of the head. Ocelli present. Eyes located at cephalic midline and well developed with 11 ommatidia at their maximum diameter.

Promesonotum convex in profile, mesonotum strongly convex and separated from pronotum. Propodeum convex with short dorsum. Metathoracic spiracles fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view. Propodeal spiracle round, separated from declivity of propodeum by a distance equal to the diameter. Petiole short, apex rounded and inclined forward.

Head and mesosoma finely punctate and opaque. Dorsum of head with some erect hairs on front and with scattered decumbent pubescence. Gaster smooth and shiny with several scattered erect hairs. Scapes with decumbent hairs that are shorter than the maximum scape diameter. Clypeus with five long, erect hairs arranged as follows: one central hair near to the anterior margin, usually conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli. Pronotum usually with two erect hairs, rest of mesosoma without hairs. Body light brown.

Queen and male. Unknown.

Etymology. After Brazil, the country of collection, in honor of its very rich ant fauna.

Distribution. Brazil: states of Goiás and Rio de Janeiro.

Remarks. Biological and ecological information of this species is lacking.

***Brachymyrmex delabiei* sp. n.**

<http://zoobank.org/17FF8984-4DCA-48B2-BC39-0DCA9B702B8A>

http://species-id.net/wiki/Brachymyrmex_delabiei

Figs 22–24, 28

Holotype worker (MZSP) [USNM ENT 00757718] and **Paratypes** 3 workers (CPDC [USNM ENT 00757719], ICN [USNM ENT 00757720], USNM [USNM

ENT 00757721)): **Brazil**, São Paulo, Tapiraí, 24°01'55.5"S 47°27'56"W, 08–14 Jan 2001, col. R.R. Silva & Eberhardt, Transecto 1 Winkler 23.

Additional material examined. 1 worker, **Brazil**, Bahia, Boa Nova, João Mata, 13 Aug 2003, cols. J.R.M. Santos & J.C.S. Carmo (CPDC) [USNM ENT 00757610]. 1 worker, **Brazil**, Bahia A61 Camacan, 27 Aug 1999. 15°36'04"S, 39°31'16"W, col. J.R.M. dos Santos, (CPDC) [USNM ENT 00757837]; 1 worker, Brazil, Santa Catharina, Palhoça, PE Serra do Tabuleiro, 02–10 Nov 2003, 27°44'28"S, 48°41'50"W, cols. R.R. Silva, B.H. Dietz and A. Tavares, (MZSP) [USNM ENT 00757725]; 1 worker, **Brazil**, São Paulo, São Bernardo do Campo, 01 Jun 1971, cols. W.L. & D.E. Brown (MCZC) [USNM ENT 00757835].

Diagnosis. This species differs from most other *Brachymyrmex* species by the presence of tumuliform metathoracic spiracles, and clypeus with five long, erect hairs arranged as follows: one central hair near to the anterior margin, usually conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli (see Fig. 17–18) and from *B. brasiliensis* by its entirely smooth and shiny body. *B. delabiei* can be diagnosed from *B. feitosai* sp. n. (see below) by the lack of dense pubescence on the first segment of the gaster and by the presence of erect hairs on the mesosoma; two on the pronotum and two on the mesonotum.

Worker. *Holotype measurements* (mm). HL₁ 0.38; HL₂ 0.29; HL₃ 0.08; HW 0.32; SL 0.32; EL 0.07; WL 0.40; PnL 0.12; PnW 0.22; ML 0.07; MW 0.13; *Indices* CI 83.7; SI₁ 102.8; SI₂ 134.4; OI 22.2.

Paratypes measurements (mm) (n=3). HL₁ 0.34 – 0.41; HL₂ 0.22 – 0.30; HL₃ 0.06 – 0.09; SL 0.31 – 0.36; EL 0.07 – 0.09; WL 0.35 – 0.43; PnL 0.09 – 0.13; PnW 0.15 – 0.24; ML 0.07 – 0.12; MW 0.13 – 0.17; *Indices* CI 83.7 – 93; SI 97 – 119; SI₂ 112 – 135; OI 21.05 – 26.

Additional material examined measurements (mm) (n=4). HL₁ 0.34 – 0.41; HL₂ 0.22 – 0.28; HL₃ 0.06 – 0.09; SL 0.31 – 0.36; EL 0.08 – 0.09; WL 0.30 – 0.43; PnL 0.10 – 0.12; PnW 0.15 – 0.20; ML 0.07 – 0.12; MW 0.15; *Indices* CI 88.8 – 92; SI₁ 97 – 100; SI₂ 71 – 78; OI 25.

Description. Head slightly longer than wide, sides slightly convex. Posterior cephalic border flat, slightly concave in the middle. Anterior clypeal margin rounded. Toruli surpassing the posterior clypeal margin (best observed in anterodorsal oblique view). Scapes surpassing the posterior margin of the head. Ocelli present. Eyes situated below the cephalic midline and well developed with 7–9 ommatidia at their maximum diameter.

Promesonotum convex in profile. Mesonotum strongly convex, rounded and separated from pronotum. Propodeum strongly convex with short dorsum. Metathoracic spiracles fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view, equidistant in diameter from metanotal groove and from the propodeal folding. Propodeal spiracle round, elevated from integument on the propodeal border. Petiole short and inclined forward.

Body smooth and shiny. Dorsum of head, promesonotum, and propodeum with short appressed hairs. Scapes with suberect and subdecumbent hairs. Clypeus with five long, erect hairs arranged as follows: one central hair near to the anterior margin, usually

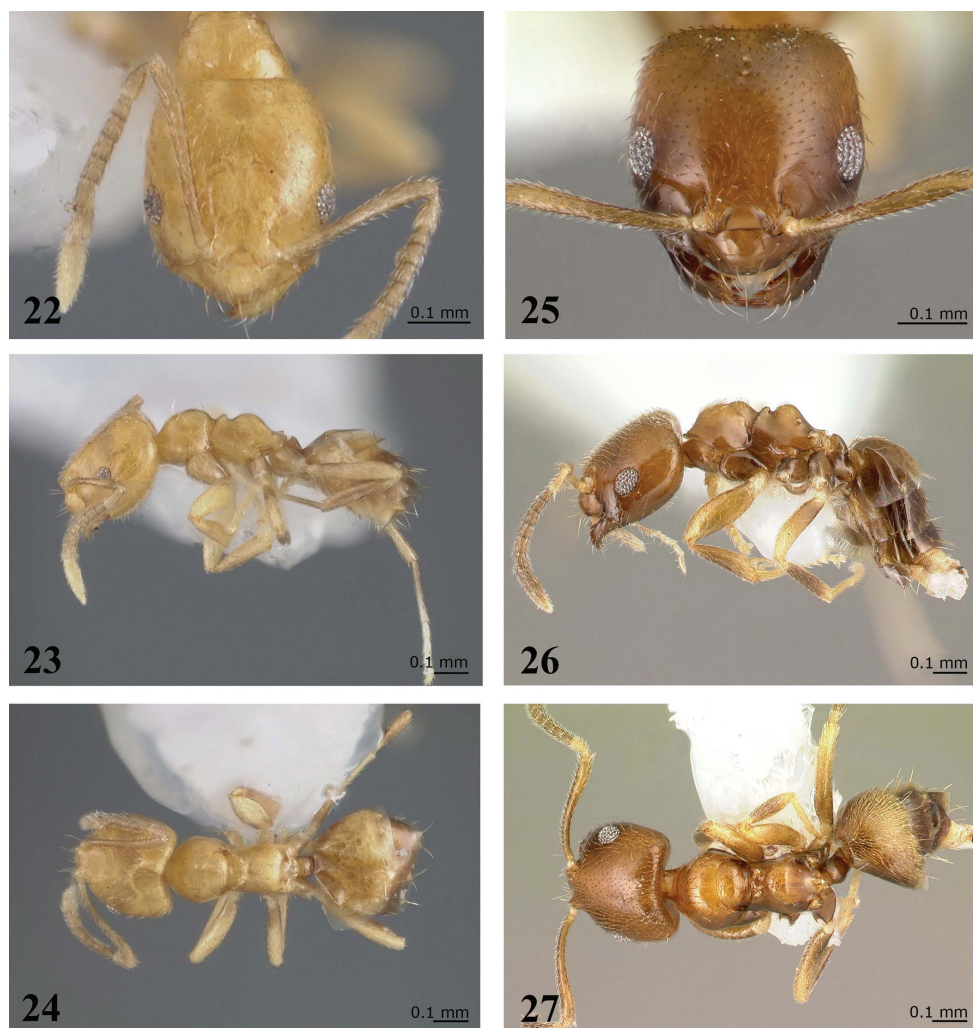


Figure 22–27. *Brachymyrmex delabiei* sp. n. (Holotype). **22** Worker, head in full-face view **23** Worker, body in lateral view **24** Worker, body in dorsal view. *Brachymyrmex feitosa* sp. n. (Paratype) **25** Worker, head in full-face view **26** Worker, body in lateral view **27** Worker, body in dorsal view (pictures taken by <http://www.antweb.org/>).

conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli. Gaster with several scattered long erect hairs, without dense pubescence. Mesosoma with erect hairs, two on the pronotum and two on the mesonotum. Body yellowish.

Queen and male. Unknown.

Distribution. Brazil: states of Bahia, Santa Catharina and São Paulo.

Etymology. We are pleased to name this ant in honor of Dr Jacques Delabie (CPDC) for his contribution to ant taxonomy and biology and his unconditional support for many ant biologists working in the Neotropics.

Remarks. The type specimens from São Paulo at Tapiraí [USNM ENT 00757718 – 00757722] were collected in a pristine region of the Brazilian Atlantic Forest (R.M. Feitosa, pers. comm.). Habitat information is lacking for the other specimens.

***Brachymyrmex feitosai* sp. n.**

<http://zoobank.org/01B69600-0156-4B6E-B162-700C921FDFBD>

http://species-id.net/wiki/Brachymyrmex_feitosai

Figs 25–28

Holotype and paratypes. 2 workers (MZSP) [USNM ENT 00757694]: **Brazil**, Rio de Janeiro, Floresta de Tijuca, D. Federal. 16 Dec 1959, C.A: Campos Seabra.

Additional material examined. 3 workers **Brazil**, Minas Gerais, Lavras, Ijaci e Perdões, 21°00'–21°19'S; 44°00'–45°07'W, Fragmento, 06 à 12/ 2002, cols. M.S. Santos & N.S. Dias (CPDC) [USNM ENT 00757836]; 1 worker, **Brazil**, São Paulo, Sete Barras, PE Carlos Botelho, 600 m, 24°12'02"S, 47°58'43"W. 11–15 May 2009, armadilha subterrânea #18, F. Esteves et al. cols. (MZSP) [ANTWEB CASENT 0217326].

Diagnosis. This species differs from most other *Brachymyrmex* species by the presence of tumuliform metathoracic spiracles, and clypeus with five long, erect hairs arranged as follows: one central hair near to the anterior margin, usually conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli (see Fig. 17–18). Like *B. delabiei* it differs from *B. brasiliensis* by its entirely smooth and shiny body. *B. feitosai* can be diagnosed from *B. delabiei* by the dense pubescence on the first gastral segment and by the presence of many suberect hairs on the pronotum and mesonotum.

Worker. *Holotype measurements* (mm). HL₁ 0.40; HL₂ 0.28; HL₃ 0.09; HW 0.36; SL 0.31; EL 0.10; WL 0.45; PnL 0.18; PnW 0.28; ML 0.09; MW 0.18; *Indices* CI 88.8; SI₁ 87.5; SI₂ 88.6; OI 27.5.

Paratypes measurements (mm) (n=2) HL₁ 0.33 – 0.43; HL₂ 0.27 – 0.29; HL₃ 0.07 – 0.10; HW 0.29 – 0.39; SL 0.26 – 0.34; EL 0.06 – 0.10; WL 0.33 – 0.45; PnL 0.08 – 0.15; PnW 0.20 – 0.24; ML 0.05 – 0.11; MW 0.13 – 0.17; *Indices* CI 82 – 90; SI₁ 88 – 103; SI₂ 105 – 113; OI 22 – 29.

Additional material examined (mm) (n=3) HL₁ 0.40 – 0.43; HL₂ 0.27 – 0.29; HL₃ 0.09; HW 0.35 – 0.39; SL 0.31; EL 0.10; WL 0.42 – 0.45; PnL 0.09 – 0.18; PnW 0.25 – 0.28; ML 0.08 – 0.12; MW 0.17 – 0.19; *Indices* CI 88 – 89; SI₁ 81 – 88; SI₂ 88 – 94; OI 25 – 28.

Description. Head slightly longer than wide. Posterior cephalic border slightly concave in the middle, and sides slightly convex. Clypeus with rounded anterior margin. Toruli surpassing the posterior clypeal margin (best observed in anterodorsal oblique view). Scapes reaching posterior margin of the head, but not surpassing it. Ocelli present. Eyes located below cephalic midline and well developed with 7–8 ommatidia at their maximum diameter.

Promesonotum convex in profile, mesonotum strongly convex and separated from pronotum. Metanotal groove present. Metathoracic spiracles dorsal, strongly protruding,



Figure 28. Distribution map of *B. micromegas*, *B. pilipes*, *B. brasiliensis* sp. n., *B. delabiei* sp. n., *B. feitosa* sp. n.

fully dorsal, tumuliform, bulging out of the metanotal groove in lateral view, equidistant from the metanotal groove and the propodeal fold. Propodeum strongly convex with short dorsum. Propodeal spiracle round, elevated from integument on the propodeal border.

Body smooth and shiny. Petiole short, apex rounded and inclined forward. Scapes with suberect hairs. Clypeus with five long, erect hairs arranged as follows: one central hair near to the anterior margin, usually conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near to toruli. Dorsum of head, promesonotum and propodeum with conspicuous semi-erect hairs lighter than body color. Gaster with several scattered long erect hairs and with dense pubescence on the first gastral segment that is lighter in color. Body brown.

Queen and male. Unknown.

Distribution. Brazil: states of Minas Gerais, Rio de Janeiro and, São Paulo.

Etymology. We are pleased to name this ant in honor of our friend and colleague, Dr Rodrigo Feitosa (Universidade Federal do Paraná) for his great contributions to ant taxonomy and his unconditional support for taxonomists, young and old.

Remarks. The specimen from São Paulo at Sete Barras [ANTWEB CASENT 0217326] was collected in a pristine region of the Brazilian Atlantic Forest. It was obtained in an underground trap, possibly indicating this species has hypogaecic habits (R.M. Feitosa, pers. comm.). Habitat information is lacking for the other specimens.

Key to workers for the *Brachymyrmex* species with tumuliform metathoracic spiracles

- 1 Clypeus with a single long apical hair near to the anterior margin, two lateral hairs medially and two hairs near the toruli (Figs 17–18); monomorphic ... **2**
- Clypeus with a continuous row of long thick hairs near the anterior margin (Fig. 15), and remaining pilosity not arranged as above; dimorphic **4**
- 2(1) Toruli surpassing the posterior clypeal margin (best observed in anterodorsal oblique view) (Fig. 17); entire body smooth and shiny **3**
- Toruli touching the posterior clypeal margin but never surpassing it (best observed in anterodorsal oblique view); head and mesosoma finely punctate and opaque; gaster smooth and shiny (Figs 20–21) ***B. brasiliensis***
- 3(2) Mesosoma without erect hairs (Fig. 26); first gastral segment with dense yellowish pubescence ***B. feitosai***
- Mesosoma with two erect hairs on pronotum and two on mesonotum (Fig. 23); gaster without pubescence (Fig. 24) ***B. delabiei***
- 4(1) Mesosoma mostly smooth and shiny, except for longitudinal striations restricted to the metapleura; body entirely light brown ***B. micromegas***
- Mesosoma with fine longitudinal striations all over (Fig. 16); gaster darker than the rest of body ***B. pilipes***

Discussion

Brachymyrmex was classified as being an entirely monomorphic genus by Bolton (2003), even though Santschi (1923) described two dimorphic species almost a century ago. Quirán et al. (2004) indicated that *Brachymyrmex* is a dimorphic genus but these authors do not treat dimorphic species in their paper, and neither do subsequent studies on *Brachymyrmex* from Argentina or elsewhere. Here, we redescribed the dimorphic *Brachymyrmex* species and we confirm that, as currently defined, *Brachymyrmex* should be added to the list of genera with monomorphic and dimorphic workers.

Moreover, while studying museum material we identified a number of specimens of described and new monomorphic *Brachymyrmex* species not dealt with here that have

intercastes (a queen-worker intermediate) (Ortiz, pers. obs.). These observations, though preliminary, raise questions about the evolution of castes in Formicinae. Some authors (Wilson 1953, Hölldobler and Wilson 1990) suggested that caste evolution may occur through disruptive selection on allometric differences among the workers and these authors used allometry to classify specimens to castes. Baroni Urbani and Passera (1996) proposed that soldiers evolved independently of workers, and that they originated directly from the queen, but this proposal was refuted by Ward (1997). Recently, Mole et al. (2012) suggested that novel castes such as soldiers and ergatoid queens evolve from rare intercastes, which consist of anomalous specimens with characteristics of both winged queens and workers. These ‘developmental mosaics’ would be erratically produced by colonies experiencing environmental or genetic perturbations; as earlier suggested by Wheeler (1991), and Anderson et al. (2008). The debate on the evolution of castes in ants is not fully settled. If *Brachymyrmex* truly contains both monomorphic and dimorphic species, the genus would provide an interesting system for studying competing hypotheses on the origin of castes in a phylogenetic framework.

One could question whether these two dimorphic species should be assigned to *Brachymyrmex* given the substantial morphological differences we observed: dimorphic species are considerably larger than the monomorphic ones and they have a long row of thick hairs near the anterior clypeal margin (Fig. 15). This contrasts sharply with the character states observed in the monomorphic species, all of which have a clypeus with five long, erect hairs arranged as follows: one central hair near to the anterior margin, usually conspicuous; one pair of lateral hairs at clypeus midlength and one pair of hairs near the toruli (Figs 17–18). Hence, the only taxonomic traits that tie these dimorphic species to *Brachymyrmex* are: antennae with nine antennal segments lacking an antennal club, and the tumuliform metathoracic spiracles. This latter character is shared with some other species in the genus (see the newly described species), but not all of them. Moreover, the petiole of *B. pilipes* and *B. micromegas* is erect, similar to the state observed in the closely related genus *Myrmelachista* and in contrast to the anteriorly inclined petiole of the monomorphic *Brachymyrmex* species. Nevertheless, given that *Brachymyrmex* is currently diagnosed based on the presence of nine antennal segments lacking an antennal club, we conservatively assign the dimorphic species to the genus for now.

The hypotheses presented here are preliminary and need further testing. Both the monophyly of *Brachymyrmex* and the placement of the dimorphic species within the genus are uncertain. To resolve this uncertainty a more thorough revision of the genus is needed, preferably one that combines morphological analysis with molecular systematics. Such a study is currently underway (Ortiz et al., in prep.) and the results should reveal much about the evolutionary history of this poorly understood ant genus.

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References

- Anderson KE, Linksvayer TA, Smith CR (2008) The causes and consequences of genetic caste determination in ants (Hymenoptera: Formicidae). *Myrmecological News* 11: 119131–139132.
- Baroni Urbani C, Passera L (1996) Origin of ant soldiers. *Nature (London)* 383: 223. doi: 10.1038/383223a0
- Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Mass., 222 pp.
- Bolton B (1995) A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Mass, 504 pp.
- Bolton B (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute* 71: 1–370.
- Bolton B (2013) An online catalog of ants of the world. <http://www.antcat.org/> [accessed June 14, 2013]
- Brady SG, Gadau J, Ward PS (2000) Systematics of the ant genus *Camponotus* (Hymenoptera: Formicidae): A preliminary analysis using data from the mitochondrial gene cytochrome oxidase I. In: Austin AD, Dowton M (Eds) *Hymenoptera. Evolution, biodiversity and biological control*. CSIRO Publishing, Collingwood, Victoria, 131–139.
- Brady SG, Schultz TR, Fisher BL, Ward PS (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the USA* 103: 18172131–13918177. doi: 10.1073/pnas.0605858103
- Brandão CRF (1991) Adendos ao catálogo abreviado das formigas da região Neotropical. *Revista Brasileira de Entomologia* 35: 319–412.
- Brown WL Jr (1973) A comparison of the Hylean and Congo-West African rain forest ant faunas. In: Meggers BJ, Ayensu ES, Duckworth WD (Eds) *Tropical forest ecosystems in Africa and South America: a comparative review*, 161–185.

- Creighton WS (1950) The ants of North America. Bulletin of the Museum of Comparative Zoology at Harvard College 104: 1–585.
- Dejean A, Fisher BL, Corbara B, Rarevohitra R, Randrianaivo R, Rajemison B, Leponce M (2010) Spatial distribution of dominant arboreal ants in a Malagasy coastal rainforest: Gaps and presence of an invasive species. PLoS ONE 5(2): e9319. doi: 10.1371/journal.pone.0009319
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Mass., xii + 732 pp.
- Kempf WW (1972) Catálogo abreviado das formigas da Região Neotropical. Studia Entomologica (N.S.) 15: 3–344.
- Kugler C (1994) A revision of the ant genus *Rogeria* with description of the sting apparatus (Hymenoptera: Formicidae). Journal of Hymenoptera Research 3: 17–89.
- Johnson RN, Agapou PM, Crozier RH (2003) A tree island approach to inferring phylogeny in the ant subfamily Formicinae, with special references to the evolution of weaving. Molecular Phylogenetics and Evolution 29: 317–330. doi: 10.1016/S1055-7903(03)00114-3
- Magrini MJ, Freitas AVL, Uehara-Prado M (2011) The effects of four types of anthropogenic disturbances on composition and abundance of terrestrial isopods (Isopoda: Oniscidea). Zoologia 28(1): 63–71. doi: 10.1590/S1984-46702011000100010
- Mayr G (1868) Formicidae novae Americanae collectae a Prof. P. de Strobel. Annuario della Società dei Naturalisti e Matematici, Modena 3: 161–178.
- Mayr G (1887) Südamerikanische Formiciden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 37: 511–632.
- Molet M, Wheeler DE, Peeters C (2012) Evolution of novel mosaic castes in ants modularity, phenotypic plasticity, and colonial buffering. The American Naturalist Vol. 180, No 3: 328–341. doi: 10.1086/667368
- Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE (2006) Phylogeny of the ants: diversification in the age of angiosperms. Science 312: 101–104. doi: 10.1126/science.1124891
- Quirán EM, Martínez JJ, Bachmann AO (2004) The Neotropical genus *Brachymyrmex* Mayr, 1868 (Hymenoptera: Formicidae) in Argentina. Redescription of the type species, *B. patagonicus* Mayr, 1868; *B. bruchi* Forel, 1912 and *B. oculatus* Santschi, 1919. Acta Zoológica Mexicana (n.s.) 20: 273–285.
- Santschi F (1917) Description de quelques nouvelles fourmis de la République Argentine. Anales de la Sociedad Científica Argentina 84: 277–283.
- Santschi F (1923) Revue des fourmis du genre *Brachymyrmex* Mayr. Anales del Museo Nacional de Historia Natural de Buenos Aires 31: 650–678.
- Santschi F (1929) Nouvelles fourmis de la République Argentine et du Brésil. Anales de la Sociedad Científica Argentina 107: 273–316.
- Shattuck SO (1992) Higher classification of the ant subfamilies Aneuretinae, Dolichoderinae and Formicinae. Systematic Entomology 17: 199–206. doi: 10.1111/j.1365-3113.1992.tb00332.x
- Ward PS (1997) Ant soldiers are not modified queens. Nature (London) 385: 494–495. doi: 10.1038/385494b0

- Ward PS (1989) Systematic studies on pseudomyrmecine ants: revision of the *Pseudomyrmex oculatus* and *P. subtilissimus* species groups, with taxonomic comments on other species. *Quaestiones Entomologicae* 25: 393–468.
- Wheeler DE (1991) The developmental basis of worker caste polymorphism in ants. *American Naturalist* 138: 1218–1238. doi: 10.1086/285279
- Wilson EO (1953) The origin and evolution of polymorphism in ants. *Quarterly Review of Biology* 28: 136–156. doi: 10.1086/399512

A new species of the *Rhinella margaritifera* species group (Anura, Bufonidae) from the montane forest of the Selva Central, Peru

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| <http://zoobank.org/097B7A2C-77FB-4BD2-8B14-819F2931F55E>

¶ <http://zoobank.org/BF30E84D-46C5-45EE-9140-E7E2154D9A66>

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Abstract

We describe a new species of the bufonid toad genus *Rhinella* from transition montane forest of the buffer zones of the Yanachaga-Chemillén National Park and the Pui Pui Protected Forest (eastern slopes of Andes, Selva Central, Peru). The new species belongs to the *Rhinella margaritifera* species group (confirmed by mtDNA data) and differs from all its members by the absence of tympanic membrane and tympanic annulus. It is characterized by medium size (SVL 57.5–65.5 mm, n = 5), moderately developed cranial crests, absence of neural crest of vertebrae, absence of bone protrusion at angle of jaw, presence of lateral rows of enlarged tubercles, and absence of subgular vocal sac and vocal slits in males. In addition, based on the molecular phylogenetic analyses of selected *Rhinella* species we propose the monophylum containing *R. chavin*, *R. festae*, *R. macrorrhina*, *R. manu*, *R. nesiotes*, *R. rostrata*, and *R. yanachaga* as a new species group under the name *Rhinella festae* species group.

