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Ceriantharia (Cnidaria) of the World: an annotated catalogue and key to species

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Abstract

The diversity of Ceriantharia is known from studies formally describing species from the late 18th Century onwards. However, no nomenclators including a list and discussion of all valid species have been produced since a list discussed by Carlgren in 1912. The present nomenclator presents a complete list of adult species of Ceriantharia of the World, including a discussion on each species. It includes the three families (Arachnactidae, Botrucnidiferidae, Cerianthidae) and the currently accepted 54 species based on their adult form. This study serves as a presentation of the "state-of-the-art" list of species of Ceriantharia, and includes a species identification key to support taxonomic identification. Additional in-depth species-by-species investigations for almost all ceriantharid species is still needed, as the information available for most of these species is quite superficial.

Keywords
Cnidaria, families, genera, identification key, tube-dwelling anemones

Introduction

The subclass Ceriantharia Perrier, 1893 (Fig. 1), a group of anthozoan species commonly known as 'tube anemones', is characterized by the presence of two tentacle discs and a tube produced by filaments of a special kind of cnida, the ptychocyst (Daly et al. 2007; Stampar et al. 2016). This group of sediment-dwelling species is recognized as some taxa are common as pets in the aquarium industry (Stampar and Silveira 2006). On the other hand, the general taxonomy of the group is rather confusing, and the literature includes some incorrect definitions of characters for both species and genera (Torelli 1961; Stampar et al. 2012; 2016).

Knowledge on Ceriantharia dates back from the late 1700s, with the description by Spallanzani (1784) of an aberrant and tubular hydroid species with a membranous tube around the body, *Tubularie* (= *Tubularia membranosa* in Gmelin, 1791: 3836). Currently, the subclass Ceriantharia is divided into three families, eight genera, and includes 54 valid species (den Hartog 1977; Stampar et al. 2016; Molodtsova 2020) (Fig. 2). Different Ceriantharia classification schemes exist, with only limited consistency with each other (e.g., Mejia et al. 2019). However, until now, there has been only one published table-style catalogue (= nomenclator) of all species of tube-anemones, which is over a century old (Carlgren 1912a) and does not contain an extensive bibliographic compilation. Additionally, many species descriptions (e.g., Arai 1965; Molodtsova 2001a) and higher-level taxonomic reorganizations have taken place since 1912, and, thus, subsequent researchers have faced difficulties in finding and organizing historical and recent citations and information on Ceriantharia. Therefore, there is an obvious need for an organized species nomenclator, as well as for an identification key to aid in further studies of this group. Here, we present a nomenclator and a key to the extant valid Ceriantharia species in their adult form (polyps), including discussions of the status of each species. Some other articles have addressed larval forms (Molodtsova 2004b; Stampar et al. 2015b) but these are not included in the present study.

Material and methods

The checklist's classification follows den Hartog (1977) for the orders and Carlgren (1912b, 1931) for genera of the subclass Ceriantharia. Cited articles have mostly been compiled from specific literature. The online databases Hexacorallians of the World (Fautin 2013) and the World Register of Marine Species (Molodtsova 2020)