Resumen

Se describe una nueva especie de sapo Bufonidae del género *Rhinella* presente en los bosques montanos transicionales de la zona de amortiguamiento del Parque Nacional Yanachaga Chemillén y el Bosque de Protección Pui Pui (Vertiente Oriental de los Andes, Selva Central, Perú). La nueva especie pertenece al grupo de especies *Rhinella margaritifera* (confirmado con datos de DNAm) y difiere de todos sus miembros por la ausencia de membrana timpánica y anillo timpánico. Se caracteriza por su tamaño mediano (SVL 57.5–65.5 mm), crestas craneales moderadamente desarrolladas, ausencia de una cresta neural, ausencia de protuberancia ósea en el ángulo mandibular, presencia de filas laterales de tubérculos agrandados, y ausencia de saco vocal subgular y hendiduras vocales en los machos. Además, basado en los análisis filogenéticos moleculares de especies seleccionadas de *Rhinella* se propone la monofilia que contiene a *R. chavin*, *R. festae*, *R. macrorhina*, *R. manu*, *R. nesiotes*, *R. rostrata* y *R. yanachaga* como un nuevo grupo de especies bajo el nombre de grupo de especies *Rhinella festae*.

Keywords

Amphibia, *Rhinella yunga*, new species, *Rhinella festae*, new species group, Andes

Palabras claves

Amphibia, *Rhinella yunga*, especie nueva, *Rhinella festae*, nuevo grupo de especies, Andes

Introduction

Neotropical toads of the *Rhinella margaritifera* species group (formerly *Bufo margaritifera* or *Bufo typhonius* species group/complex) are represented by several members of anuran communities inhabiting floor of tropical humid rainforest of South America. These medium-sized (SVL ca. 31–81 mm; e.g., Hoogmoed 1986, Caldwell 1991) ground dwelling toads show obvious adaptations to the life on leaf litter of primary and secondary forests. Their cryptic coloration resembles dark partly decomposed fallen leaves (“dead-leaf pattern”). Effect of this coloration is multiplied by body outline disruptive function of elevated and laterally widely expanded cranial crests, bone protrusions at angle of jaws and neural crests of vertebrae of some species (often sexually dimorphic), which also serve as direct antipredator mechanism. Similar overall external body constitution and typical “dead-leaf” color pattern on one side and substantial intra- and interpopulational variation in the individual morphological characteristics on the other has shown a limited value of external morphology for proper understanding of taxonomy within the *R. margaritifera* species group. Therefore, unusually high cryptic species diversity has been expected within this species group. Reliability of this premise has been confirmed by modern studies based on non-morphological research methods (see Fouquet et al. 2007a).

Currently, 16 species of the *Rhinella margaritifera* species group are recognized (Frost 2013, Lavilla et al. 2013): *R. acutirostris* (Spix, 1824); *R. alata* (Thomiot, 1884); *R. castaneotica* (Caldwell, 1991); *R. dapsilis* (Myers & Carvalho, 1945); *R. hoogmoedi* Caramaschi & Pombal, 2006; *R. lescurei* Fouquet, Gaucher, Blanc & Velez-Rodriguez, 2007; *R. magnussoni* Lima, Menin & Araújo, 2007; *R. margaritifera* (Laurenti, 1768);

R. martyi Fouquet, Gaucher, Blanc & Velez-Rodriguez, 2007; *R. ocellata* (Günther, 1858), *R. paraguayensis* Ávila, Pansonato & Strüssmann, 2010; *R. proboscidea* (Spix, 1824), *R. roqueana* (Melin, 1841); *R. sclerocephala* (Mijares-Urrutia & Arends-R, 2001); *R. scitula* (Caramaschi & Niemeyer, 2003); and *Rhinella stanlaidi* (Lötters & Köhler, 2000). Out of these 16 species, six occur in western part of Amazonia (*R. acutirostris*, *R. castaneotica*, *R. dapsilis*, *R. margaritifera*, *R. proboscidea*, and *R. roqueana*) and only one species (*R. stanlaidi*) is reported from the humid montane rainforest of the Amazonian versant of the Andes in central Bolivia (elevation range 1600–2000 m a.s.l.; Lötters and Köhler 2000).

During herpetological surveys in the Yanachaga-Chemillén National Park (Cordillera Yanachaga; see Lehr et al. 2012) and Pui Pui Protected Forest (Bosque de Protección Pui Pui) in central Peru, we discovered an apparently unnamed species of *Rhinella margaritifera* species group living in montane forest in the buffer zones of both protected areas. This contribution is aimed to its formal description.

Materials and methods

Morphological characters

Collected specimens were fixed in 96% ethanol and stored in 70% ethanol. Measurements are given in millimetres (mm) and were taken by the senior author to the nearest 0.1 mm using a dissecting microscope and electronic digital callipers. Notes on color in life were taken from field notes and color photographs. Webbing formula follows the standards of Myers and Duellman (1982), whereas all other terminology is that of Duellman (1970) and Duellman and Lehr (2009). Format of the description follows the standards of Duellman and Mendelson (1995) and Köhler and Lötters (1999). Measurement abbreviations used throughout the text are: SVL, snout–vent length; TL, tibia length; FL, foot length (distance from proximal margin of inner metatarsal tubercle to tip of Toe IV); HL, head length (from angle of jaw to tip of snout); HW, head width (at level of angle of jaw); ED, horizontal eye diameter; IOD, interorbital distance; EW, upper eyelid width; IND, internarial distance; E–N, eye–nostril distance (straight line distance between anterior corner of orbit and posterior margin of external nares). Fingers and toes are numbered preaxially to postaxially from I–IV respectively I–V. We determined comparative lengths of Toes III and V by adpressing both toes against Toe IV; lengths of Fingers I and II were determined by adpressing the fingers against each other. Condition of the tympanum was assessed by visual examination under microscope. Specimens were sexed externally based on the presence or absence of nuptial pads and internally based on the type of gonads. Photographs taken in the field by JM were used for descriptions of color in life. As locality traits we used GPS coordinates collected in the field based on WGS84 datum. Specimens were deposited in the herpetological collections of the Field Museum, Chicago (FNHM), Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM) in Lima,

Peru, and the National Museum Prague, Czech Republic (NMP). The referred material is registered in the Illinois Wesleyan University, Bloomington, USA (IWU). For specimens examined, see Appendix.

Molecular phylogenetic analysis

Species selection: We included three specimens of the putative new species from the *Rhinella margaritifera* species group from the montane forests of the Cordillera Yanachaga (Selva Central, Peru) and, for comparison, several specimens from the same species group from different lowland localities in the Peruvian and Bolivian Amazonia tentatively identified as *R. cf. margaritifera* and *R. cf. castaneotica*. We also tested distinctiveness and phylogenetic position of sympatric *R. yanachaga* Lehr, Pramuk, Hedges & Córdova, 2007 and *R. cf. leptoscelis* (Boulenger, 1912) collected in the same area of the Cordillera Yanachaga, both from the *R. veraguensis* species group (Lehr et al. 2007, Padial et al. 2009), i.e., a presumed closely-related outgroup (cf. Pramuk 2006). As a definite outgroup we employed a sample of *R. poeppigii* (Tschudi, 1845) from a distant species group of the *R. marina* species group (Pramuk 2006; Maciel et al. 2010). Our dataset was further supplemented by sequences from GenBank to include representatives of all earlier published genetic lineages of the *R. margaritifera* species group (Pramuk 2006; Fouquet et al. 2007a, 2012a, b; Jansen et al. 2011). In addition, some other closely related species outside the *R. margaritifera* species group were also included following phylogenies from Pramuk (2006), Chaparro et al. (2007), Van Bocxlaer et al. (2010), and Pyron and Wiens (2011) [*R. amboroensis* (Harvey & Smith, 1993), *R. chavin* (Lehr, Köhler, Aguilar & Ponce, 2001), *R. nesiotes* (Duellman & Toft, 1979), and *R. veraguensis* (Schmidt, 1857), all presumably from the *R. veraguensis* species group (cf. Padial et al. 2006; Pramuk 2006), and *R. festae* (Peracca, 1904) sequences from GenBank (Frost et al. 2006; Pramuk 2006)]. The resulting dataset was composed of 43 samples with 32 samples from the *R. margaritifera* species group.

Laboratory procedure: The genomic DNA was extracted from tissues stored in 96% ethanol. The mitochondrial 16S rRNA gene, which is widely used in the amphibian DNA barcoding (e.g., Vences et al. 2012), was targeted using the primers 16SL1 and 16SH1 adapted or directly taken from Palumbi et al. (1991). For more details, PCR conditions and sequencing see Moravec et al. (2009). The gained sequences have been deposited in GenBank (KF992143–KF992154).

Computational analysis: Maximum likelihood (ML) and Bayesian inference (BI) approaches were applied to construct phylogenetic trees to infer evolutionary positions of our samples in the context of published phylogenies of closely related groups of South American toads (cf. Pramuk 2006; Fouquet et al. 2007a). The DNA multiple sequence alignment was carried out in MAFFT v7.1 (Katoh and Standley 2013) producing a 415 bp-long alignment. Ambiguously aligned positions were eliminated by Gblocks v0.91b under options for a less stringent selection (Castresana 2000)

producing a final alignment of 400 bp. The software jModelTest v2.1.4 (Darriba et al. 2012) using the PhyML algorithm (Guindon and Gascuel 2003) was used to find the best-fitting model of nucleotide evolution, which was under the Akaike information criterion the GTR+I+G model. The ML analysis was performed in PhyML v3.0 (Guindon et al. 2010) using the best option of a combination of the nearest neighbour interchange and the subtree pruning and regrafting algorithm of tree improvement, and with optimization of the topology and branch lengths. The branch support was assessed by 1000 bootstrap pseudoreplicates. The BI analysis was run in MrBayes v3.2.2 (Ronquist et al. 2012) with two runs and four chains in each run for 6×10^6 generations, sampling every 100th generation. Appropriate sampling was justified by examining the stationarity of log-likelihood scores against the generation time using Tracer v1.5 (Rambaut and Drummond 2009; all parameters had effective sample size > 200), and convergence between the two simultaneous runs was confirmed by the convergence diagnostics of the average standard deviation of split frequencies and the potential scale reduction factor values. From the sampled trees, 25% were discarded as a burn-in and a 50% majority-rule consensus tree was produced from the remaining post burn-in trees. The posterior probabilities (pp) were calculated as the frequency of samples recovering any particular clade. Clades supported with pp values ≥ 0.95 and ML bootstrap values $\geq 70\%$ were considered highly supported (Huelsenbeck and Rannala 2004). Genetic uncorrected p -distances were calculated in PAUP* (Swofford 2003).

Results

Phylogenetic analysis and systematics

The observed morphological differences of the *Rhinella margaritifera* species group specimens from the buffer zone of the Yanachaga-Chemillén National Park were supported by results of the molecular phylogenetic analyses. Both phylogenetic methodological approaches (ML and BI) resulted in essentially same trees (BI tree in Fig. 1). Their common character is a clear division into three well-supported main clades beside the outgroup lineage of the *R. marina* species group (*R. cf. poeppigii*). The three species of toads collected in the Cordillera Yanachaga mountains are represented in all three main clades. *Rhinella cf. leptoscelis* forms a clade with *R. veraguensis* and *R. amboroensis* (Bayesian pp 1.00/ML bootstrap 98), i.e., the *R. veraguensis* clade. The recently described *R. yanachaga* shows up as a sister species of *R. chavin* and both are members of a well-supported clade (1.00/98) together with *R. festae* and *R. nesiotes* outside the *R. veraguensis* clade. The third species from the Cordillera Yanachaga, the putative new species, is positioned with a high support in the *R. margaritifera* group (1.00/95). This species appears as an independent lineage sister to all other studied (lowland) members of the species group. However, there was low statistical support for this topology similarly like general low supports for

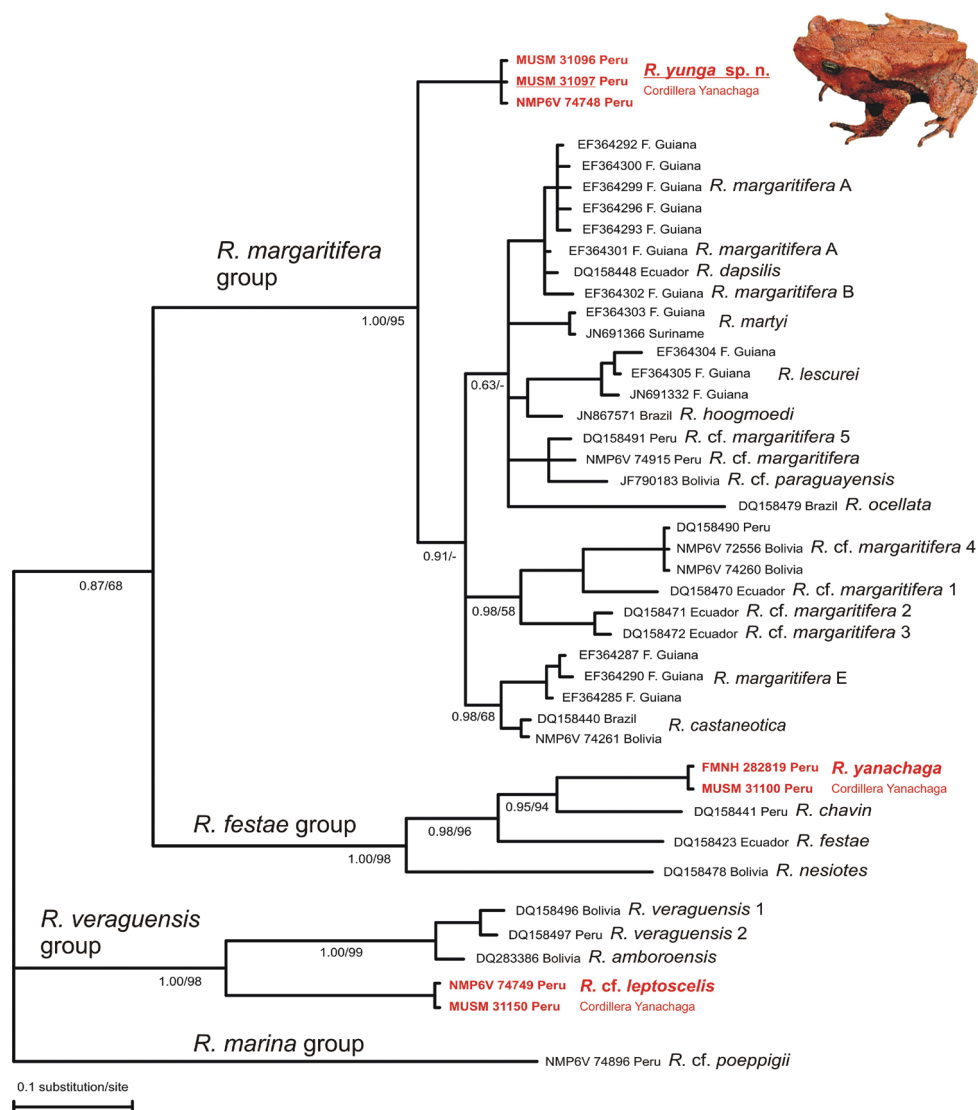


Figure 1. The Bayesian phylogeny of South American *Rhinella* toads with a focus on the *R. margaritifera* group and closely related species. Numbers below the branches correspond to the Bayesian posterior probabilities and ML bootstrap values. Nodes were collapsed if appeared in less than 50% of the post burn-in tree samples. In red the three toad species collected in the Cordillera Yanachaga mountains, Selva Central, Peru, representing members of three different species groups.

the branching inside the group keeping the phylogenetic arrangement within the *R. margaritifera* species group an open question. Genetic distances (16S) of the species of the *R. margaritifera* group from the Cordillera Yanachaga from the other taxa of the group were 3.3% (*R. castaneotica*) – 6.0% (*R. cf. margaritifera* 1) with the average distance 4.9%.

***Rhinella yunga* sp. n.**

<http://zoobank.org/36EB4C22-3BCB-4371-90AA-8F5CE2E6B571>

http://species-id.net/wiki/Rhinella_yunga

Holotype (Figs 2–4). MUSM 31097 (GenBank *16S rRNA*: KF992151), adult male, collected at Quebrada San Alberto (ca. 10°34'S, 75°23'W) at 1950 m a.s.l., in the buffer zone of the Yanachaga-Chemillén National Park (Sector San Alberto), Distrito de Oxapampa, Provincia de Oxapampa, Región Pasco, Peru, on 15 January 2012 at 18:40h by Edgar Lehr, Jiří Moravec, and Juan Carlos Cusi.

Paratypes. MUSM 31096, NMP6V 74748 (GenBank *16S rRNA*: KF992150, KF992152), two adult males, collected with the holotype; MUSM 31148 (Fig. 5), an adult female, same locality as holotype, collected on 3 February 2012 at 18:25h by Edgar Lehr, Jiří Moravec, and Juan Carlos Cusi.

Referred specimens. NMP6F 28 (photovoucher), adult male (Fig. 6A), observed on the left bank of the Rio Huancabamba, ca. 5 km W of Oxapampa (10°36'S, 75°30'W) at ca. 1885 m a.s.l. on 5 February 2012 by Edgar Lehr, Jiří Moravec, and Juan Carlos Cusi; IWU 236, an adult female (Fig. 6B), collected in the area of Rio Huatziroki (ca. 11°07'04.2"S, 75°12'05.6"W) at 2075 m a.s.l., in the buffer zone of the Protected Forest Pui Pui, Provincia Chanchamayo, Región Junín, Peru, on 13 June 2013 by Rudolf von May and Juan Carlos Cusi; IWU 235 and IWU 273, subadult specimens, collected in the area of Rio Huatziroki (ca. 11°07'04.2"S, 75°12'05.6"W, and 11°07'40.6"S, 75°11'15.7"W), at 1915 and 2230 m a.s.l., in the buffer zone of the Protected Forest Pui Pui, Provincia Chanchamayo, Región Junín, Peru, on 13 and 16 June 2013 by Edgar Lehr, Jiří Moravec, Rudolf von May, and Juan Carlos Cusi.

Diagnosis. A medium-sized species of the *Rhinella margaritifera* species group characterized by the presence of cephalic crests, distinct parotoid glands, lateral row of tubercles, dorsal “dead-leaf” pattern, and mtDNA data (see Ávila et al. 2010 and Fig. 1). The new species can be distinguished by the following combination of characters: (1) medium size SVL 57.5–59.5 mm in males ($n = 3$), 53.5–65.5 mm in females ($n = 2$); (2) snout slightly pointed in dorsal view, protruding beyond the margin of lip, rounded above and curved posteroventrally in profile; (3) nostrils protuberant, directed dorsolaterally, anterior part exceeding anterior margin of lower jaw; (4) canthal, supraorbital and supratympanic crests continuous, slightly elevated in males, distinctly elevated in female; supratympanic crest moderately expanded dorsolaterally in female; (5) tympanic membrane and tympanic annulus absent; (6) bone protrusion at angle of jaw absent; (7) neural crest of vertebrae absent; (8) parotoid glands elongate, elliptical to subtriangular, slightly protruding laterally, incorporated into lateral row of tubercles; (9) lateral row of tubercles present; tubercles rounded to subconical in males, conical in female; (10) skin on dorsum smooth with scattered flat tubercles in male, tubercles conical in female; (11) skin on dorsal surfaces of limbs smooth with scattered low tubercles in males, spinulose in female; (12) first finger slightly longer than the second in males, both fingers equal in length in single female; (13) palmar tubercle large, ovoid, two to four times size of subtri-



Figure 2. Holotype of *Rhinella yunga* sp. n. (MUSM 31097) in life, **(A)** laterodorsal, and **(B)** ventral views. Photographs by J. Moravec.

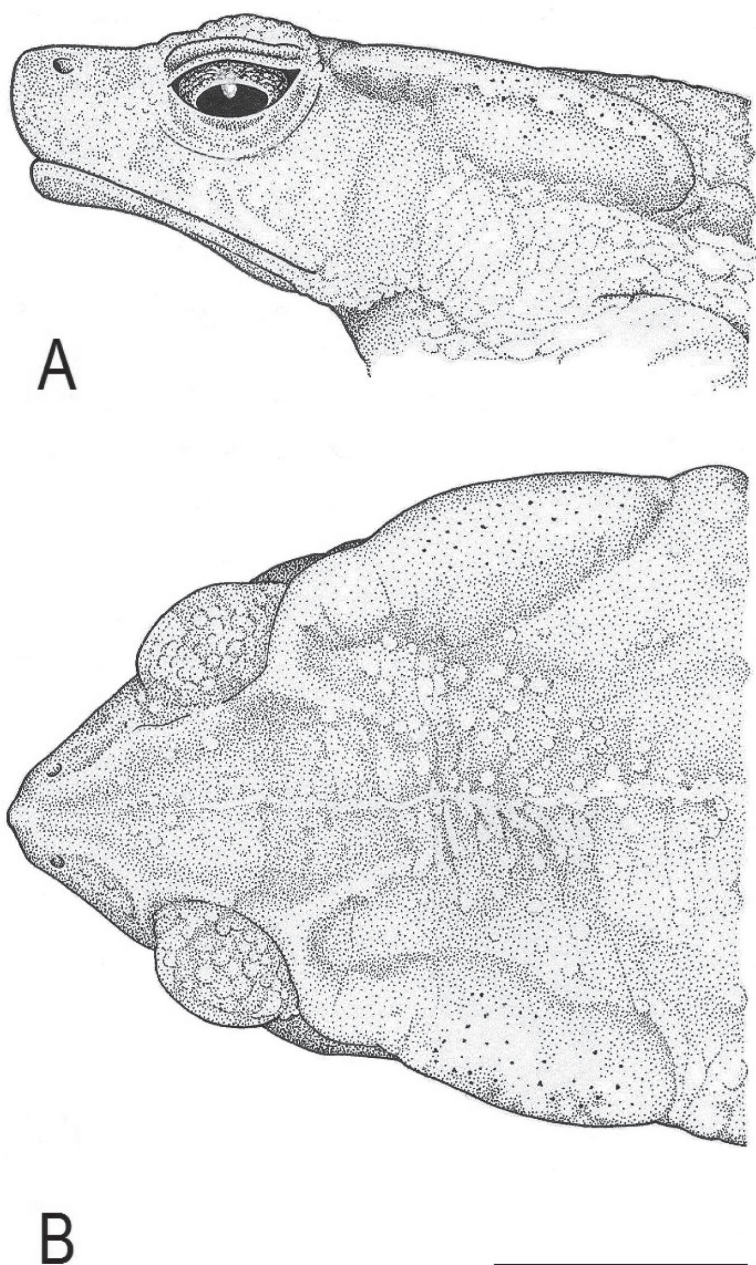


Figure 3. Holotype of *Rhinella yunga* sp. n. (MUSM 31097), (A) lateral, and (B) dorsal views of head. Scale bar equals 10 mm. Drawings by J. Moravec.



Figure 4. Holotype of *Rhinella yunga* sp. n. (MUSM 31097), (A) palmar, and (B) plantar views of right hand and foot. Scale bar equals 5 mm. Drawings by J. Moravec.

angular thenar tubercle; (14) inner metatarsal tubercle ovoid, protruding distally, ca. two times size of outer rounded to ovoid subconical metatarsal tubercle; (15) modal webbing on foot: I $0^{1/4}$ – $0^{1/4}$ II $0^{1/4}$ –2– III 1– 3 IV 3– $0^{1/4}$ V in males and I 1–2 II $0^{1/3}$ – $2^{1/2}$ III 1– $3^{1/4}$ IV $3^{1/4}$ –1– V in the single female; (16) subarticular tubercles prominent, round to oval; supernumerary tubercles round, one half to same size of former; (17) subgular vocal sac and vocal slits absent, and nuptial excrescences

present in males; (18) dorsum light yellowish tan to reddish-brown, with irregular brown, dark brown or back markings; whitish or pale yellow middorsal stripe present; venter light orange-tan with irregular dark brown spots, iris silvery greenish with irregular black mottling.

Comparisons. Morphologically, *R. yunga* differs from all members of the *Rhinella margaritifera* species group by the absence of tympanum. From the currently recognized species of the *R. margaritifera* species group occurring in the area of the eastern slopes of the Andes and lowland Western Amazonia, the new species can also be distinguished by following combinations of characters: from *R. acutirostris* by larger size, absence of bone protrusion at angle of jaw and by coloration (*R. acutirostris*: SVL up to 47 mm in males [35.3 mm in adult male holotype] and 57 mm in females, weak bone protrusion at angle of jaw, belly cream in holotype; Spix 1824, Hoogmoed 1986, Lötters and Köhler 2000); from *R. castaneotica* by larger size, presence of lateral rows of enlarged tubercles and absence of bone protrusion at angle of jaw (*R. castaneotica*: SVL 30.9–36.8 mm in males, 33.8–42.6 mm in females, lateral rows of enlarged tubercles absent, weak bone protrusion at angle of jaw present; Caldwell 1991, Köhler and Lötters 1999, Ávila et al. 2010); from *R. dapsilis* by smaller size, absence of fleshy process in the snout, and tuberculate to spinulose skin (*R. dapsilis*: SVL 77 mm in female holotype, snout developed in a fleshy proboscis, skin smooth; Myers and Carvalho 1945, Rodrigues and Duellman 1994, Fouquet et al. 2007b); from *R. margaritifera* by less developed cranial crests, absence of neural crest of vertebrae, and absence of bone protrusion at angle of jaw (*R. margaritifera*: supraorbital and supratympanic crests hypertrophied, bone protrusion at angle of jaw and vertebral apophyses present; Hoogmoed 1986, Fouquet et al. 2007b, Ávila et al. 2010, type specimen ZISP 257.1 in Milto and Barabanov 2011: fig. 17, Lavilla et al. 2013); from *R. proboscidea* by less prominent and less pointed snout, distinct parotid glands, tuberculate to spinulose skin, and presence of lateral row of tubercles (*R. proboscidea*: snout distinctly prominent and pointed, parotid glands indistinct, smooth skin, lateral row of tubercles absent; Spix 1824, Hoogmoed 1986); from *R. roqueana* by smaller size, less expanded supratympanic crest, absence of bone protrusion at angle of jaw, absence of neural crest of vertebrae, and presence of lateral row of tubercles (*R. roqueana*: SVL up to 72 mm in males and 81 mm in females, supratympanic crest large, bone protrusion at angle of jaw well developed, crest of vertebrae present, lateral row of tubercles absent; Hoogmoed 1986); from *R. stanlarii* by larger size, absence of bone protrusion at angle of jaw, and by coloration (*R. stanlarii*: SVL 39.1–54.1 mm in males and 57.2–59.4 mm in females, well developed bone protrusion at angle of jaw, ventral colors brown and cream; Lötters and Köhler 2000).

Description of holotype. Adult male; body robust; SVL 59.5 mm; head wider than long; snout slightly pointed in dorsal view, protruding beyond the margin of lip, rounded above and curved posteroventrally in profile; nostrils protuberant, directed dorsolaterally, anterior part exceeding anterior margin of lower jaw; canthus rostralis concave in lateral view, rounded in profile; loreal region barely concave, horizontal eye diameter larger than distance between nostril and anterior corner of eye; tempo-



Figure 5. Female paratype of *Rhinella yunga* sp. n. (MUSM 31148) in alcohol, (A) lateral, and (B) dorsal views. Photographs by J. Moravec.



Figure 6. Referred specimens of *Rhinella yunga* sp. n., (A) adult male (NMP6F 28) in water, ca. 5 km W of Oxapampa, and (B) adult female (IWU 236) from the area of Rio Huatziroki. Photographs by J. Moravec.

ral region curved caudomedially; tympanic membrane and tympanic annulus absent; canthal, supraorbital, and supratympanic crests continuous; canthal crest low, barely distinct; supraorbital and supratympanic crests slightly elevated, supratympanic crest slightly expanded laterally, not exceeding markedly outer edge of upper eyelid; bone protrusion at angle of jaw absent; neural crest of vertebrae absent; parotoid glands well developed, elongate, subtriangular, slightly protruding laterally; lateral row of rounded to subconical tubercles from posterior margin of parotoid gland to groin (the first tubercle separated from the gland). Skin on dorsal and lateral surfaces smooth with scattered low to conical tubercles lacking keratinized tips; cranial crests and parotoid glands smooth; loreal and temporal areas smooth with sporadic inconspicuous flat tubercles; upper eyelids with prominent round tubercles; skin on throat and belly coarsely areolate to warty. Forelimb hypertrophied; relative length of fingers $II < IV < I < III$; palmar tubercle prominent, ovoid; thenar tubercle conspicuously prominent, subtriangular, about one third size of the palmar tubercle; subarticular tubercles large, prominent, distal subarticular tubercle under Finger III bifid; supernumerary tubercles numerous, about half size or less of subarticular tubercles; basal webbing between fingers; nuptial excrescences present on thenar tubercle, dorsal and lateral surfaces of Fingers I–II and inner lateral surface of finger III. Foot longer than tibia; relative length of toes $I < II < V < III < IV$; inner metatarsal tubercle ovoid, protruding distally; outer metatarsal tubercle ovoid, subconical, about half the size of inner metatarsal tubercle; subarticular tubercles prominent, round to oval; supernumerary tubercles round, about half to same size of subarticular tubercles; toes with moderate webbing, webbing formula $I \ 0^{1/4} - 0^{1/4} \ II \ 0^{1/4} - 2 \ III \ 1 - 3 \ IV \ 3 - 0^{1/4} \ V$; lateral fringes broad; tips of digits terminating in indistinct discs. Tongue elongate, attached to anterior part of mouth floor; choanae small, oval; vocal slits absent; subgular vocal sac absent.

Measurements of holotype provided in Table 1.

Coloration of holotype in alcohol. Dorsal surfaces of head, body, and limbs light grey with slightly darker irregular markings forming very inconspicuous “dead-leaf pattern” from between eyes to cloacal region; whitish grey middorsal stripe from snout to cloaca. Middle area of shank, tibia, and tarsus with obscure dark grey spots forming one transverse bar on flexed leg. Dark grey transverse bar on forearm. Ground color of lateral side of head and body light grey. Two inconspicuous oblique darker grey bars below eye, one darker grey bar in temporal area from posterior edge of eye to angle of jaw. Dorsal side of parotoid glands and lateral row of tubercles light grey, sharply contrasting with dark grey to black longitudinal stripe leading from posterior margin of orbit, along lateral side of parotoid gland and below the lateral row of tubercles. Throat, belly, and ventral surfaces of legs whitish with irregular dark grey spots.

Coloration of holotype in life. General pattern same as in alcohol. Ground color yellow tan dorsally, orange tan ventrally; larger scattered dorsal tubercles light orange.

Iris silvery greenish with irregular black mottling.

Variation. For variation in measurements see Table 1. The male paratypes are similar to the holotype in body form and coloration. An uncollected male observed ca. 5 km W of Oxapampa (Fig. 6A) differed in more contrast “dead leaf pattern”. The female

Table 1. Measurements (mm) of the holotype and the paratypes of *Rhinella yunga* sp. n. (see text for abbreviations).

Measurements	Holotype	Paratypes		
	MUSM 31097	MUSM 31096	NMP6V 74748	MUSM 31148
Sex	Male	Male	Male	Female
SVL	59.5	57.5	58.0	65.5
TL	22.9	23.0	23.8	23.4
FL	25.7	24.4	24.8	25.0
HL	17.9	17.3	17.4	19.9
HW	20.0	19.6	20.0	22.7
ED	6.2	6.1	6.1	6.0
IOD	7.1	6.9	6.7	7.7
EW	4.2	4.0	4.0	4.1
IND	2.8	2.9	2.9	3.5
E-N	4.2	4.0	3.9	4.0
PL	14.2	12.3	11.6	9.9
PW	5.7	5.9	5.9	6.0

paratype (Fig. 5) is larger than the holotype, is more tuberculate (larger tubercles possess keratinized tips), has distinctly elevated cranial crests with supratympanic crest moderately expanded dorsolaterally, and differs in less developed webbing (see Diagnosis). The overall dorsal coloration of the female paratype is darker and the dark spots on the throat and belly are denser than in the holotype. The morphological characters of the three referred specimens from the buffer zone of the Pui Pui Protected Forest correspond, in general, to those of the type series. The referred adult female (IWU 236; Fig. 6B) measured 53.5 mm in SVL and its coloration (in life) is intense reddish-brown.

Etymology. The specific name *yunga* is derived from the Quechua expression *yungas* meaning “warm valley”, which is widely used for an ecoregion of montane rainforests covering the eastern Andean slopes of Peru and Bolivia. The name is used as a noun in apposition and refers to the general habitat of the new species.

Distribution, ecology, and threat status. Besides from its type locality, *Rhinella yunga* is also known from the area on the left bank of the Rio Huancabamba (ca. 5 km W of Oxapampa, ca. 1885 m a.s.l.), from Quebrada Yanachaga valley at the settlement Prosoya (10°25.118'S, 75°31.126'W, ca. 1800 m. a.s.l.) and from the area of Rio Huatziroki (elevation 1915–2230 m a.s.l.) lying in the buffer zone of the Pui Pui Protected Forest ca. 60 km straight southeast of the type locality (see the referred material; Fig. 7). To date, *R. yunga* is known from an altitudinal range 1800–2230 m a.s.l., which represents a contact belt between the transitional montane forest (“Bosque de transición”, 1000–2000 m a.s.l.) and montane cloud forest (“Bosque de neblina”, 2000–3400 m a.s.l.; altitudinal zonation adopted from Milanovich et al. 2006). It is likely that *R. yunga* is distributed in a wider area of montane forests in the Peruvian regions Pasco and Junín (Selva Central).

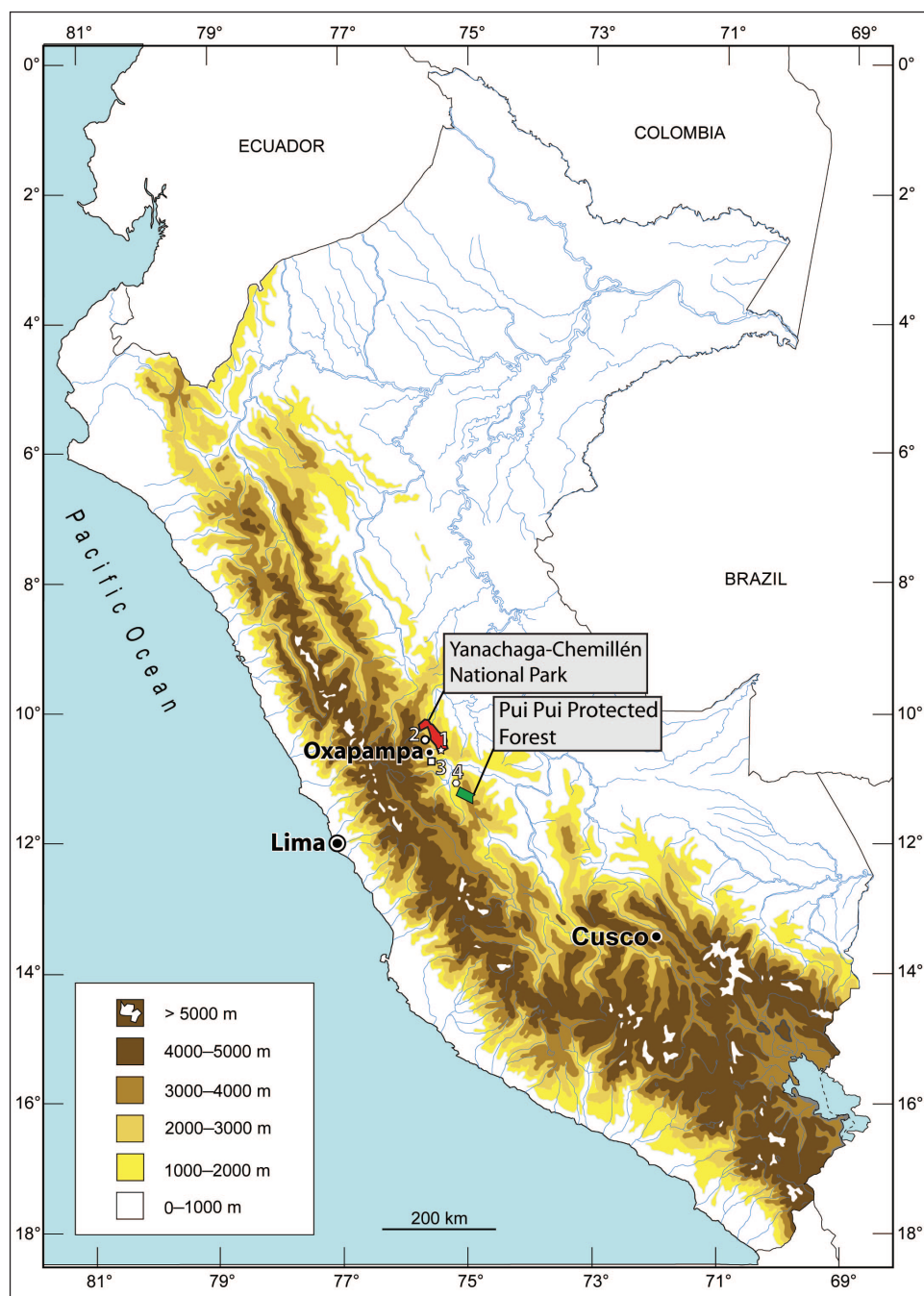


Figure 7. Schematic map of central and southern Peru showing known distribution of *Rhinella yunga* sp. n. **1** type locality **2** Quebrada Yanachaga valley at the settlement Prosoya (elevation ca. 1800 m. a.s.l.) **3** Rio Huancabamba (ca. 5 km W of Oxapampa, ca. 1885 m a.s.l.) **4** Rio Huatziroki (elevation 1915–2230 m a.s.l.) lying in the buffer zone of the Pui Pui Protected Forest ca. 60 km straight southeast of the type locality. Map by E. Lehr.



Figure 8. Habitat of *Rhinella yunga* sp. n., (A) a road margin at the type locality, and (B) closed cloud forest in the area of Rio Huatziroki (ca. 2200 m a.s.l.). Photographs by J. Moravec.

All collected and observed specimens were in breeding condition. The female paratype contained numerous small pigmented oviductal eggs. At the type locality, the males were sitting in shallow water of small temporal water bodies along a narrow unpaved road (Fig. 8A). The males entered the water in the late afternoon. The female paratype was collected on the ground in close vicinity of breeding puddles at night. In the vicinity of Huancabamba-Prosoya (Programa Social Yanachaga, former Hacienda Yanachaga) one adult male was observed (not collected) in a small artificial pond at night. The three referred specimens from the area of Rio Huatziroki were found in low dense forest covering a sharp montane ridge (Fig. 8B). Tadpole and call are unknown. Observed sympatric anurans include *Rhinella* cf. *leptoscelis* (MUSM 31150, NMP6V 74749), *Hypsiboas aguilari* Lehr, Faivovich & Jungfer, 2010 (MUSM 31147), *Pristimantis* cf. *bipunctatus* (Duellman & Hedges, 2005), and *Pristimantis* sp. We classify *Rhinella yunga* as “Data Deficient” according to the IUCN red list criteria and categories (IUCN Standards and Petitions Subcommittee 2013) based on the limited information on its geographic range.

Discussion

It appears that large number of still unnamed cryptic species remains hidden under some nominal species of the *Rhinella margaritifera* species group (e.g., Pramuk 2006; Fouquet et al. 2007a; Lavilla et al. 2013). The main reason of this fact is a limited use of traditional morphological methods for a proper delimitation of many of still undescribed taxa. Nevertheless, the newly recognized *R. yunga* is a rare exception. It differs from all members of the *R. margaritifera* species group by an absence of an external tympanum. Lack of tympanum in combination with other morphological features shows that *R. yunga* is a separate, morphologically well-defined species. In addition, this finding is supported also by genetic data. Despite the very preliminary character of the obtained phylogeny of the selected species of the genus *Rhinella*, it is evident that *R. yunga* represents a separate lineage within the radiation of the *R. margaritifera* species group (Fig. 1). Its current position in the phylogenetic tree seems to be sister to all other studied members of the species group (lowland), suggesting a possible basal split between the montane Andean and lowland Amazonian taxa. However, the statistical support for this scenario is presently rather low and a further testing with more complete taxon sampling is necessary. *Rhinella yunga* is distributed in the area of montane forest at the western limit of the range of the *R. margaritifera* species group, where it occurs syntopically with morphologically and genetically clearly divergent members of the *R. veraguensis* species group (*R.* cf. *leptoscelis*; Fig. 1). The recently described *R. yanachaga* was expected to be a part of the *R. veraguensis* group (Lehr et al. 2007), however this species shows up in a well-supported clade outside the *R. veraguensis* clade (Fig. 1). A similar topology of such an outside clade has been already shown in former studies (however without *R. yanachaga*; Pramuk 2006; Chaparro et al. 2007; Van Bocxlaer et al. 2010; Pyron and Wiens 2011). Therefore, based on this phylogenetic arrangement, which makes the *R. veraguensis* species group (sensu Pramuk 2006; Padial et al. 2006) paraphyletic, we propose the clade containing *R. yanachaga*

as a new species group under the name *Rhinella festae* species group. According to the currently available data (Pramuk 2006; Chaparro et al. 2007; Van Bocxlaer et al. 2010; Pyron and Wiens 2011), the *R. festae* species group contains the following species: *R. chavin*, *R. festae*, *R. macrorhina* (Trueb, 1971), *R. manu* Chaparro, Pramuk & Gluesenkamp, 2007, *R. nesiotes*, *R. rostrata* (Noble, 1920), and *R. yanachaga*.

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References

- Ávila RW, Pansonato A, Strüßmann C (2010) A new species of the *Rhinella margaritifera* group (Anura: Bufonidae) from Brazilian Pantanal. *Zootaxa* 2339: 57–68.
- Caldwell JP (1991) A new species of toad in the genus *Bufo* from Pará, Brazil, with an unusual breeding site. *Papéis Avulsos de Zoologia* 37: 389–400.
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540–552. doi: 10.1093/oxfordjournals.molbev.a026334
- Chaparro JC, Pramuk JB, Gluesenkamp AG (2007) A new species of arboreal *Rhinella* (Anura: Bufonidae) from cloud forest of southeastern Peru. *Herpetologica* 63: 203–212. doi: 10.1655/0018-0831(2007)63[203:ANSOAR]2.0.CO;2
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772. doi: 10.1038/nmeth.2109
- Duellman WE (1970) The hylid frogs of Middle America. *Monographs of the Museum of Natural History, The University of Kansas* 1: 1–753.
- Duellman WE (2005) *Cuzco Amazónico. The lives of amphibians and reptiles in an Amazonian rainforest*. Comstock Publishing Associates, Cornell University Press, Ithaca, London, 433 pp.

- Duellman WE, Lehr E (2009) Terrestrial-breeding frogs (Strabomantidae) in Peru. Natur- und Tier-Verlag, Naturwissenschaft, Münster, 382 pp.
- Duellman WE, Mendelson JR (1995) Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. University Kansas Science Bulletin 55: 329–376.
- Fouquet A, Vences M, Salducci M-D, Meyer A, Marty C, Blanc M, Gilles A (2007a) Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups. Molecular Phylogenetics and Evolution 43: 567–582. doi: 10.1016/j.ympev.2006.12.006
- Fouquet A, Gaucher P, Blanc M, Velez-Rodriguez CM (2007b) Description of two new species of *Rhinella* (Anura: Bufonidae) from the lowlands of the Guiana Shield. Zootaxa 1663: 17–32.
- Fouquet A, Noonan BP, Rodrigues MT, Pech N, Gilles A, Gemmell NJ (2012a) Multiple Quaternary refugia in the eastern Guiana Shield revealed by comparative phylogeography of 12 frog species. Systematic Biology 61: 461–489. doi: 10.1093/sysbio/syr130
- Fouquet A, Recoder R, Teixeira M Jr., Cassimiro J, Amaro RC, Camacho A, Damasceno R, Carnaval AC, Moritz C, Rodrigues MT (2012b) Molecular phylogeny and morphometric analyses reveal deep divergence between Amazonia and Atlantic Forest species of *Dendrophryniscus*. Molecular Phylogenetics and Evolution 62: 826–838. doi: 10.1016/j.ympev.2011.11.023
- Frost DR (2013) Amphibian Species of the World: an Online Reference. Version 5.6 (9 January 2013). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA.
- Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto B, Moler P, Drewes RC, Nussbaum RA, Lynch J, Green DM, Wheeler WC (2006) The amphibian tree of life. Bulletin of the American Museum of Natural History 297: 1–370. doi: 10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2
- Guindon S, Gascuel O (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Systematic Biology 52: 696–704. doi: 10.1080/10635150390235520
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59: 307–321. doi: 10.1093/sysbio/syq010
- Hoogmoed M (1986) Biosystematic studies of the *Bufo „typhonius“* group. A preliminary progress report. In: Roček Z (Ed) Studies in Herpetology. Charles University, SEH, Prague, 147–150.
- Huelsenbeck JP, Rannala B (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biology 53: 904–913. doi: 10.1080/10635150490522629
- IUCN Standards and Petitions Subcommittee (2013) Guidelines for using the IUCN Red List categories and criteria. Version 10.1. Prepared by the Standards and Petitions Subcommittee. Downloadable from <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Jansen M, Bloch R, Schulze A, Pfenninger M (2011) Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. Zoologica Scripta 40: 567–583. doi: 10.1111/j.1463-6409.2011.00498.x

- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. doi: 10.1093/molbev/mst010
- Köhler J, Lötters S (1999) Annotated list of amphibian records from the Departamento Pando, Bolivia, with description of some advertisement calls. *Bonner zoologische Beiträge* 48: 259–273.
- Lavilla EO, Caramaschi U, Langone JA, Pombal JP Jr., de Sá RO (2013) The identity of *Rana margaritifera* Laurenti, 1768 (Anura, Bufonidae). *Zootaxa* 3646: 251–264. doi: 10.11646/zootaxa.3646.3.4
- Lehr E, Pramuk JB, Hedges SB, Córdova JH (2007) A new species of arboreal *Rhinella* (Anura: Bufonidae) from Yanachaga-Chemillén National Park in central Peru. *Zootaxa* 1662: 1–14.
- Lehr E, Moravec J, Cusi JC (2012) Two new species of *Phrynomys* (Anura, Strabomantidae) from high elevations in the Yanachaga-Chemillén National park in Peru (Departamento de Pasco). *ZooKeys* 235: 51–71. doi: 10.3897/zookeys.235.3885
- Lötters S, Köhler J (2000) A new toad of the *Bufo typhonius* complex from humid montane forests of Bolivia (Amphibia, Anura, Bufonidae). *Spixiana* 23: 293–303.
- Maciel NM, Collevatti RG, Colli GR, Schwartz EF (2010) Late Miocene diversification and phylogenetic relationships of the huge toads in the *Rhinella marina* (Linnaeus, 1758) species group (Anura: Bufonidae). *Molecular Phylogenetics and Evolution* 57: 787–797. doi: 10.1016/j.ympev.2010.08.025
- Moravec J, Aparicio J, Guerrero-Reinhard M, Calderón G, Jungfer K-H, Gvoždík V (2009) A new species of *Osteocephalus* (Anura: Hylidae) from Amazonian Bolivia: first evidence of tree frog breeding in fruit capsules of the Brazil nut tree. *Zootaxa* 2215: 37–54.
- Myers GS, Carvalho AL (1945) Notes on some new or little-known Brazilian amphibians, with an examination of the history of the Plata salamander *Ensatina platensis*. *Boletim do Museu Nacional* 35: 1–24.
- Milanovich JL, Rodríguez IZ, García L, Andaluz T, Verde M, Calderón N, Melgarejo K (2006) Plan Maestro 2005–2009, Parque Nacional Yanachaga Chemillén. INRENA, Corporación Gráfica Andina, Surco.
- Padial JM, Reichle S, McDiarmid RW, De la Riva I (2006) A new species of arboreal toad (Anura: Bufonidae: *Chaunus*) from Madidi National Park, Bolivia. *Zootaxa* 1278: 57–58.
- Padial JM, Chaparro JC, Köhler J, De la Riva I (2009) Rediscovery, resurrection and redescription of *Rhinella leptoscelis* (Boulenger, 1912) (Anura: Bufonidae). *Zootaxa* 2115: 56–64.
- Palumbi S, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR. Version 2. University of Hawaii, Honolulu, 47 pp.
- Pramuk JB (2006) Phylogeny of South American *Bufo* (Anura: Bufonidae) inferred from combined evidence. *Zoological Journal of the Linnean Society* 146: 407–452. doi: 10.1111/j.1096-3642.2006.00212.x
- Pyron RA, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of advanced frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61: 543–583. doi: 10.1016/j.ympev.2011.06.012
- Rambaut A, Drummond AJ (2009) Tracer. MCMC Trace Analysis Tool Version v1.5.0. <http://tree.bio.ed.ac.uk/software/tracer/>

- Rodríguez LO, Duellman WE (1994) Guide to the frogs of the Iquitos region, Amazonian Peru. University of Kansas Natural History Museum Special Publications 22: 1–80.
- Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. doi: 10.1093/sysbio/sys029
- Spix JB de (1824) *Animalia nova sive species novae Testudinum et Ranarum, quas in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis. Monachii*: 4 pp, 1–53, pls. 1–7, 1–22.
- Swofford DL (2003) PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland.
- Van Bocxlaer I, Loader SP, Roelants K, Biju SD, Menegon M, Bossuyt F (2010) Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. *Science* 327: 679–682. doi: 10.1126/science.1181707
- Vences M, Nagy ZT, Sonet G, Verheyen E (2012) DNA barcoding amphibians and reptiles. In: Kress WJ, Erickson DL (Eds) *DNA Barcodes: Methods and Protocols. Methods in Molecular Biology*, 79–107. doi: 10.1007/978-1-61779-591-6_5

Appendix

Specimens examined

- Rhinella castaneotica*: BOLIVIA: Pando, Federico Roman: Santa Crucito, ca. 150 m a.s.l.: NMP6V 74261 (GenBank *16S rRNA*: KF992144).
- Rhinella* cf. *margaritifera*: PERU: Ucayali: Pucallpa: 17.4 km S of Masisea, ca. 160 m a.s.l.: NMP6V 74915 (GenBank *16S rRNA*: KF992143).
- Rhinella* cf. *margaritifera*: BOLIVIA: Pando: Nicolas Suarez: Bioceanica, ca. 250 m a.s.l.: NMP6V 72556 (GenBank *16S rRNA*: KF992146).
- Rhinella* cf. *margaritifera*: BOLIVIA: Pando: Manuripi: San Antonio, ca. 270 m a.s.l.: NMP6V 74260 (GenBank *16S rRNA*: KF992145).
- Rhinella yanachaga*: PERU: Pasco: Oxapampa: Quebrada Yanachada, 2900 m a.s.l.: FNHM 282819 (GenBank *16S rRNA*: KF992148), MUSM 31100 (GenBank *16S rRNA*: KF992149).
- Rhinella* cf. *leptoscelis*: PERU: Pasco: Oxapampa: Quebrada San Alberto, 1950 m a.s.l., NMP6V 74749 (GenBank *16S rRNA*: KF992153).
- Rhinella* cf. *leptoscelis*: PERU: Pasco: Oxapampa: ca 5 km W Oxapampa, ca. 1885 m a.s.l., MUMS 31150 (GenBank *16S rRNA*: KF992154).
- Rhinella* cf. *poepigii*: PERU: Ucayali: Boquerón Padre Abad, ca. 415 m a.s.l.: NMP6V 74896 (GenBank *16S rRNA*: KF992147).

The “*Fungia patella* group” (Scleractinia, Fungiidae) revisited with a description of the mini mushroom coral *Cycloseris boschmai* sp. n.

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Abstract

The recent taxonomic history of extant free-living *Cycloseris* species is briefly reviewed, resulting in the description of *Cycloseris boschmai* sp. n. (Scleractinia, Fungiidae) and a discussion on the validity of two other recently described species. Some *Cycloseris* species were previously considered to belong to the *Fungia patella* group, which also concerned misidentified museum specimens that actually belong to the new species. Other specimens of *C. boschmai* sp. n. were photographed and collected in the course of 30 years of fieldwork. The new mushroom coral is compared with other free-living *Cycloseris* species by means of an identification key. With a maximum diameter of 50 mm, it is the smallest free-living mushroom coral discovered so far. It can also be distinguished by its large primary order costae and variable colouration. Its distribution range is limited to the Coral Triangle, where it can be observed as an uncommon species on lower reef slopes.

Keywords

Coral reef, free-living, fungiid, solitary, budding, collection, fieldwork, Coral Triangle, Indo-Pacific

Introduction

Mushroom corals (Scleractinia, Fungiidae) form a common element in the fauna of most Indo-Pacific coral reefs. Depending on the species, full-grown specimens are either attached or free-living, which are character states occurring in various evolutionary lineages and therefore do not necessarily reflect phylogenetic relationships among the Fungiidae (Cairns 1984, Hoeksema 1989, 1991b, 2009, Gittenberger et al. 2011, Benzoni et al. 2012). After settlement, each fungiid individual starts as a small attached coral (anthocaulus). While corals of attached species obtain a foliaceous or encrusting growth form (Hoeksema 1989, 1993a, 2009, Gittenberger et al. 2011, Benzoni et al. 2012), those of free-living species eventually become detached from their stalk, reaching the anthocyathus stage (Wells 1966, Hoeksema 1989, Hoeksema and Yeemin 2011, Hoeksema and Waheed 2012). Owing to their charismatic appearance, abundance and large polyp size, these free-living fungiids are usually easy to find. By growing large and occurring in high densities, they may form mono- or multi-species assemblages covering extensive reef areas (Littler et al. 1997, Hoeksema 2004, 2012a, Elahi 2008, Hoeksema and Koh 2009, Hoeksema and Gittenberger 2010, Hoeksema and Matthews 2011, Hoeksema and Benzoni 2013). They can live on various kinds of reef substrates, ranging from silt to solid rock, from nearshore to offshore and from shallow reef flats to deep reef bases (e.g., Hoeksema and Moka 1989, Hoeksema 1991a, Hoeksema 2012a, 2012b, Waheed and Hoeksema 2013, in press). Mushroom corals themselves may in turn act as habitat to associated faunas consisting of molluscs, crabs, shrimps, acoel flatworms, comb jellies, and fish, some of which are host-specific (Hoeksema and Kleemann 2002, Kleemann and Hoeksema 2002, Gittenberger and Gittenberger 2005, 2011, Hoeksema and Fransen 2011, Owada and Hoeksema 2011, Bos 2012, Hoeksema et al. 2012, 2013a, 2013b, Hoeksema and Farenzena 2012, Gittenberger and Hoeksema 2013, Van der Meij and Hoeksema 2013). The various mushroom coral species vary in size (Hoeksema 1989, 1991b, Gittenberger et al. 2011) and it is obvious that corals with large surface area and thick skeletons offer most habitat space for associated fauna in contrast to small species (Hoeksema et al. 2012).

The smallest species among free-living mushroom corals appear to be among the most difficult to identify because they show relatively few distinguishing characters and much ecophenotypic variation (Hoeksema and Moka 1989, Hoeksema 1993d). Döderlein (1901, 1902) classified them as the “*patella* group” within the genus *Fungia* Lamarck, 1801. He considered them to be the most “primitive” species owing to their small size, imperforate (solid) corallum wall, and rudimentary, hardly discernible costal spines and septal dentations (see Scholtz et al. 2012). The fossil record of this *F. patella* group could be traced back to the Cretaceous, while its distribution ranged from eastern Africa to the west coast of America and its maximum depth was known to be over 100 m (Döderlein 1901).

Previously, species of the *F. patella* group were considered to belong to the genera *Cycloseris* Milne Edwards & Haime, 1849, consisting of complete corals, and *Diaseris* Milne Edwards & Haime, 1849, representing radially fragmenting corals of the

same species (see Hoeksema 1989). Döderlein (1902) already considered complete and fragmenting corals to be different forms that can be found within each species. He recognized the following six species and synonyms: 1. *F. patella* Ellis & Solander, 1786 (including *F. patellaris* Lamarck, 1801, *F. tenuis* Dana, 1846, *F. hexagonalis* Milne Edwards & Haime, 1849, *Diaseris fragilis* Alcock, 1893); 2. *F. erosa* Döderlein, 1901; 3. *F. distorta* Michelin, 1842; 4. *F. cyclolites* Lamarck, 1816; 5. *F. elegans* Verrill, 1868; 6. *F. costulata* Ortmann, 1889. Some authors still consider *Diaseris* a separate genus (e.g. Veron 2000, Claereboudt 2006) while there is morphological evidence for their synonymy (Hoeksema 1989, Hoeksema and Waheed 2011, 2012).

Oddly, both *F. patella* and *F. patellaris* are junior synonyms of *F. fungites* (Linnaeus, 1756), the type species of *Fungia* (see Hoeksema 1989). However, Döderlein's (1902) photographs of his *F. patella* corals show that he referred to complete and fragmenting specimens of the free-living species *Cycloseris fragilis* (Alcock, 1893) and *C. sinensis* Milne Edwards & Haime, 1851 (see Hoeksema 1989). The outlines of Döderlein's (1902: pls. 1–2) smallest specimens are either circular or hexagonal.

Van der Horst (1921) mentioned six specimens of *Fungia patella* (*sensu* Döderlein), which he obtained from the Siboga Expedition collections: “The 3 *Cycloseris*-forms of Stat. 315 have both surfaces flat. Two of these specimens have the ribs obviously only at the edge of the corallum, the centrum of the under surface being irregularly covered by fine granulations. The septa of these two specimens are equal in height and very much grained. They have the appearance of *F. patella* var. *filigrana* Död. In the third specimen (dimensions 52 × 52 m.M.) the ribs reach the centrum, the scar of the attachment is here obvious. The edge of the corallum is slightly undulating.”

Boschma (1923a) had access to only the first two of these specimens and also to mushroom corals collected during the Danish Expedition to the Kei Islands in the Banda Sea, eastern Indonesia, and to other corals from Hawaii, among which were small specimens that according to him belonged to “Döderlein's, *patella*-group”. He recognized eight separate species besides *F. pattella* (*sensu* Döderlein 1902), which previously were considered synonyms: 1. *F. patelliformis* Boschma, 1923; 2. *F. fragilis* (Alcock, 1893); 3. *F. marginata* Boschma, 1923; 4. *F. distorta* (Michelin, 1842); 5. *Fungia* sp.; 6. another *Fungia* sp.; 7. *Stephanophyllia neglecta* Boschma, 1923; 8. *F. vaughani* Boschma, 1923. Several species were represented by complete and fragmenting shapes. Among the complete corals, several had a hexagonal outline, such as juvenile specimens of *F. tenuis* (Boschma 1923a: pl. 9), which actually belong to *F. hexagonalis* (see Boschma 1925, Hoeksema 1989). He had many specimens available to him that he identified as *F. marginata*; some of these were illustrated together with the original description (Boschma 1923a) and other ones in a subsequent publication (Boschma 1925). In the diagnosis of *F. marginata*, Boschma (1923a) refers to a circular corallum outline, although he also states that young stages are hexagonal in shape. According to him this species could be distinguished by its thick corallum margin, which might be true if compared with for instance his *Fungia patelliformis* (a synonym of *Cycloseris fragilis* (see Hoeksema 1989) but not with some other species, such as *C. costulata* (see Hoeksema 1989).

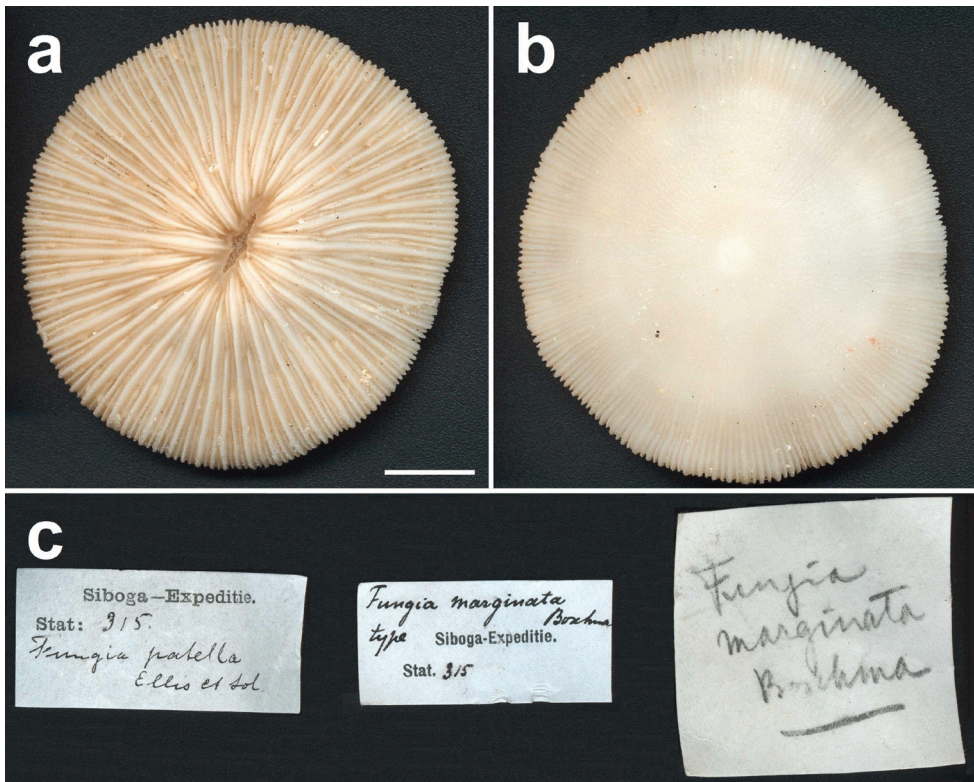


Figure 1. Lectotype of *Fungia marginata* Boschma, 1923 (ZMA Coel. 604, ethanol), which is a specimen of *Cycloseris costulata* Ortmann, 1889, collected at Siboga Expedition Sta. 315, Anchorage East of Sailus Besar, in the Paternoster islands, Indonesia. **a** Upper side **b** Lower side **c** Collection labels indicating the first identification by Van der Horst (*Fungia patella*) and the later one by Boschma (*Fungia marginata*). Scale bar: 0.5 cm.

The two specimens (ZMA Coel. collection) earlier described by Van der Horst (1921) as *F. patella* from Siboga Expedition Station 315 in the Paternoster Islands, Indonesia were considered syntypes (Van Soest 1979). One of these syntypes is a coral with a circular outline and a diameter of 48.5 mm (ZMA Coel. 604, herein designated lectotype; Figure 1), whereas the other is a smaller specimen with hexagonal outline, a diameter of 13 mm, and relatively thick primary costae (ZMA Coel. 723, herein designated paralectotype; Figure 2). Based on these two types, *F. marginata* is considered a junior synonym of *F. costulata* (Hoeksema 1989). Because of its doubtful identity, the juvenile specimen is not useful as type. Boschma (1923a) assumed that *F. costulata* does not have a solid corallum wall and has more or less equal costae and therefore described *F. marginata* as a species with a solid corallum wall, unequal costae, and thick corallum margin as distinguishing characters. Actually, the type of *F. costulata* does have a solid wall, whereas costae of all mushroom coral species may be dissimilar in size, including *F. costulata* (Hoeksema 1989, Gittenberger and Hoeksema 2006). Furthermore, the



Figure 2. Paralectotype of *Fungia marginata* Boschma, 1923 (ZMA Coel. 723, dry), which may be a juvenile specimen of *Cycloseris costulata* Ortmann, 1889 or *C. hexagonalis* Milne Edwards & Haime, 1849, collected at Siboga Expedition Sta. 315, Anchorage East of Sailus Besar, in the Paternoster islands, Indonesia **a** Specimen with collection box and labels; scale bar: 1 cm. Collection labels indicating the first identification by Van der Horst (*Fungia patella*) and the later one by Boschma (*Fungia marginata*) **b** Close-up upper side **c** Close-up lower side.

identity of *F. marginata* has never been really clear, because most subsequent authors confused it with other species (see Hoeksema 1989).

Boschma (1925) had access to many more *F. marginata* specimens according to the accompanying identification labels, but he did not mention them in the original species description. These specimens are still available in the collections of the Zoological Museum - University of Copenhagen (UZMK) and Naturalis Biodiversity Center (RMNH Coel.). Among these corals, several specimens are slightly larger than the syntypes and they actually do show enlarged lower order costae, although this was not clearly illustrated in his plates (Boschma 1925: pls. 5–6). These specimens are re-examined in the present study along with many small mushroom corals collected during various recent field surveys (1983–2013). The last ones were striking because of their outstanding long and thick costae and their colorful appearance in comparison with the usual brown hues found in individuals of related species (Hoeksema 1989, Gittenberger and Hoeksema 2006). Based on this unique set of characters consisting of a relatively small adult size, enlarged primary order costae and variable coloration, these corals are considered to belong to a new species, herein described as *Cycloseris boschmai* sp. n.

All species of the former *Fungia patella*-group belong to *Cycloseris*, previously considered a subgenus of *Fungia* (see Hoeksema 1989). As a consequence of recent molecular phylogenetic studies, so far 13 species have been recognized in the genus *Cycloseris*,

three of which are attached (Gittenberger et al. 2011, Benzoni et al. 2012) and not part of the old *F. patella*-group. The new species, here described as the free-living *Cycloseris boschmai* sp. n., is the fourteenth. Specimens were either available in museum collections or were photographed and sampled during SCUBA diving in the field. In addition to a detailed description, many illustrations are presented to show the phenotypic variation of this small *Cycloseris* species, following in the foot steps of Döderlein (1902) and Boschma (1923a, 1925). For the purpose of specimen identification, a key to the presently known free-living extant *Cycloseris* species is given.

Abbreviations

BWH = B.W. Hoeksema; Exp. = Expedition; I. = Island; Sta. = Station; MTQ = Museum of Tropical Queensland, Townsville, Australia; RMNH Coel. = Rijksmuseum van Natuurlijke Historie, Coelenterate collection (Naturalis Biodiversity Center), Leiden, the Netherlands; UZMK = Zoological Museum - University of Copenhagen, Denmark; ZMA Coel. = Zoological Museum of Amsterdam Coelenterate collection (Naturalis Biodiversity Center), Leiden, the Netherlands.

Systematic section

Order Scleractinia Bourne, 1900

Suborder Fungiina Verrill, 1856

Superfamily Fungiicae Dana, 1846

Family Fungiidae Dana, 1846

Genus *Cycloseris* Milne Edwards & Haime, 1849

<http://species-id.net/wiki/Cycloseris>

Type species. *Fungia cyclolites* Lamarck 1816. Designation by monotypy.

Synonymy. *Cycloseris* Milne Edwards and Haime 1849: 72; Milne Edwards and Haime 1850: xlix; Milne Edwards and Haime 1851: 111–112; Milne Edwards 1860: 49; Tenison-Woods 1878: 328; Duncan 1883: 149–150; Quelch 1886: 119–120; Gardiner 1899: 171; Gardiner 1905: 944; Vaughan and Wells 1943: 139; Wells 1956: 388; Wells 1966: 235–236; Veron and Pichon 1980: 107–108; Ditlev 1980: 54; Nemenzo 1981: 182; Scheer and Pillai 1983: 74; Nemenzo 1986: 140; Pillai 1986: 153; Veron 1986: 320–321; Chevalier and Beauvais 1987: 710; Veron 1992: 123; Veron 1993: 199; Latypov 1995: 88; Nishihira and Veron 1995: 234; Veron 2000: 236; Suharsono 2004: 191; Claereboudt 2006: 187; Latypov 2006: 178; Suharsono 2008: 215; Wallace et al. 2009: 46.

Diaseris Milne Edwards and Haime 1849: 72; Milne Edwards and Haime 1850: xlix; Milne Edwards and Haime 1851: 117; Milne Edwards 1860: 54–55; Duncan 1883: 150; Gardiner 1905: 945; Veron and Pichon 1980: 119–121; Veron 1986: 326–

327; Veron 1992: 127; Veron 1993: 205; Latypov 1995: 95; Nishihira and Veron 1995: 239; Veron 2000: 248; Suharsono 2004: 197; Claereboudt 2006: 190; Latypov 2006: 185; Suharsono 2008: 222. (Type species: *Fungia distorta* Michelin, 1842. Designation by monotypy.

Fungia (*Cycloseris*) – Hoeksema 1989: 30–31; Hoeksema and Van Ofwegen 2004.

Characters. Adult corals either encrusting and polystomatous or free-living and monostomatous (Gittenberger et al. 2011, Benzon et al. 2012). Outline of free-living, unfragmented specimens varying from circular to oval. Juveniles may be hexagonal. Free-living corals may fracture repeatedly into regenerating wedge-shaped pieces (Hoeksema 1989, Yamashiro et al. 1989, Yamashiro and Nishihira 1994, 1998, Hoeksema and Waheed 2011, 2012). Fragmenting corals may produce extra stomata along fracture lines. Corallum wall without perforations. Septal margins ornamented by fine, sharp dentations. Costae covered by fine spiny protuberances, which may become granular and blunt in large specimens. Tentacles small and usually translucent in extended state.

***Cycloseris boschmai* sp. n.**

<http://zoobank.org/8FA4CA99-7074-4425-A7ED-D051D6AB3311>

http://species-id.net/wiki/Cycloseris_boschmai

Figures 3–13

Fungia marginata (partim) Boschma 1923: 141–142; 1925: 199–202.

Fungia (*Cycloseris*) *costulata* (partim) – Hoeksema 1989: 64–69.

Fungia (*Cycloseris*) spec. – Hoeksema et al. 2004: 15; Hoeksema 2008: 11–12; 2010: 24–25.

Cycloseris sp. 1 – Gittenberger et al. 2011: 117; Hoeksema 2012a: 188.

Cycloseris sp. – Hoeksema et al. 2012: 652.

Cycloseris spec. – Waheed and Hoeksema 2013: 41.

Type material. Type specimens of *Cycloseris boschmai* from Banda, Moluccas, Indonesia (Danish Exp. to the Kei Islands, 1922), previously identified as *Fungia marginata* by Boschma 1925). **Holotype:** RMNH Coel. 8333 (1 dry specimen: 28 mm; Figure 3), Banda, 1922. **Paratypes:** RMNH Coel. 8334 (1 dry specimen: 29 mm), Banda, Lontor, 12.vi.1922; RMNH Coel. 8335 (5 dry specimens: 20–30 mm), Banda, off Lontor, 10–20 m depth, 4°33'S, 129°52'E, 1922.

Other material: Indonesia. Bali: RMNH Coel. 40146 (2 dry specimens: 25, 31 mm), NE Bali, Tulamben, 3–5 m, 08°16'36"S, 115°35'37"E, Bali Lombok Strait Exp. Sta. BAL.20, 09.iv.2001, coll. BWH; RMNH Coel. 40147 (1 dry specimen: 18 mm), NE Bali, Tulamben, 5 m depth, 08°16'26"S, 115°35'28"E, Bali Lombok Strait Exp. Sta. BAL.21, 11.iv.2001, coll. BWH. **Nusa Tenggara Timur (Lesser Sunda Islands):** RMNH Coel. 21471 (1 dry specimen: 38 mm), NE Komodo, S Gili Lawa Laut, 08°27'00"S, 119°34'24"E, Snellius-II Exp. Sta. 4.253, 27.x.1984,

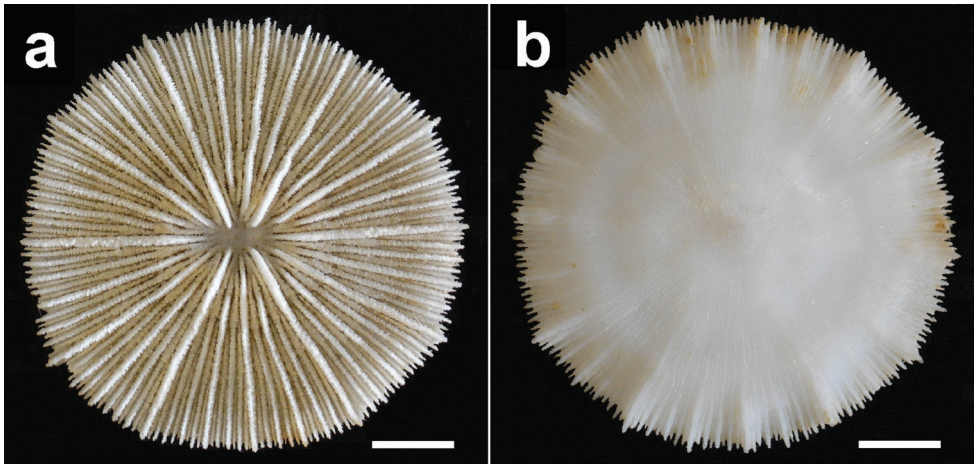


Figure 3. Holotype of *Cycloseris boschmai* sp. n. (RMNH Coel. 8333). Indonesia, Banda, Danish Exp. to the Kei Islands, 1922. **a** Upper side **b** Lower side. Scale bar: 0.5 cm.

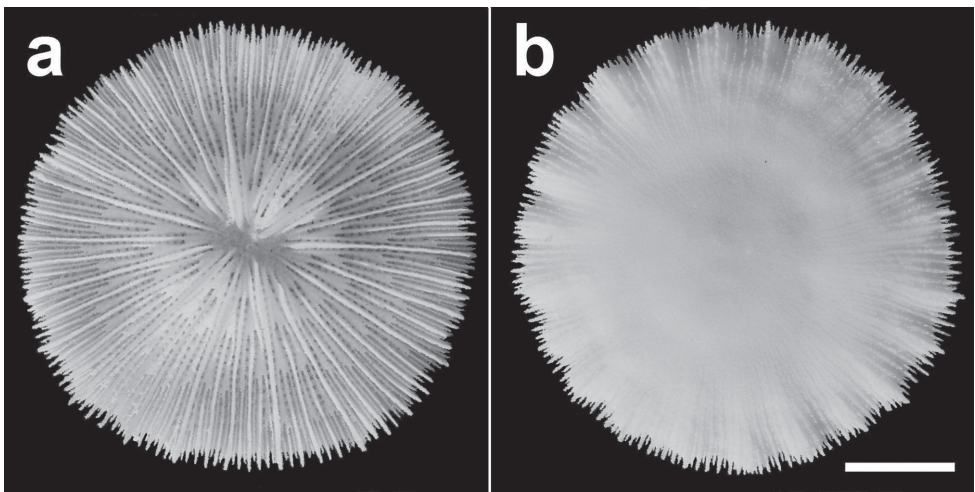


Figure 4. Specimen of *Cycloseris boschmai* sp. n. (RMNH Coel. 21471). Indonesia, NE Komodo, S Gili Lawa Laut, Snellius-II Exp. Sta. 4.253, 27 October 1984. **a** Upper side **b** Lower side. Scale bar: 0.5 cm.

coll. BWH; RMNH Coel. 40145 (4 dry specimens: 24–32 mm), SE Komodo, N side bay S of Tanjung Lohnamu, 08°38'19"S, 119°28'45" E, TNC Komodo Rapid Ecological Assessment Sta. KOM.16, coll. BWH; RMNH Coel. 31190 (1 dry specimens: 32 mm), N Sumbawa, Bay of Sanggar, 08°19'36"S, 118°15'12"E, Snellius-II Exp. Sta. 4.132, 30.x.1984, coll. BWH. **South Sulawesi.** RMNH Coel. 31188 (1 dry specimen: 31 mm), Spermonde Archipelago, N Bone Tambung Island, 05°01'50"S, 119°16'25"E, 13.vi.1986, coll. BWH; RMNH Coel. 31189 (5 dry specimens: 29–50 mm), Spermonde Archipelago, W Kudingareng Keke I., 9–18 m depth, 05°06'30"S, 119°17'04"E, 6.xii.1984, coll. BWH; RMNH Coel. 31192

(5 dry specimens: 17–31 mm), SW Selayar I., NW Bahuluang I., 06°28'00"S, 120°25'30"E, Snellius-II Exp. Sta. 4.202, 10.x.1984, coll. BWH; RMNH Coel. 31191 (3 dry specimens: 35–37 mm), NE Taka Bone Rate, E Tarupa Besar, 06°28'S, 121°08'E, Snellius-II Exp. Sta. 4.140, 25.ix.1984, coll. BWH. **Central Sulawesi, Tomini Bay, Togian Islands:** RMNH Coel. 24278 (2 dry specimens: 34, 39 mm), S Talatakoh I., 00°26'34"S, 122°06'07"E, Tethyana Exp. Sta. 10, 21.ix.1999, coll. BWH; RMNH Coel. 24291 (1 dry specimen: 48 mm), S Togian I., 00°20'10"S, 121°59'00"E, Tethyana Exp. Sta. 14, 23/24.ix.1999, coll. BWH; RMNH Coel. 24706 (5 dry specimens: 30–42 mm), S Batudaka I., 00°35'25"S, 121°41'38"E, Tethyana Exp. Sta. 15, 24.ix.1999, coll. BWH; RMNH Coel. 31193 (7 dry specimens: 29–50 mm), S Waleabahi I., 00°26'16"S, 122°15'16"E, Tethyana Exp. Sta. 8, 19.ix.1999, coll. BWH. **North Sulawesi:** RMNH Coel. 40156 (4 dry specimens: 36–40 mm), Lembah Strait, Tanjung Mawali, 14 m depth, 01°26'36"N, 125°13'46"E, Lembah Strait Exp. Sta. LEM.04, 31.i.2012, coll. BWH. **SE Sulawesi, Tukang Besi Islands (Wakatobi):** RMNH Coel. 40143 (1 dry specimen: 12 mm), NW Tomia, 05°43'59"S, 123°53'35"E, TNC-WWF Wakatobi Rapid Ecological Assessment Sta. WAK.25, 13.v.2003, coll. BWH; RMNH Coel. 40144 (1 dry specimen: 40 mm), SW Karang Kaledupa, lagoon, 05°51'46"S, 123°43'17"E, TNC-WWF Wakatobi Rapid Ecological Assessment Sta. WAK.28, 14.v.2003, coll. BWH. **Moluccas:** RMNH Coel. 33586 (2 dry specimens: 47, 58 mm), Ambon, N coast near Morela, 03°33'S, 128°12'E, Fauna Malesiana Maluku Exp. Sta. MAL.12, 13.xi.2002, coll. BWH; **Northern Moluccas:** RMNH Coel. 8286 (10 dry specimens, some with buds, 32–50 mm, previously identified as *Fungia marginata*), Banda, off Lontor, to 13 m depth, 4°33'S, 129°52'E, Danish Exp. to the Kei Islands, 15.vi.1922; UZMK (5 specimens in ethanol, 13–40 mm, previously identified as *Fungia marginata*), Gunung Api, 20–25 m depth, Danish Exp. to the Kei Islands, 13.vi.1922; UZMK (9 specimens in ethanol, 26–50 mm, previously identified as *Fungia marginata*), Lontor, 13 m depth, Danish Exp. to the Kei Islands, 15.vi.1922; RMNH Coel. 40096 (1 dry specimen: 29 mm), Halmahera, East coast Teluk Dodinga, Karang Galiasa, 00°50'46"N, 127°35'07"E, Ternate Exp. Sta. TER.38, 14.xi.2009, coll. BWH; RMNH Coel. 40102 (1 dry specimen: 34 mm), Hiri I., Tanjung Ngafauda, 00°54'38"N, 127°19'03"E, Ternate Exp. Sta. TER.14, 16 m depth, 31.x.2009, coll. BWH; RMNH Coel. 40103 (1 dry specimen: 30 mm), Ternate, Sulamadaha I., 00°52'04"N, 127°19'33"E, Ternate Exp. Sta. TER.22, 18 m depth, 6.xi.2009, coll. BWH; RMNH Coel. 40104 (1 dry specimen: 19 mm), Ternate, Dufadufa, Benteng Toloko, 00°48'49"N, 127°23'22"E, Ternate Exp. Sta. TER.24, 8 m depth, 7.xi.2009, coll. BWH; RMNH Coel. 40105 (1 dry specimen: 31 mm), Halmahera, W Pasir Lamo, 00°53'21"N, 127°27'34"E, Ternate Exp. Sta. TER.26, 8.xi.2009, coll. BWH; RMNH Coel. 40106 (1 dry specimen: 48 mm), Tidore, north Pilonnga, 00°42'50"N, 127°28'45"E, Ternate Exp. Sta. TER.34, 12 m depth, 12.xi.2009, coll. BWH; RMNH Coel. 40173 (1 dry specimen: 29 mm), Ternate, Tanjung Tabam, 00°50'05"N, 127°23'10"E, Ternate Exp. Sta. TER.12, 11 m depth, 30.x.2009, coll. BWH; RMNH Coel. 40174 (1 dry

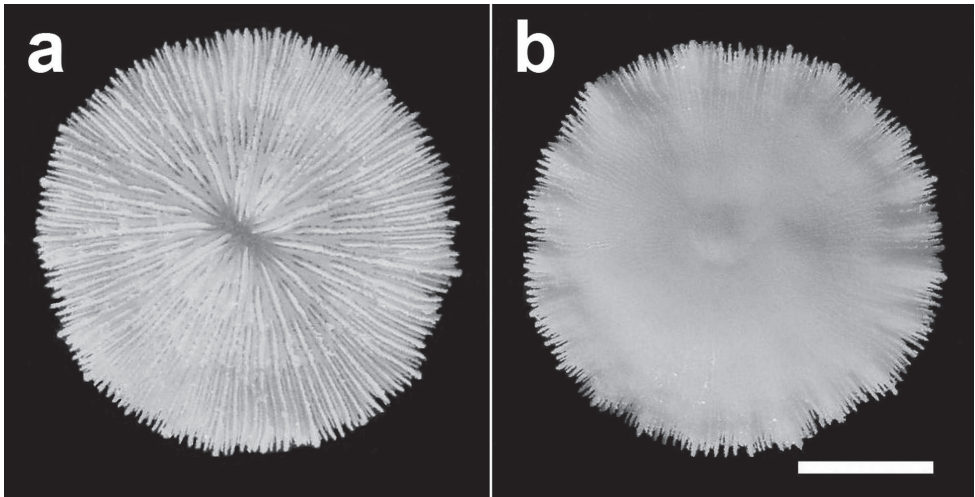


Figure 5. Specimen of *Cycloseris boschmai* sp. n. (RMNH Coel. 31190). Indonesia, N Sumbawa, Bay of Sanggar, Snellius-II Exp. Sta. 4.132, 30 October 1984 **a** Upper side **b** Lower side. Scale bar: 0.5 cm.

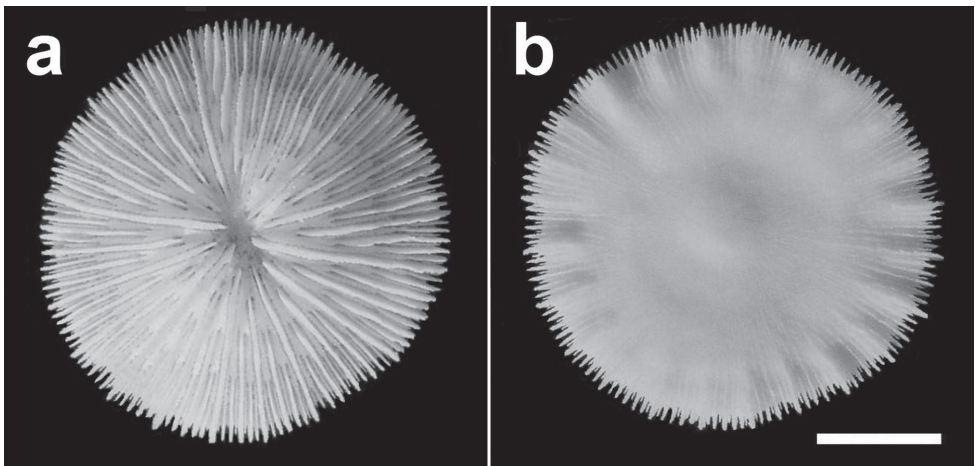


Figure 6. Specimen of *Cycloseris boschmai* sp. n. (RMNH Coel. 31188). Indonesia, South Sulawesi, Spermonde Archipelago, north side of Bone Tambung Island, 13 June 1986. **a** Upper side **b** Lower side. Scale bar: 0.5 cm.

specimen: 17 mm), Ternate, outside harbor to the east, 00°46'55"N, 127°30'20"E, Ternate Exp. Sta. TER.25, 8 m depth, 7.xi.2009, coll. BWH. **East Kalimantan, Berau Islands:** RMNH Coel. 31922 (1 dry specimen: 19 mm), W Derawan I., 7 m depth, 02°16'53"N, 118°13'39"E, East Kalimantan Berau Exp. Sta. BER.02, 4.x.2003, coll. BWH; RMNH Coel. 31923 (1 dry specimen: 15 mm), Berau Delta, Lighthouse-2 Reef, 6 m depth, 02°09'34"N, 118°10'11"E, East Kalimantan Berau Exp. Sta. BER.05, 5.x.2003, coll. BWH; RMNH Coel. 31924 (2 dry specimen: 22, 31 mm), Samama I., 8 m depth, 02°07'32"N, 118°20'10"E, East Kalimantan Berau

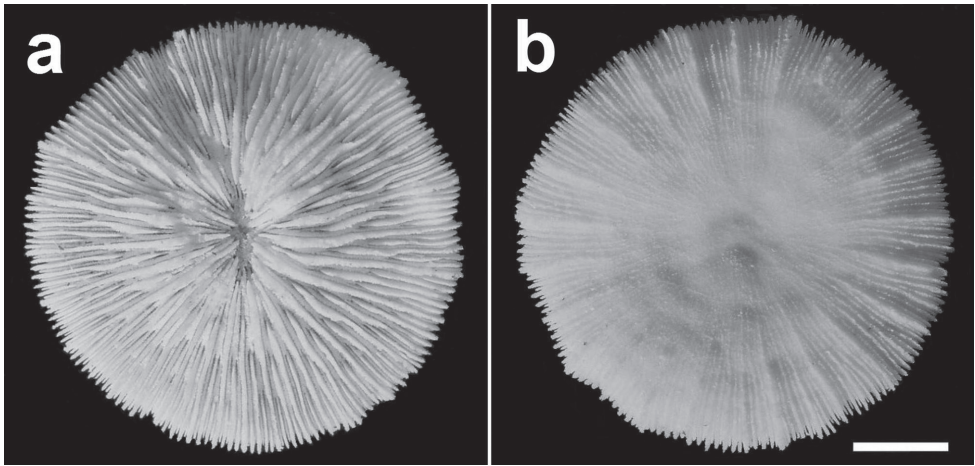


Figure 7. Specimen of *Cycloseris boschmai* sp. n. (RMNH Coel. 24291). Indonesia, Central Sulawesi, Togian Islands, S Togian I., Tethyana Exp. Sta. 14, 23/24 September 1999 **a** Upper side **b** Lower side. Scale bar: 0.5 cm.

Exp. Sta. BER.10, 7.x.2003, coll. BWH; RMNH Coel. 31925 (1 dry specimen: 42 mm), NE Kakaban I., 14 m depth, 02°08'53" 118°32'32"E, East Kalimantan Berau Exp. Sta. BER.49, 28.x.2003, coll. BWH; RMNH Coel. 40149 (1 dry specimen: 14 mm), S of Samama I., NE Buliulin I., 14 m depth, 02°07'07"N, 118°20'32"E, East Kalimantan Berau Exp. Sta. BER.26, 15.x.2003, coll. BWH; RMNH Coel. 40153 (1 dry specimen: 46 mm), N Maratua I., near entrance lagoon, 9 m depth, 02°14'53"N, 118°37'36"E, East Kalimantan Berau Exp. Sta. BER.29, 17.x.2003, coll. BWH; RMNH Coel. 40154 (1 dry specimen: 21 mm), S Derawan I., 13 m, 02°15'04"N, 118°15'04"E, East Kalimantan Berau Exp. Sta. BER.04a, 18.x.2003, coll. BWH; RMNH Coel. 40155 (1 dry specimen: 50 mm), E Sangalaki I., Light-house, 12 m depth, 02°04'54"N, 118°24'30"E, East Kalimantan Berau Exp. Sta. BER.22, 14.x.2003, coll. BWH. **West Papua, Raja Ampat Islands:** RMNH Coel. 40140 (1 dry specimen: 30 mm), S. Mansuar (Sawandarik village), 00°35'26"S, 130°36'12"E, Raja Ampat Exp. Sta. RAJ.06, 20.xi.2007, coll. BWH; RMNH Coel. 40141 (1 dry specimen: 33 mm), Yeffam I., E Penemu I., 8 m depth, 00°35'20"S, 130°17'06"E, Raja Ampat Exp. Sta. RAJ.66, 13.xii.2007, coll. BWH. **Malaysia, Sabah, northern Borneo:** RMNH Coel. 33545 (1 dry specimen: 20 mm), W Sabah, Gaya Islands off Kota Kinabalu, W Sapi I., 06°00'26"N, 116°00'13"E, 28.vii.2005, coll. BWH. **Layang-Layang:** RMNH Coel. 40095 (2 dry specimens: 18 mm attached, 37 mm free-living), Easternmost point, Sta. LAC.14, 15-25 m depth, 07°22'34"N, 113°51'15"E, 28.iii.2013, coll. BWH. **Philippines:** RMNH Coel. 24908 (2 dry specimens: 20, 32 mm), Cebu Strait, West of Bohol, NW Cabilao I., 09°53'20"N, 123°45'53"E, 2.x.1999, coll. BWH. **Palau:** RMNH Coel. 40225 (1 dry specimen), SE off Garreru I., S Goraklbud Passage, 07°19'15"N, 134°35'50"E, 29.vii.2002, coll BWH.

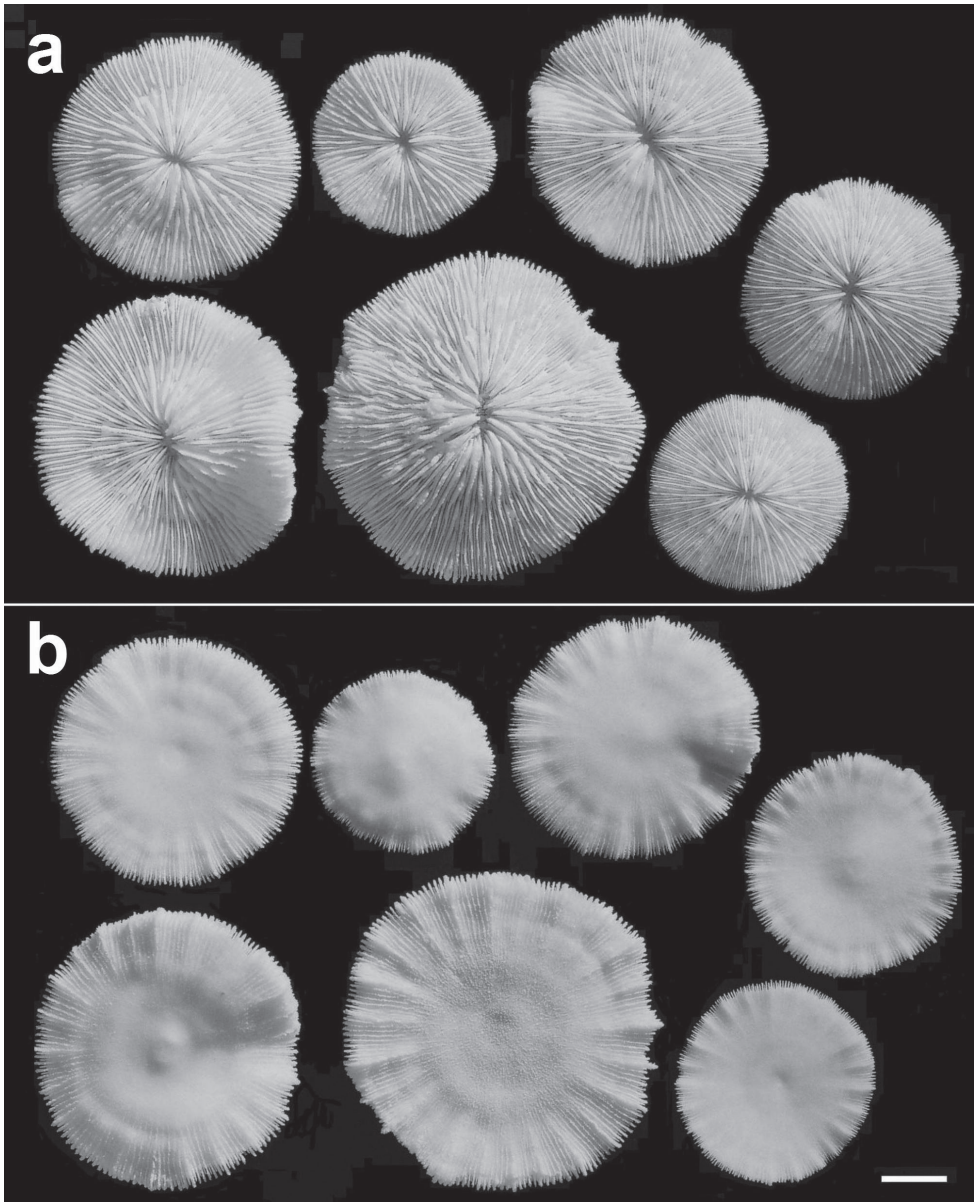


Figure 8. Specimens of *Cycloseris boschmai* sp. n. (RMNH Coel. 31193). Indonesia, Central Sulawesi, Togian Islands, S Waleabahi I., Tethyana Exp. Sta. 8, 19 September 1999 **a** Upper side **b** Lower side. Scale bar: 0.5 cm.

Characters. (Figures 3–13) The diameter of the examined specimens ranges between 12 and 50 mm. Corals mostly flat, moderately thick and robust. Adult animals unattached and monostomatous with septa-costae extending outside the circular to slightly oval corallum outline. Juvenile specimens vary from round to slightly hexagonal.

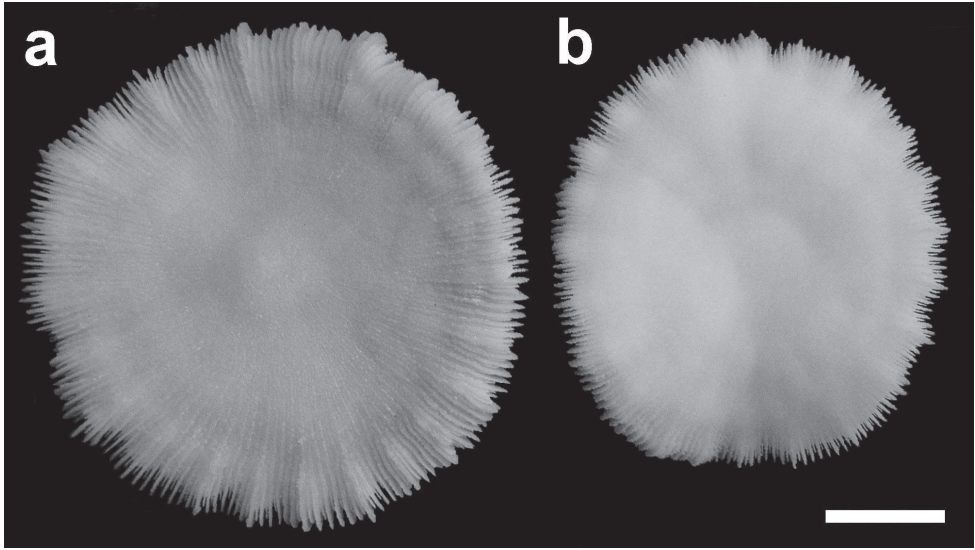


Figure 9. Two specimens of *Cycloseris boschmai* sp. n. (RMNH Coel. 24278). Indonesia, Central Sulawesi, Togian Islands, S Talatakoh I., Tethyana Exp. Sta. 10, 21 September 1999. Scale bar: 0.5 cm.

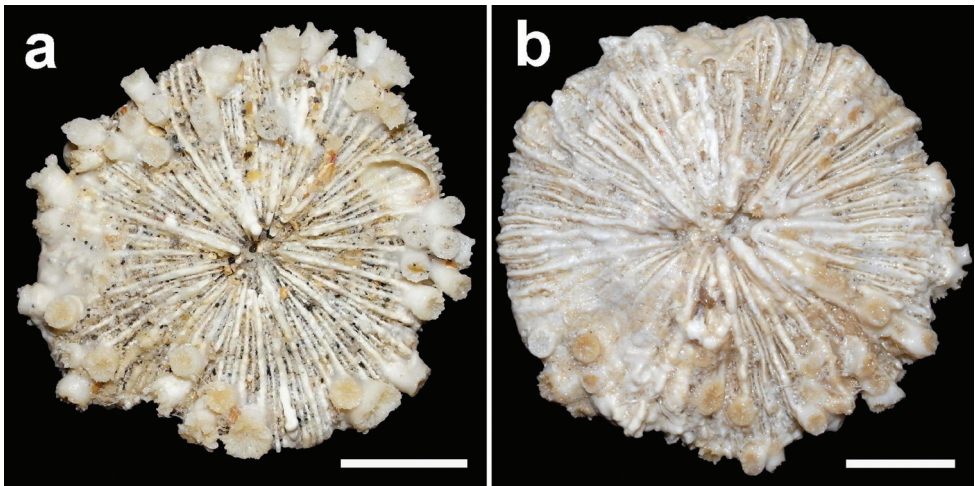


Figure 10. Two specimens of *Cycloseris boschmai* sp. n. (RMNH Coel. 8286) with marginal buds and sand in the mouths. Indonesia, Banda, off Lontor, Danish Exp. to the Kei Islands, 15 June 1922.

Wedge-shaped, regenerating fragments not known. The length of the fossa, measured at its bottom, is 1/9 to 1/6 of the corallum length. The columella is formed by a mingled mass of tightly to loosely packed trabeculae. Septa densely packed and straight, unequal in thickness and height. The relatively thick and high septa of lower orders are solid; they are flanked by perforated septa of higher orders. Tentacular lobes absent. Septal margins are finely ornamented with sharp and granular dentations. Their number varies

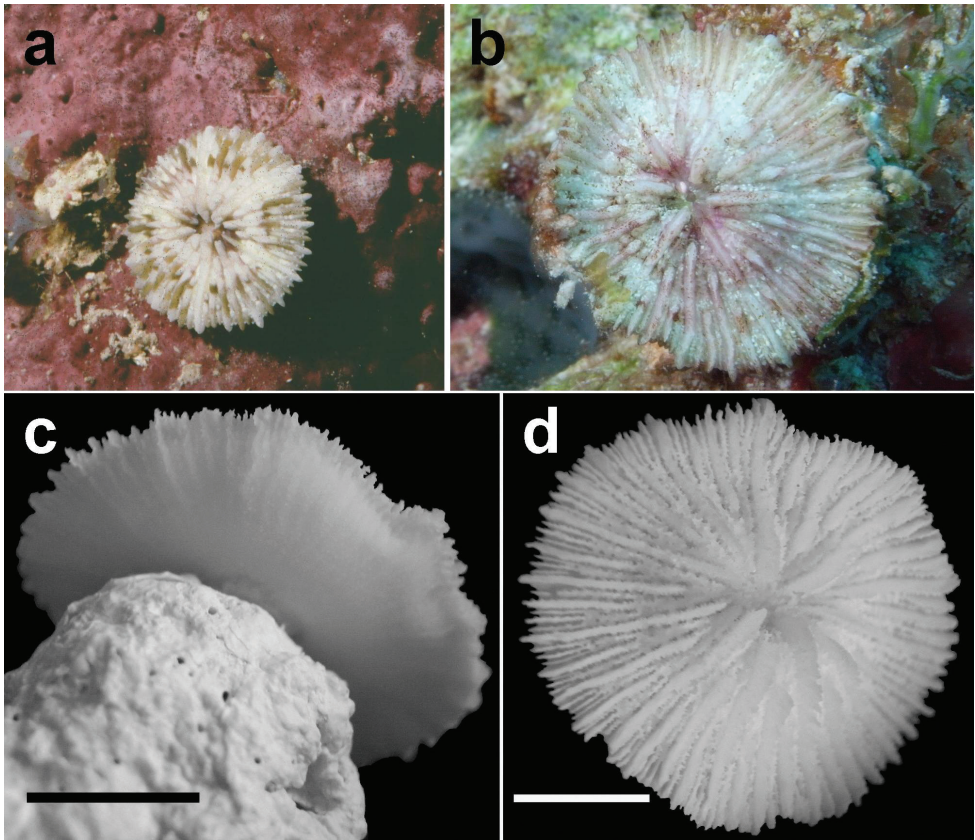


Figure 11. Juvenile, attached specimens of *Cycloseris boschmai* sp. n. **a** Papua New Guinea, Bismarck Sea, Madang, June 1992 **b–d** Malaysia, South China Sea, Layang Layang, Easternmost point, (RMNH Coel. 40095), 28 March 2013 **b** In situ (bleached) **c** Lower side **d** Upper side. Scale bars: 0.5 cm.

from 20 to 70 per cm. Septal sides are densely covered by fine granulations, which are irregularly dispersed or arranged in rows perpendicular to the septal margin. Compound synapticulae (fulturae) connecting the septa laterally cannot easily be distinguished because of tight septal arrangement. The solid corallum wall is granulated and may show a detachment scar. The lower side varies from flat to slightly convex. Costae unequal in size, straight and prominent near the corallum margin but less distinct at the centre. Corallum margin may be slightly undulating because of enlarged lower order costae. Costae ornamented with fine granular or acute spines. Their number varies from 15 to 80 per cm. Some individuals have small buds over their surface, especially in the proximity of the corallum margin (Figure 10). Attached juveniles (anthocaulus stage) are rare (Figure 11). The color of the living animal is variable with hues of red or green (Figures 11–13). Tentacles small and transparent with white acrospheres at their tips (Figure 13).

Geographical distribution (Figure 14). The distribution range is limited to the Coral Triangle (Hoeksema 2007): eastern Malaysia (Sabah and Layang Layang), east-

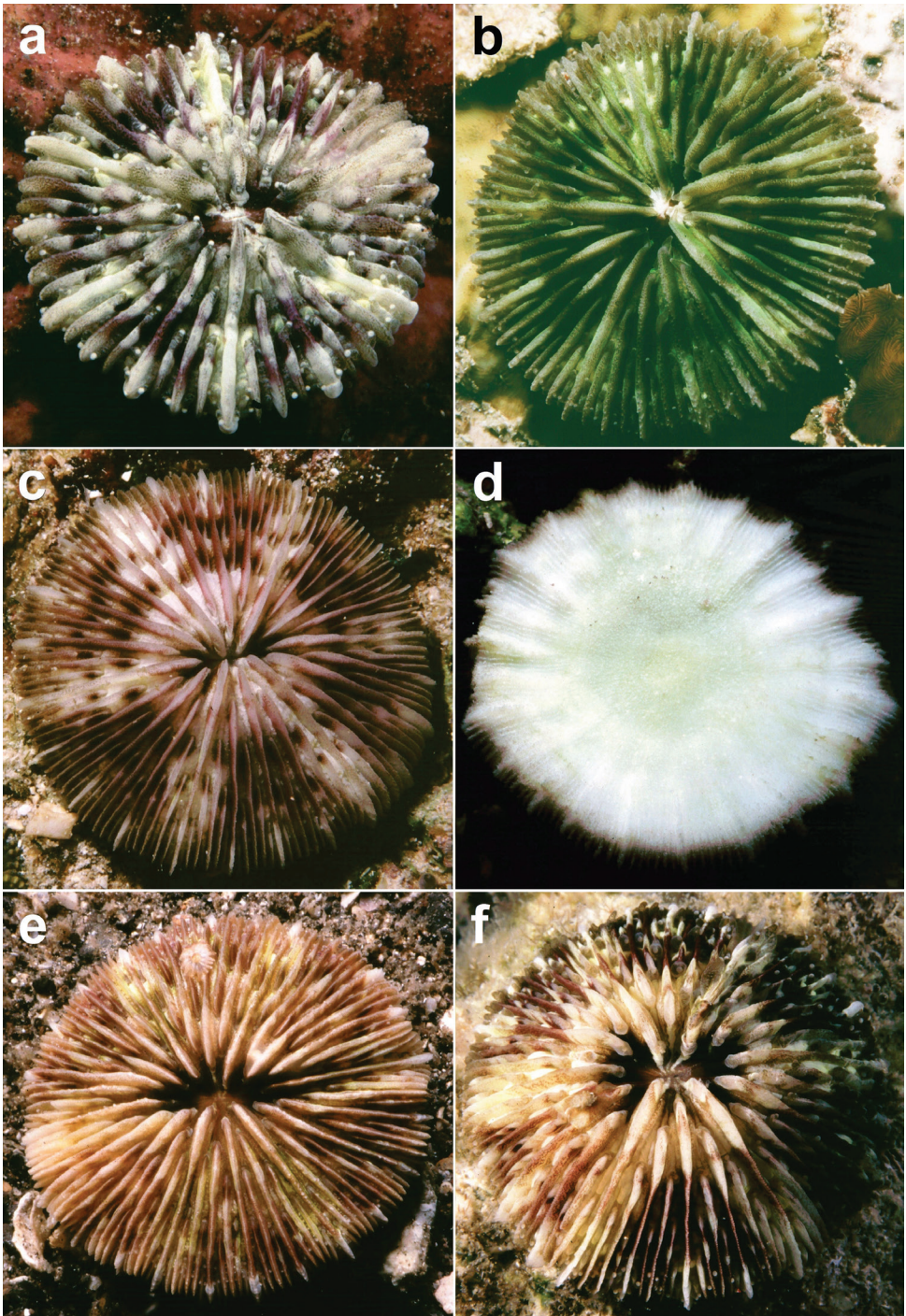


Figure 12. *Cycloseris boschmai* sp. n. **a** Indonesia, Bali, Tulamben, September 1997 **b** Philippines, Cebu, November 1999 **c–e** Indonesia, Central Sulawesi, Togian Islands, September 1999 **f** Indonesia, South Sulawesi, Spermonde Archipelago, Bone Lola reef, August 1997.

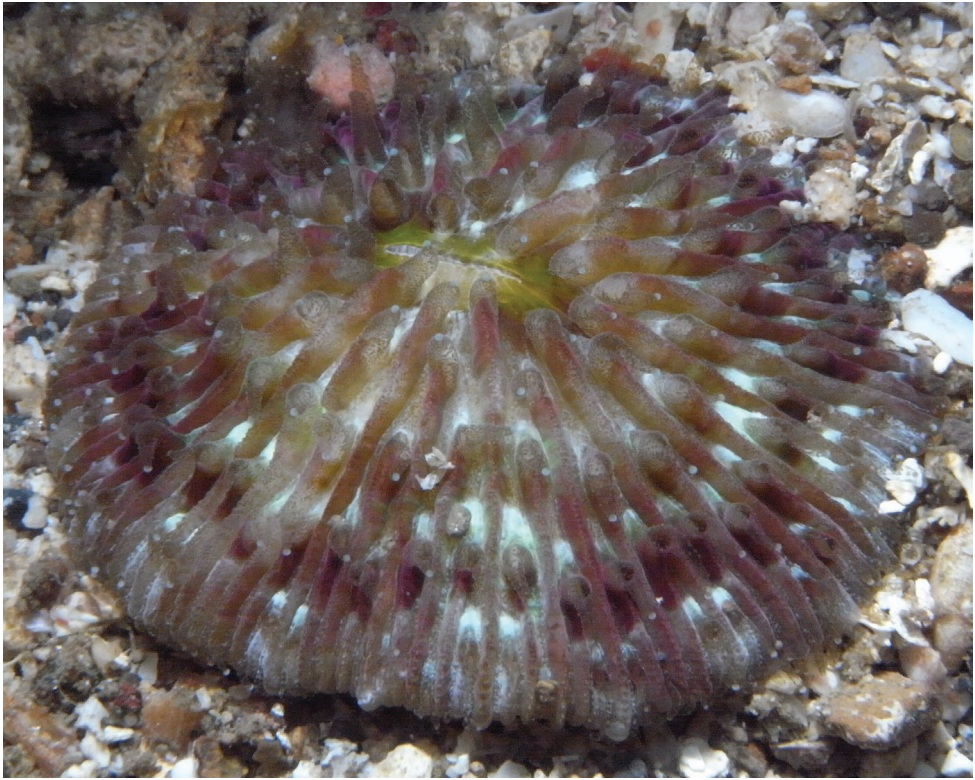


Figure 13. *Cycloseris boschmai* sp. n. specimen showing transparent extended tentacles with white acrospheres at their tips; Indonesia, North Sulawesi, Lembah Strait, Lobangbatu, February 2012.

ern Indonesia (from Bali to West Papua), central Philippines (Cebu Strait), Papua New Guinea (Madang Lagoon), and Palau.

Etymology. The species is named after the late Prof. Hilbrand Boschma, former director of the Rijksmuseum van Natuurlijke Historie (now Naturalis Biodiversity Center), who devoted much of his research time to the study of mushroom corals, including specimens of the new species.

Diagnosis. Adult corals small (< 50 mm) with uneven circular corallum margin owing to enlarged costae. Live specimens with variable, patchy colouration.

Key to recent free-living *Cycloseris* species (full-grown, unfragmented specimens), partly after Hoeksema (1989)

- 1a Lower order costae distinctly larger than other ones.....2
- 1b Costae fine, adjacent ones equal to almost equal5
- 2a Coralla flat and thin, corallum outline circular3
- 2b Coralla thick and slightly arched, corallum outline slightly or much oval....4

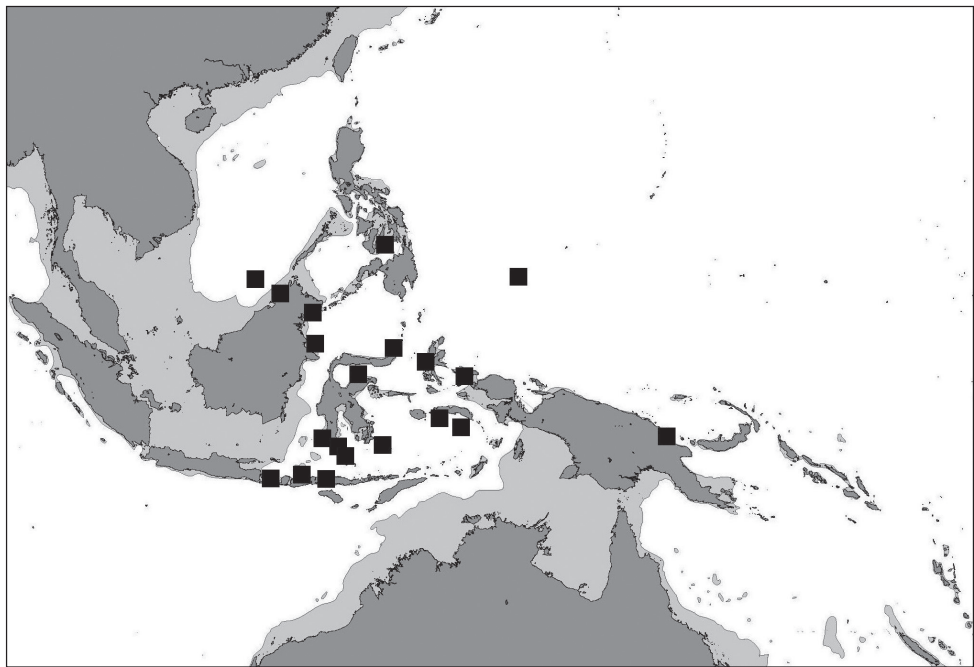


Figure 14. Map of the Central Indo-Pacific indicating localities where *Cycloseris boschmai* sp. n. has been recorded.

- 3a Lower order costae thicker and longer than higher order costae, ornamentation fine (20–70 / cm), maximum corallum diameter 5 cm, habitat mostly consisting of reef slopes and sandy reef bases..... *Cycloseris boschmai* sp. n.
- 3b Lower order costae sharp, ornamentation very fine (40–80 / cm) on lower order costae and indistinct on higher order costae, maximum corallum diameter 8 cm, habitat mostly consisting of deep, sandy reef bases.....
..... *Cycloseris vaughani*
- 4a Corallum outline slightly oval, lower order costae irregularly and roughly ornamented (20–70 / cm), maximum corallum diameter 8.5 cm, habitat consisting of upper reef slopes *Cycloseris tenuis*
- 4b Corallum outline clearly oval, lower order costae sharp, costal ornamentation very fine (40–90 / cm) and nearly absent on higher order costae, maximum corallum diameter 12.5 cm, habitat mostly consisting of deep, sandy reef bases *Cycloseris somervillei*
- 5a Septa densely packed and (almost) equal in height..... 6
- 5b Septa loosely packed, septa of lower orders thicker and more exsert than others ..7
- 6a Central fossa short (< 10% of corallum diameter); all septa perforated, nearly equal in size and tightly packed with little space in between them, maximum corallum diameter 8.5 cm, habitat mostly consisting of deep, sandy reef bases *Cycloseris sinensis*

- 6b Length of central fossa > 10% of corallum diameter, septa of lower order solid and thicker than adjacent septa with distinct space in between them, maximum corallum diameter 7.5 cm, habitat consisting of deeper reef slopes or reef bases *Cycloseris distorta*
- 7a Corallum outline oval 8
- 7b Corallum outline circular or irregularly round with folds or undulations 9
- 8a Coralla thick; underside flat or arched, costae equal, maximum corallum diameter 9 cm, habitat consisting of lower reef slopes or sandy reef bases *Cycloseris cyclolites*
- 8b Coralla convex around fossa (humped), costae equal in juveniles, maximum corallum diameter 12.5 cm, habitat mostly consisting of deep, sandy reef bases *Cycloseris somervillei*
- 9a Coralla with folded, undulating margin 10
- 9b Coralla with regular, smooth periphery 11
- 10a Coralla thin, central fossa short (< 10% of corallum diameter), margin undulating (hexagonal in juveniles) maximum corallum diameter 8.5 cm, habitat consisting of sandy reef slopes or sandy reef bases *Cycloseris hexagonalis*
- 10b Coralla thick and usually strongly arched, margin with folds, maximum corallum diameter 8.5 cm, habitat consisting of lower reef slopes or sandy reef bases *Cycloseris curvata*
- 11a Coralla and septa thin, adjacent costae slightly alternating in size maximum corallum diameter 15 cm, habitat mostly consisting of sandy reef bases *Cycloseris fragilis*
- 11b Coralla moderately thick, lower order septa thicker than others, costae nearly similar in size, maximum corallum diameter 12 cm, habitat consisting of lower reef slopes or sandy reef bases *Cycloseris costulata*

Discussion

Although some material of *Cycloseris boschmai* sp. n. was already available in museum collections (RMNH, UZMK), the species could only be discovered because of much fieldwork (1983–2013) with proportionate opportunities for observations and sampling to enable separation of the new species from resembling ones. Boschma (1923a, 1925) might have had the same species in mind when he described and studied *Fungia marginata*, but his selection of type specimens from the Paternoster Islands and the unclear comparison with other species of Döderlein's, *Fungia patella* group are not convincing. He described this species because of its supposedly thick corallum margin as compared to the other species in the *F. patella* group, but this character is not useful when applied several other *Cycloseris* species.

The *F. marginata* material from Banda is suitable as type material of the new species. Because the Banda specimens were wrongly identified by him, this does not concern a new name for an existing species but an entirely new species (Hoeksema 1993b).

These old museum specimens are not just useful as type material but also because they supply information about habitat (field data) and asexual reproduction by budding. They also constitute the oldest material of *C. boschmai*, which gives them potential historical value as baseline material in studies on changing coral faunas (Hoeksema and Koh 2009, Van der Meij et al. 2010, Hoeksema et al. 2011, Van der Meij and Visser 2011, Hoeksema and Wirtz 2013).

Cycloseris boschmai sp. n. is the smallest mushroom coral known so far (see key). Superficially, it resembles *C. costulata*, which has less prominent costae, a more even corallum margin (not undulating), a larger maximum size and less colourful appearance (see Hoeksema 1989, Hoeksema and Van Ofwegen 2004, Gittenberger and Hoeksema 2006). Both species can be found on reef slopes and sandy reef bases. *C. costulata* is common and wide-spread (Hoeksema 1989, 2012a) and has a variable growth form (Hoeksema and Moka 1989, Gittenberger and Hoeksema 2006), which is why much material had to be examined to find sufficient consistency in the diagnostic characters of the new species.

C. boschmai sp. n. also resembles *C. tenuis*, which is more oval, less colourful (see Gittenberger and Hoeksema 2006), and with lower order costae that are rougher and more irregularly ornamented. *C. tenuis* is most common on upper reef slopes (Hoeksema 2012a), whereas the rarer *C. boschmai* shows a deeper depth range. The new species also resembles *C. vaughani*, which has sharper lower order costae, a brown colouration (Hoeksema 1989, Hoeksema and Van Ofwegen 2004) and a much deeper depth range (Hoeksema 2012a).

With the inclusion of *C. boschmai* sp. n., 11 free-living *Cycloseris* species are distinguished. Since the taxonomic revision of the Fungiidae by Hoeksema (1989) various other mushroom coral species were reported as new to science (Veron 1990, 2000, 2002, Hoeksema and Dai 1991, Hoeksema 1993a, 1993c, 2009, 2012c, Latypov 1995, 2006, Ditlev 2003, Mondal and Raghunathan 2013). Two of these were originally classified as *Cycloseris* but they appear to be synonyms of previously described species and one of these is not a *Cycloseris*.

Cycloseris colini Veron, 2000 is a synonym of *Lithophyllon spinifer* (Claereboudt and Hoeksema 1987). The central dome and upward margins, combined with the large corallum size as described by Veron (2002) are characters commonly found in *L. spinifer* (see Hoeksema 1993a: fig. 14, Veron 2000, Hoeksema and Van Ofwegen 2004, Hoeksema 2008: fig. 9). A specimen from Palau (MTQ G55817) was designated holotype by Veron in 2002, but since the species was described in 2000 this designation was invalid (ICZN 2011). Hence, this specimen is hereby designated lectotype.

Cycloseris densicolummelus Latypov, 2006 has not been described in an official publication but in an electronic document that was distributed via a CD-ROM. This work should have contained a clear publication date and a statement naming at least five major publicly accessible libraries in which copies of the optical disc were to have been deposited (ICZN 2012). Since only the year of translation has been mentioned in the introduction and no names of libraries were given, this name is not valid. Although the publication by Latypov (2006) is said to be an English translation of an original

book in Russian, the latter does not mention *C. densicolummelus* but “*Cycloseris* sp. 1” (Latypov 1995: 95, pl. 28 fig. 2). The specimen indicated as “holotype”, spec. 1/95158 deposited in the Museum of Institute Marine Biology, Vladivostok 69041, Russia, is from Mai Rut Island, Gulf of Thailand. The illustration with the species description (Latypov 2006: figs 46–8) shows that it is a specimen of *C. costulata*. The well developed tentacular lobes, the intensive granulation of the lateral septal surfaces and the densely packed trabeculae of columella, which are indicated as diagnostic characters, do not really distinguish *C. densicolummelus* from *C. costulata* (see Hoeksema 1989, Gittenberger and Hoeksema 2006).

Because *C. boschmai* is a rare species (considering that most material was gathered during fieldwork in a time span of 30 years) and its geographic distribution range is restricted to the Coral Triangle, not much can be said about its ecology. Specimens are difficult to find, owing to their small body size compared to other mushroom coral species (Hoeksema 1991b, Gittenberger et al. 2011), which may be restrictive to the settlement of associated fauna and therefore none of its symbionts was reported previously (Hoeksema et al. 2012: “*Cycloseris* sp.”). In the present study, one of the photographed specimens shows a coral barnacle (Figure 11e), which is now the only known associated animal.

Small-sized free-living mushroom corals have been reported to show much mobility (Hoeksema 1988, Yamashiro and Nishihira 1995), which may help them to escape from competition for space with other organisms (Chadwick 1988, Hoeksema and De Voogd 2012). The distinctive large lower order costae may be useful as ridges in stabilizing the corals in order to prevent them to slide too rapidly downslope to deeper reef zones with sandy substrate (Hoeksema 1988). The enlarged ridge-like costae can also be seen in some other *Cycloseris* species (see key) and in the small-sized free-living deep-sea coral *Deltocyathus rotulus* (Alcock, 1898) (see Cairns and Kitahara 2012: fig 18Q).

Although free-living *Cycloseris* species were previously considered primitive, this is not the case according to their phylogeny reconstruction (Gittenberger et al. 2011). Their predominant habitat of deeper sandy substrates can also be considered an advanced trait (Hoeksema 2012b). The sand in the mouth of nearly dead specimens from Banda (Figure 10) suggests that they were collected from a sandy substrate, which may not be their preferred habitat. During the author's fieldwork (1983–2013), no specimens were observed on sandy reef bases. *C. boschmai* corals are small but not thin, which may not facilitate mobility and sediment-shedding as seen in large-polyped corals (Bongaerts et al. 2012, Erftemeijer et al. 2012). The presence of buds in several of the specimens from Banda, in addition to the sand in their stomata, (Boschma 1925; Figure 10) may also indicate that specimens have been buried (Gilmour 2002). Specimens of *C. hexagonalis* have been observed to show a similar abundance of buds on a sandy slope in eastern Sabah (BWH personal observation 2009). Budding may be a mushroom coral's last resort of survival when its mouth is clogged and not capable of food intake anymore (Boschma 1922, 1923b, 1923c).

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References

- Alcock A (1893) On some newly-recorded corals from the Indian Seas. *Journal of the Asiatic Society of Bengal (Natural History)* 62: 138–149, pl. 5.
- Alcock A (1898) An account of the deep-sea Madreporaria collected by the Royal Indian marine survey ship Investigator. Trustees Indian Museum, Calcutta, 29 pp., 3 pls.
- Benzoni F, Arrigoni R, Stefani F, Reijnen BT, Montano S, Hoeksema BW (2012) Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): lost mushroom corals find their way home. *Contributions to Zoology* 81: 125–146.
- Bongaerts P, Hoeksema BW, Hay KB, Hoegh-Guldberg O (2012) Mushroom corals overcome live burial through pulsed inflation. *Coral Reefs* 31: 399. doi: 10.1007/s00338-011-0862-z
- Bos AR (2012) Symbiotic fishes (Gobiidae and Labridae) of the mushroom coral *Heliofungia actiniformis* (Scleractinia; Fungiidae). *Coral Reefs* 31: 133. doi: 10.1007/s00338-011-0834-3
- Boschma H (1922) On budding and coalescence of buds in *Fungia fungites* and *Fungia actiniformis*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, Amsterdam 24: 257–268.
- Boschma H (1923a) The Madreporaria of the Siboga Expedition IV. *Fungia patella*. Siboga-Expedition XVI. Brill, Leiden, 129–148, pls. 9–10.
- Boschma H (1923b) Experimental budding in *Fungia fungites*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, Amsterdam 26: 88–96, pls. 1–2.
- Boschma H (1923c) Knospung und verwandte Erscheinungen bei *Fungia fungites* und *Fungia actiniformis*. *Treubia* 3: 149–179.

- Boschma H (1925) Madreporaria I. Fungiidae. Papers from Dr. Mortensen's, Pacific Expedition 1914–16. Videnskabelige meddelelser fra Dansk Naturhistorisk Forening 79: 185–259, pls. 5–11.
- Cairns SD (1984) An application of phylogenetic analysis to the Scleractinia: Family Fungiidae. Paleontographica Americana 54: 49–57.
- Cairns SD, Kitahara MV (2012) An illustrated key to the genera and subgenera of the Recent azooxanthellate Scleractinia (Cnidaria: Anthozoa), with an attached glossary. ZooKeys 227: 1–47. doi: 10.3897/zookeys.227.3612
- Chadwick NE (1988) Competition and locomotion in a free-living fungiid coral. Journal of Experimental Marine Biology and Ecology 123: 189–200. doi: 10.1016/0022-0981(88)90041-X
- Chevalier JP, Beauvais L (1987) Ordre des Scléractiniaires. In: Grassé PP (Ed) Traité de Zoologie tome III, fasc. 3. Masson, Paris, 679–753.
- Claereboudt MR (2006) Reef corals and coral reefs of the Gulf of Oman. Historical Association of Oman, Oman, 344 pp.
- Claereboudt M, Hoeksema BW (1987) *Fungia* (*Verrillofungia*) *spinifer* spec. nov., a new scleractinian coral (Fungiidae) from the Indo-Malayan region. Zoologische Mededelingen, Leiden 61: 303–309.
- Dana JD (1846–1849) United States Exploring Expedition during the years 1838–1842. Zoophytes 7. Lea and Blanchard, Philadelphia, 740 pp.
- Ditlev H (1980) A Field-guide to the Reef-building Corals of the Indo-Pacific. Backhuys, Rotterdam, and Scandinavian Science press, Klampenborg, 291 pp.
- Ditlev H (2003) New scleractinian corals (Cnidaria: Anthozoa) from Sabah, north Borneo. Description of one new genus and eight new species, with notes on their taxonomy and ecology. Zoologische Mededelingen, Leiden 77: 193–219.
- Döderlein L (1901) Die Korallengattung *Fungia*. Zoologischer Anzeiger 24: 351–360.
- Döderlein L (1902) Die Korallengattung *Fungia*. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 27(1): 1–162, pls. 1–25.
- Duncan PM (1883) Observations on the madreporarian family the Fungidae with special reference to the hard structures. Journal of the Linnean Society of London, Zoology 17: 137–163, pls. 5–6.
- Elahi R (2008) Effects of aggregation and species identity on the growth and behavior of mushroom corals. Coral Reefs 27: 881–885. doi: 10.1007/s00338-008-0403-6
- Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes. White and Son, London, 1–208, pls. 1–63.
- Erftemeijer PLA, Riegl B, Hoeksema BW, Todd PA (2012) Environmental impacts of dredging and other sediment disturbances on corals: a review. Marine Pollution Bulletin 64: 1737–1765. doi: 10.1016/j.marpolbul.2012.05.008
- Gardiner JS (1899) On the postembryonic development of *Cycloseris*. In: A. Willey's, Zoological Results, Zoological Results based on Material from New Britain, New Guinea, Loyalty Islands and Elsewhere, Cambridge 2: 171–180, pls. 19–20.
- Gardiner JS (1905) Madreporaria III. Fungida IV. Turbinolidae. In: Fauna and geography of the Maldives and Laccadives Archipelagoes, Cambridge 2: 933–957, pls. 89–93.

- Gilmour JP (2002) Acute sedimentation causes size-specific mortality and asexual budding in the mushroom coral, *Fungia fungites*. Marine and Freshwater Research 53: 805–812. doi: 10.1071/MF01219
- Gittenberger A, Gittenberger E (2005) A hitherto unnoticed adaptive radiation: epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia). Contributions to Zoology 74: 125–204.
- Gittenberger A, Gittenberger E (2011) Cryptic, adaptive radiation of parasitic snails: sibling species of *Leptoconchus* (Gastropoda: Coralliophilidae) in corals. Organisms, Diversity and Evolution 11: 21–41. doi: 10.1007/s13127-011-0039-1
- Gittenberger A, Hoeksema BW (2006) Phenotypic plasticity revealed by molecular studies on reef corals of *Fungia* (*Cycloseris*) spp. (Scleractinia: Fungiidae) near river outlets. Contributions to Zoology 75: 195–201.
- Gittenberger A, Hoeksema BW (2013) Habitat preferences of coral-associated wentletrap snails (Gastropoda: Epitoniidae). Contributions to Zoology 82: 1–25.
- Gittenberger A, Reijnen BT, Hoeksema BW (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. Contributions to Zoology 80: 107–132.
- Hoeksema BW (1988) Mobility of free-living fungiid corals (Scleractinia), a dispersion mechanism and survival strategy in dynamic reef habitats. Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia 2: 715–720.
- Hoeksema BW (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zoologische Verhandelingen, Leiden 254: 1–295.
- Hoeksema BW (1991a) Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. Marine Ecology Progress Series 74: 225–237. doi: 10.3354/meps074225
- Hoeksema BW (1991b) Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. Netherlands Journal of Zoology 41: 122–139.
- Hoeksema BW (1993a) Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: an annotated checklist with the description of *Cantharellus jebbi* spec. nov. Zoologische Mededelingen, Leiden 67: 1–19.
- Hoeksema BW (1993b) Some misapplied nomina nova in reef coral taxonomy (Scleractinia). Zoologische Mededelingen, Leiden 67: 41–47.
- Hoeksema BW (1993c) Historical biogeography of *Fungia* (*Pleuractis*) spp. (Scleractinia: Fungiidae), including a new species from the Seychelles). Zoologische Mededelingen, Leiden 67: 639–654.
- Hoeksema BW (1993d) Phenotypic corallum variability in Recent mobile reef corals. Courier Forschungs-Institut Senckenberg 164: 263–272.
- Hoeksema BW (2004) Impact of budding on free-living corals at East Kalimantan, Indonesia. Coral Reefs 23: 492. doi: 10.1007/s00338-004-0402-1
- Hoeksema BW (2007) Delineation of the Indo-Malayan Centre of maximum marine biodiversity: the Coral Triangle. In: Renema W (Ed) Biogeography, Time and Place: Distributions, Barriers and Islands, Springer, Dordrecht, 117–178. doi: 10.1007/978-1-4020-6374-9_5

- Hoeksema BW (2008) Stony corals (Fungiidae). In: Hoeksema BW, Van der Meij SET (Eds) Cryptic marine biota of the Raja Ampat Islands group. Naturalis, Leiden, 8–12.
- Hoeksema BW (2009) Attached mushroom corals (Scleractinia: Fungiidae) in sediment-stressed reef conditions at Singapore, including a new species and a new record. Raffles Bulletin of Zoology, Supplement 22: 81–90.
- Hoeksema BW (2010) Stony corals (Fungiidae). In: Hoeksema BW, Van der Meij SET (Eds) Crossing marine lines at Ternate: Capacity building of junior scientists in Indonesia for marine biodiversity assessments. Naturalis, Leiden, 19–24.
- Hoeksema BW (2012a) Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde Shelf, South Sulawesi. Raffles Bulletin of Zoology 60: 183–212.
- Hoeksema BW (2012b) Evolutionary trends in onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae). Contributions to Zoology 81: 199–221.
- Hoeksema BW (2012c) Mushroom corals (Scleractinia: Fungiidae) of Espiritu Santo (Vanuatu, West Pacific) with the description of a new species. Zoosystema 34: 429–443. doi: 10.5252/z2012n2a14
- Hoeksema BW, Benzoni F (2013) Multispecies aggregations of mushroom corals in the Gambier Islands, French Polynesia. Coral Reefs 32: 1041. doi: 10.1007/s00338-013-1054-9
- Hoeksema BW, Dai CF (1991) Scleractinia of Taiwan. II Family Fungiidae (with the description of a new species). Bulletin Zoological Institute, Academia Sinica, Taipei 30: 201–226.
- Hoeksema BW, De Voogd NJ (2012) On the run: free-living mushroom corals avoiding interaction with sponges. Coral Reefs 31: 455–459. doi:10.1007/s00338-011-0856-x
- Hoeksema BW, Farenzena ZT (2012) Tissue loss in corals infested by acoelomorph flatworms (*Waminoa* sp.). Coral Reefs 31: 869. doi: 10.1007/s00338-012-0919-7
- Hoeksema BW, Franssen CHJM (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. Coral Reefs 30: 519. doi: 10.1007/s00338-011-0736-4
- Hoeksema BW, Gittenberger A (2010) High densities of mushroom coral fragments at West Halmahera, Indonesia. Coral Reefs 29: 691. doi: 10.1007/s00338-010-0616-3
- Hoeksema BW, Kleemann K (2002) New records of *Fungiacava eilatensis* Goreau et al., 1968 (Bivalvia: Mytilidae) boring in Indonesian mushroom corals (Scleractinia: Fungiidae). Basteria 66: 25–30.
- Hoeksema BW, Koh EGL (2009) Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. Raffles Bulletin of Zoology, Supplement 22: 91–101.
- Hoeksema BW, Matthews JL (2011) Contrasting bleaching patterns in mushroom coral assemblages at Koh Tao, Gulf of Thailand. Coral Reefs 30: 95. doi: 10.1007/s00338-010-0675-5
- Hoeksema BW, Moka W (1989) Species assemblages and ecomorph variation of mushroom corals (Scleractinia: Fungiidae) related to reef habitats in the Flores Sea. Netherlands Journal of Sea Research 23: 149–160. doi: 10.1016/0077-7579(89)90009-4
- Hoeksema BW, Van Ofwegen LP (2004) Indo-Malayan reef corals: a generic overview. World Biodiversity Database, CD-ROM Series, ETI, Amsterdam.
- Hoeksema BW, Waheed Z (2011) Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. Coral Reefs 30: 1087. doi: 10.1007/s00338-011-0807-6

- Hoeksema BW, Waheed Z (2012) Onset of autotomy in an attached *Cycloseris* coral. *Galaxea Journal of Coral Reef Studies* 14: 25–26. doi: 10.3755/galaxea.14.25
- Hoeksema BW, Wirtz P (2013) Over 130 years of survival by a small, isolated population of *Favia gravida* corals at Ascension Island (South Atlantic). *Coral Reefs* 32: 551. doi: 10.1007/s00338-012-1002-0
- Hoeksema BW, Yeemin T (2011) Late detachment conceals serial budding by the free-living coral *Fungia fungites* in the Inner Gulf of Thailand. *Coral Reefs* 30: 975. doi: 10.1007/s00338-011-0784-9
- Hoeksema BW, Suharsono Cleary DFR (2004) Stony corals. In: Hoeksema BW (Ed) Marine biodiversity of the coastal area of the Berau region, East Kalimantan, Indonesia. Progress report East Kalimantan Program - Pilot phase (October 2003). Naturalis, Leiden, 7–16.
- Hoeksema BW, Van der Land J, Van der Meij SET, Van Ofwegen LP, Reijnen BT, Van Soest RWM, De Voogd NJ (2011) Unforeseen importance of historical collections as baselines to determine biotic change of coral reefs: the Saba Bank case. *Marine Ecology* 32: 135–141. doi: 10.1111/j.1439-0485.2011.00434.x
- Hoeksema BW, Van der Meij SET, Franssen CHJM (2012) The mushroom coral as a habitat. *Journal of the Marine Biological Association of the United Kingdom* 92: 647–663. doi: 10.1017/S0025315411001445
- Hoeksema BW, Scott C, True JD (2013a) Dietary shift in corallivorous *Drupella* snails following a major bleaching event at Koh Tao, Gulf of Thailand. *Coral Reefs* 32: 423–428. doi: 10.1007/s00338-012-1005-x
- Hoeksema BW, Waheed Z, Alamaru A (2013b) Out of sight: aggregations of epizoic comb jellies underneath mushroom corals. *Coral Reefs* 32: 1065. doi: 10.1007/s00338-013-1078-1
- ICZN (2011) Coral taxon names published in ‘Corals of the world’ by J.E.N. Veron (2000): potential availability confirmed under Article 86.1.2. *Bulletin of Zoological Nomenclature* 68: 162–166.
- ICZN (2012) Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *ZooKeys* 219: 1–10. doi: 10.3897/zookeys.219.3944
- Kleemann K, Hoeksema BW (2002) *Lithophaga* (Bivalvia: Mytilidae), including a new species, boring in mushroom corals (Scleractinia: Fungiidae) at South Sulawesi, Indonesia. *Basteria* 66: 11–24.
- Lamarck JBPA de M de (1801) *Système des Animaux sans vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution d’après les considérations de leurs rapports naturels et de leur organisation, et suivant l’arrangement établi dans les galeries du Muséum d’Histoire naturelle, parmi leurs dépouilles conservées; précédé du Discours d’ouverture de l’an VIII de la République*. Déterville, Paris, 432 pp.
- Lamarck JBPA de M de (1816) *Histoire naturelle des animaux sans vertèbres*. Vol. 2. Verdier, Paris, 568 pp.
- Latypov YY (1995) Scleractinian corals of Vietnam. Part III. Faviidae, Fungiidae. Nauka, Moscow, 140 pp. [in Russian]
- Latypov YY (2006) The scleractinian corals of Vietnam. Pdf file on CD-ROM, Far East Branch Russian Academy of Sciences, Institute of Marine Biology, Vladivostok, 405 pp.

- Linnaeus C (1758) *Systema naturae* (ed. 10), 1. Laurentii Salvii, Holmiae, 824 pp.
- Littler MM, Littler DD, Brooks BL, Koven JF (1997) A unique coral reef formation discovered on the Great Astrolabe Reef, Fiji. *Coral Reefs* 16: 51–54. doi: 10.1007/s003380050059
- Michelin H (1842) Description d'une nouvelle espèce de Zoophyte du genre Fongie. *Revue Zoologique par La Société Cuvierienne* 5: 316.
- Milne Edwards H (1860) *Histoire naturelle des coralliaires ou polypes proprement dits* 3. Librairie Encyclopédique de Roret, Paris, 560 pp.
- Milne Edwards H, Haime J (1849) Mémoire sur les polypiers appartenant a la famille des Oculinides, au groupe intermédiaire des Pseudoastréides et a la famille des Fongides. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 29: 67–73.
- Milne Edwards H, Haime J (1850) Classification of polypi. A monograph of the British fossil corals 1. Palaeontographical Society of London, London, viii-lxxxv.
- Milne Edwards H, Haime J (1851) Recherches sur les polypiers. Mémoire 6. Monographie des Fongides. *Annales des Sciences Naturelles, Zoologie, Series 3*, 15: 73–144.
- Mondal T, Raghunathan C (2013) Description of a new coral species (Scleractinia: Fungiidae) from Andaman Islands, India. *Journal of Threatened Taxa* 5: 4653–4659. doi: 10.11609/JoTT.o3194.4653-9
- Nemenzo F (1981) Philippine corals. *Guide to the Philippine Flora and Fauna* 2: 1–320.
- Nemenzo F (1986) Corals. *Guide to the Philippine Flora and Fauna* 5: 1–273.
- Nishihira M, Veron JEN (1995) *Hermatypic corals of Japan*. Kaiyusha Publishers, Tokyo, 439 pp.
- Ortmann A (1889) Beobachtungen an Steinkorallen von der Südküste Ceylons. *Zoologische Jahrbüchern, Abteilung für Systematik, Biologie und Biogeographie der Tiere* 4: 493–590, pls. 11–17.
- Owada M, Hoeksema BW (2011) Molecular phylogeny and shell microstructure of *Fungiacava eilatensis* Goreau et al. 1968, boring into mushroom corals (Scleractinia: Fungiidae), in relation to other mussels (Bivalvia: Mytilidae). *Contributions to Zoology* 80: 169–178.
- Pillai CSG (1986) Recent corals from the south-east coast of India. In: James PSBR (Ed) *Recent Advances in Marine Biology. Today and Tomorrow'S, Printers and Publishers*, New Delhi, 107–198.
- Quelch JJ (1886) Report on the reef-corals collected by H.M.S. Challenger during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–79. *Zoology* 16(3): 1–203, pls. 1–12.
- Scholtz J, Hoeksema BW, Pawson DL, Ruthensteiner B (2012) Ludwig Döderlein (1855–1936): Some aspects of his life, research, and legacy. *Spixiana* 35: 177–191.
- Scheer G, Pillai CSG (1983) Report on the stony corals from the Red Sea. *Zoologica, Stuttgart* 45(133): 1–198, pls. 1–41.
- Suharsono (2004) *Jenis-jenis karang di Indonesia*. Pusat Penelitian Oseanografi - LIPI, Jakarta, 343 pp.
- Suharsono (2008) *Jenis-jenis karang di Indonesia*. LIPI Press, Jakarta, 372 pp.
- Tenison-Woods JE (1878) On the extra tropical corals of Australia. *Proceedings of the Linnean Society of New South Wales* 2: 292–341, pls. 4–6.
- Van der Horst CJ (1921) The Madreporaria of the Siboga Expedition II. *Madreporaria Fungida*. Siboga-Expedition XVIb. Brill, Leiden, 53–98, pls. 1–6.

- Van der Meij SET, Hoeksema BW (2013) Distribution of gall crabs inhabiting mushroom corals on Semporna reefs, Malaysia. *Marine Biodiversity* 43: 53–59. doi: 10.1007/s12526-012-0135-2
- Van der Meij SET, Visser RR (2011) The *Acropora humilis* group (Scleractinia) of the Snellius expedition (1929–30). *Raffles Bulletin of Zoology* 59: 9–17.
- Van der Meij SET, Suharsono, Hoeksema BW (2010) Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). *Marine Pollution Bulletin* 60: 1442–1454. doi: 10.1016/j.marpolbul.2010.05.011
- Van Soest RWM (1979) A catalogue of the Coelenterate type specimens of the Zoological Museum of Amsterdam IV. Gorgonacea, Actinaria, Scleractinia. *Beaufortia* 29: 81–126.
- Vaughan TW, Wells JW (1943) Revision of the suborders, families and genera of the Scleractinia. *Special Papers of the Geological Society of America* 44: 1–363.
- Veron JEN (1986) *Corals of Australia and the Indo-Pacific*. Angus & Robertson, North Ryde (N.S.W.), 644 pp.
- Veron JEN (1990) New Scleractinia from Japan and other Indo-Pacific countries. *Galaxea* 9: 95–173.
- Veron JEN (1992) Hermatypic corals of Japan. *Australian Institute of Marine Science Monograph Series* 9: 1–234.
- Veron JEN (1993) A biogeographic database of hermatypic corals. *Australian Institute of Marine Science Monograph Series* 10: 1–433.
- Veron JEN (2000) *Corals of the World*. Volume 2. Australian Institute of Marine Science, Townsville, 429 pp.
- Veron JEN (2002) New species described in *Corals of the World*. *Australian Institute of Marine Science Monograph Series* 11: 1–209.
- Veron JEN, Pichon M (1980) Scleractinia of Eastern Australia – Part III. Family Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectinidae, Caryophyllidae, Dendrophylliidae. *Australian Institute of Marine Science Monograph Series* 4: 1–459.
- Verrill AE (1868) Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. No. 6. Review of the polyps and corals of the West Coast of America. *Transactions of the Connecticut Academy of Arts and Sciences* 1: 377–558, pls. 5–10.
- Waheed Z, Hoeksema BW (2013) A tale of two winds: species richness patterns of reef corals around the Semporna peninsula, Malaysia. *Marine Biodiversity* 43: 37–51. doi: 10.1007/s12526-012-0130-7
- Waheed Z, Hoeksema BW (in press) Diversity patterns of scleractinian corals at Kota Kinabalu, Malaysia, in relation to depth and exposure. *Raffles Bulletin of Zoology*.
- Wallace CC, Fellegara I, Muir PR, Harrison PL (2009) The Scleractinian Corals of Moreton Bay, Eastern Australia: high latitude, marginal assemblages with increasing species richness. *Memoirs of the Queensland Museum – Nature* 54: 1–118.
- Wells JW (1956) Scleractinia. In: Moore RC (Ed) *Treatise on Invertebrate Paleontology*. F. Coelenterata. Geological Society of America & University of Kansas Press, 328–440.
- Wells JW (1966) Evolutionary development in the scleractinian family Fungiidae. In: Rees WJ (Ed) *The Cnidaria and their Evolution*. Symposia of the Zoological Society London 16. Academic Press, London, 223–246, pl. 1.

- Yamashiro H, Nishihira M (1994) Radial skeletal dissolution to promote vegetative reproduction in a solitary coral *Diaseris distorta*. *Experientia* 50: 497–498. doi: 10.1007/BF01920756
- Yamashiro H, Nishihira M (1995) Phototaxis in Fungiidae corals (Scleractinia). *Marine Biology* 124: 461–465. doi: 10.1007/BF00363920
- Yamashiro H, Nishihira M (1998) Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin, 1843), a free-living fungiid coral. *Journal of Experimental Marine Biology and Ecology* 225: 253–267. doi: 10.1016/S0022-0981(97)00229-3
- Yamashiro H, Hidaka M, Nishihira M, Pong-In S (1989) Morphological studies on skeletons of *Diaseris fragilis*, a free-living coral which reproduces asexually by natural autotomy. *Galaxea* 8: 283–294.

Book Review: An adventurous life of Victor Ivanovich Motschulsky, described by himself

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It is difficult to review the book one is editing. One sees the flaws, having already received comments from colleagues, zoologists and historians of science. But V.I. Motschulsky is such a compelling yet little-known personality that we find it our duty to review the book even though one of us is its editor.

Among entomologists, rumors abound that Motschulsky, an outstanding specialist in insect systematics as well as an avid collector, stole beetle specimens from famous collections and argued with his European colleagues. He had a difficult personality. It is no accident that Walter Horn called him “the infernal entomologist.”

History and natural history are intertwined in the book, which consists in large part of memoirs recorded in Russian and German, and in part of reverse translations of Motschulsky’s articles published in the 1850s–60s mostly in French. The first part is, first and foremost, a history, while the second is largely natural history. (Let us not forget that “biology”, while coined as a term, was not widely used until the late 19th century). The translation from German of the biographical and highly biased essay by W. Horn, which was written in the 1920s, is placed in the end of the book.

V.I. Motschulsky was born in 1810. A military man, he participated in the suppression of the Polish uprising, where he was wounded and lost hearing in the left ear. Later, he served in the Caucasus, the so-called Kyrgyz steppe, East Siberia, and

Orenburg. The biographical account ends in 1841, followed by reverse translations of entomological expeditions to the outskirts of St. Petersburg as well as abroad to Europe and America in 1852–55. There remains no account of the period from 1841 to 1851 and from 1856 on. All that remains are headings: “Military service in Chuguyev,” “Travels in the Crimea,” “Travels abroad. Egypt,” “Paris. London. Dalmatia. Montenegro,” “My survey on the gnawing of the French army’s lead bullets by the grub *Urocerus juvenicus* in the Crimea”, etc. In 1863, Motschulsky permanently relocated to the Crimea, was very ill in the last years of his life and died in 1871.

While reading his memoirs, one is stunned by the breadth of Motschulsky’s interests as well as his integrity and patriotism. Motschulsky was a direct participant in such events as the repression of the Polish uprising in 1830–31 and the conquest of the Caucasus and Central Asia. He witnessed the horrific flooding of Kronstadt in November 1824. The Decembrists’ uprising took place when he was a youth and the War of 1812 while he was a baby. In one way or another, all these and other events are reflected in his memoirs. Motschulsky’s book offers a few novel historical facts and interpretations. Apparently, Empress Catherine II was murdered: Lady Perekusikhina served her poisoned chocolate (p. 20). The book recounts the story of a man who impersonated the murdered Emperor Paul (pp. 21, 164). Halfway through the book there appears an authoritative confirmation that Count Araktshejew was, in fact, murdered after stealing the signed letterhead of the late Emperor Alexander I and forging 13 royal decrees (p. 105). Motschulsky purportedly heard this last shocking story directly from Count P.A. Kleinmichel: the book marks its first appearance in scientific literature. Other anecdotes are interspersed among the memoirs. To his credit, Motschulsky had a sober view of the tsarist administration. “Emperor Nicholas exclusively favored the military, whereas members of other professions had to make do elsewhere.” (p. 23). “And, given that everyone must serve in the military, and that all young men are groomed exclusively for military service, their remaining talents are stunted. This is truly unfortunate for the empire, because as a result, the landed gentry is weakened, estates are abandoned by their owners and fall into disrepair, families grow destitute, trade is chilled outside of large urban centers, and the country as a whole grows poor.” (p. 23). This is what came of the incompetently run Polish campaign and intrigues and thievery in the Caucasus. It is abundantly clear that the principles and methods of governance in Russia have not changed much since the reign of Nicholas I.

It appears that Motschulsky’s career in the military was not very successful, but he did not aim to succeed there. “On one hand, it instilled in me distaste for the unlawful and on the other, honesty, contrary to which I could not act and due to which I often got in trouble given my volatile temper.” (p. 18). For example, “on two occasions, I was demoted due to my temper: the first time, I called our French teacher a scoundrel and the second time, I could not stop laughing at a demented duty officer.” (p. 22). While stationed in the Caucasus, Motschulsky successfully submitted to his superiors a report on “the Persian and Afghan question” and received recognition for it. As a result, he was to be dispatched to Persia, but the

plan fell through because of his poor health. Instead, he was allowed to go on leave “abroad” even though at that time, trips abroad were largely discouraged. On his return in 1836, Motschulsky was offered to continue serving in St. Petersburg, but he chose to return to the Caucasus. Notwithstanding his heroism and professional acclaim, he was ultimately forced out. Later, after his work in the so-called Kyrgyz steppe and East Siberia, the following happened. “I wanted to join the diplomatic corps, to make use of my knowledge of the East, but the Ministry of Foreign Affairs dragged its feet, delaying for many months and many questionable reasons. Tired of waiting, I decided to accept a position as special envoy for the Committee and Commission for the Construction of the Moscow Railway. Thus, all I had assembled and studied over the course of many years bore no fruit.” (p. 169). And, by way of a bitter recap, “After all, in this country, an educated and honest man can find few ways to earn a living.” (p. 22).

Motschulsky’s luck and courage – and even, to a degree, his recklessness – are astounding. Here is an anecdote from the Polish campaign: “A grenade exploded under my horse, and as a result I was thrown in the air but not injured. The horse itself received a mild shrapnel wound. Because we had not eaten anything in two days, one of our Cossacks brought me a pot of beef from camp. My fellow soldiers and I rode off a distance, so as to enjoy the delicacy without running the risk of being shot. We got off our horses, set the pot down on the ground, and sat on the grass, eagerly awaiting a chance to partake of the beef. I reached out with a fork for a piece of beef when we were all covered with a cloud of dust and lost consciousness. The pot and fork disappeared – they were smashed by a ricocheted cannonball. Our food was scattered everywhere in miniscule bits. It appears that we had picked a poor place for a meal.” (p. 40). And here is an account of the Swiss Alps: “When crossing the snowy peaks of Appenzell, we had to walk on very narrow paths, where snow that had melted in the June heat frequently slid out from under our feet. Once, we started slipping downhill – I fell on my back and with terrifying speed began to slide down. But I kept my wits about me and tried to stop my descent, using an iron pick of the kind that every traveler carries. This I succeeded in doing a few feet before the edge of a cliff. Another time, when I slipped and fell in the same area, I was sliding so fast, I could not see anything and everything turned black, when I felt a terrifying jolt resonate through my body. I stopped, my feet pressed against a ridge of rocks and ice that had formed at the edge of a cliff where goats had traveled in the fall – just a couple of feet from a drop of over 250 feet.” (p. 86)

Motschulsky’s descriptions of nature and people are full of incisive observations. He describes Caucasian mineral waters; Prince Sevardzelidze, a man of legendary strength; the bazaars of Tiflis; the Georgian temperament; oil spills in Dagestan; Caucasian mountain peaks; and jackals who stole the boots he had treated with cured pig fat, as he slept outside, fearing the fleas that abounded indoors.

At the time of Motschulsky’s early travels, oil was not yet widely used. “In the 1820s, near Sary island in the Caspian Sea, a new island had formed and Mr. Ménétriés [a renowned naturalist from St. Petersburg – *K.M. & S.G.*] traveled by boat to

inspect it. One of the sailors carelessly lit a pipe, a spark fell, and the island went up in flames. Ménétrés and his men barely managed to save the boat, but the sea was covered in oil and also lit up. They barely made it out, rowing as fast as they could.” (p. 64). Describing Astrakhan and its vicinity, Motschulsky justly notes, “Extracting oil from the islands and coastal regions of the Caspian Sea alone could form a substantial basis for trade if petroleum were adopted for illuminating streets and houses, where it may well replace gas and, even more so, other oils.” (p.147)

During his travels abroad, Motschulsky was interested not only in beetles, but also museums, architecture (cathedrals, monuments, tombs), and the memorial museum of Andreas Hofer, a famous partisan from Tyrol, who fought against Napoleon’s invasion. In the museum, which was once Hofer’s residence, “visitors can see his trousers and even snip off a piece as a souvenir.” (p. 90–91)

Motschulsky engaged in occasional discussions on economics, concerned about a well-run economy. Here is what he writes about the fishing trades in Astrakhan: “To strengthen the fishing trades, we must clean Volga’s polluted estuary so that fish may enter the river from the sea, which is presently difficult if not impossible. It is noticeable how sturgeon and beluga get stranded in the shallows and cannot get out: it is hardly surprising that many fish return to the sea and seek out other estuaries to fulfill their natural cycles. It also bears noting that now, fishermen leave on the shore small fish not intended for trade, whereas previously, they released it back into the sea, thus preserving the young. At present, however, one can smell millions of rotting fish, dying for no good reason around fishing rafts and boats.” (p. 147)

But Motschulsky’s primary passion was, of course, beetles and, to a lesser degree, other insects. He collected them on every suitable occasion – in the Caucasus, in the outskirts of St. Petersburg, in America. The beetles he caught he literally stuffed in his pockets (in pill boxes) and later emptied out onto sticky sheets covered with gum arabic. He then divided the sheets into segments and mounted them on entomological pins. These sheets are still part of his beetle collection. Motschulsky actively communicated with the leading entomologists of his day, frequently arguing with them and engaging in disputes. Motschulsky’s collection was bequeathed to the Moscow Society of Naturalists, where it was abandoned. It was not re-discovered until the early 20th century and is currently housed in Moscow University’s Zoological Museum. It has partly been re-examined and many beetles have been reclassified according to modern standards. But the boxes with other insects, myriapods and crustaceans are in very poor shape. They have been ravaged by dermestid beetle larvae, an entomologist’s worst enemy. The small collection of spiders has been lost altogether.

In fact, beetles saved Motschulsky’s life when he was sent on a reconnaissance mission together with several locals loyal to the Russian government. Pretending to be deaf and dumb, he was captured by highlanders in the Caucasus in 1838. He was “made” when his captors noticed that his hood was stitched in silk, as was customary in Tiflis, and not in wool, as in the mountains. “Suddenly, we were surrounded by highlanders, who took our horses and weapons. They put each of us in a separate hut under guard.” (p. 135). “As soon as I realized what danger I was in, I did not fail to make friends. The

first was this woman [a highlander's wife who was told to guard Motschulsky – *K.M. & S.G.*]. Dinnertime was approaching, and I was helping her with the preparations, fixing the fire, making flatbread, and otherwise assisting with small chores – all was done as in accordance with the highlanders' customs. In the meantime, I slipped into the fire a pencil I was carrying in my pocket, which, if found, would undoubtedly have costed me my life." (p. 136). The prisoner was led into a clearing between cliffs and a precipice in the hopes that he would start talking to his travel companions and reveal his purpose. "Knowing quite well that our enemies were watching us, I remained true to my assumed role and, paying no attention to my travel companions, I lay down on the ground and started playing with rocks, putting them in my mouth and spitting them out into the abyss. In the meantime, I was shredding into bits the piece of paper I was carrying in my pocket, chewing and swallowing the bits. Thus, I got rid of a dangerous and incriminating item which contained notes from my travels. [A while later,] the highlanders came and searched my pockets, where they found a few crushed insects I had gathered along the way, the discovery of which caused uproarious laughter, and which they carefully returned to my pocket." (p. 136)

The chapter titled "1833. Lithuania. Magnetism" stands out somewhat. In it, Motschulsky encounters magnetism, or lunacy, in his cousin Louisa. This condition, together with Louisa's youth – Motschulsky planned to marry her upon her recovery – greatly appealed to the scientist. But the marriage did not take place, most likely due to his numerous travels and growing interest in beetles. The chapter remains unfinished, ending literally mid-word.

The manuscript containing Motschulsky's memoirs was illustrated with landscapes and drawings of beetles and other arthropods, but unfortunately, far from all of these illustrations have survived. The book contains all that could be located. Certain peculiarities of Motschulsky's language should also be kept in mind, for clarity's sake. For example, he calls robbers predators and beggars the bedraggled.

In the introduction, the compiler of the book compares Motschulsky to Paganel, but this fictional geographer and naturalist had not yet been created by Jules Verne and came into existence somewhat later, in 1859. A more accurate comparison might be made to Cousin Benedict, an entomologist, and also a creation of Jules Verne.

Despite prolonged – even drawn out – preparations, the book has not been sufficiently edited, and typos have crept in. There is also a noticeable dearth of reference tools: footnotes, index, and list of Latin titles. For example, Motschulsky writes that Lake Baikal supports "a marvelous fish, as large as a ruff, and consisting entirely of fat." (p. 167). There is no further commentary. Meanwhile, he is apparently speaking of the big Baikal oilfish (Y.V. Tchaikovsky, personal comment). Many names and geographic locations are given multiple spellings, which somewhat interferes with reading the book. Regretfully, Latin names are also sloppily written.

It is difficult to describe in a book review our awe and delight with this wonderful book. The author's language is perfect, albeit somewhat obsolete Russian, while his views are almost modern. We recommend that you read this book for yourself. Orders from abroad can be made through Pensoft Publishers, <www.pensoft.net>.

Far from all biographic materials of V.I. Motschulsky have been made available to scholars. Research remains to be done in military archives, including his personal file and report on “the Eastern question”. As far as we know, Motschulsky’s business correspondence may still be found in various civil archives in Moscow and St. Petersburg. But an academic biography of our hero is a task for the future.

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References

Krivokhatsky VA (2013) An adventurous life of Victor Ivanovich Motschulsky, described by himself. KMK Scientific Press, Moscow & St. Petersburg, 261 pp. [in Russian]