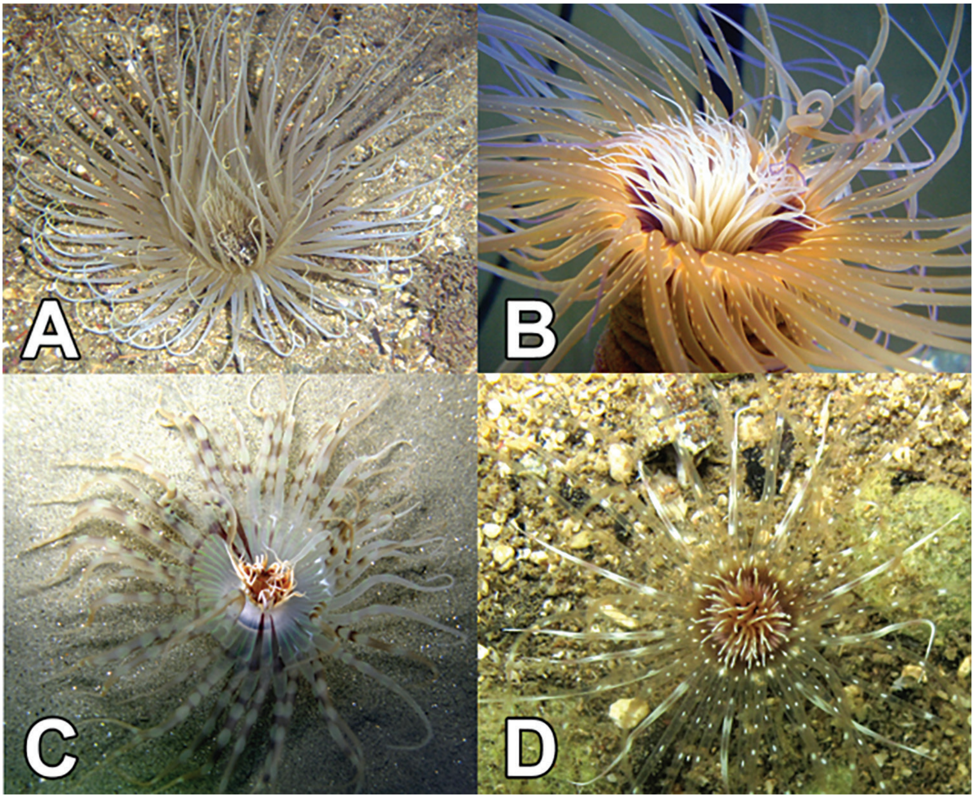

Figure 1. Examples of Ceriantharia: **A** Cerianthidae, *Ceriantheomorphe brasiliensis* **B** *Pachycerianthus schlenzae* **C** Arachnactidae, *Isarachnanthus nocturnus* **D** Botrucnidiferidae, *Botruanthus mexicanus* (Photograph Ricardo Gonzalez-Muñoz).

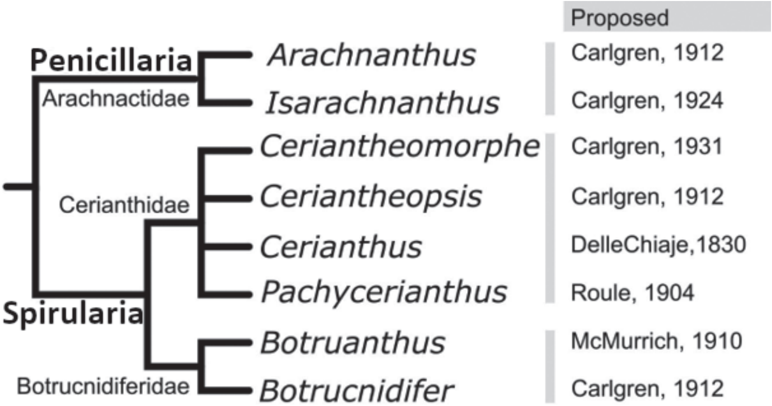

Figure 2. Classification of Ceriantharia (adapted from Stampar et al. 2016a).

were used to assist in bibliographic compilations. Information on deposited specimens was obtained directly from the original descriptions and/or collections of mentioned museums for each species. If the type material was not found, this information is indicated for each species. In terms of life cycle, larval forms of cerianthids were not added to this study, as it is still not possible to make proper correlations with adult forms without the aid of molecular-based re-examinations (e.g., Stampar et al. 2015c). The identification key was constructed with the characters available for each species, although unfortunately some species have sparse descriptions and only a few distinctive characters are known.

Results

The compilation of species resulted in a list of 54 valid species (Fig. 2) of adult forms of Ceriantharia. The current classification divides the species into the families Arachnactidae (nine species, 16%); Botrucnidiferidae (four species, 8%), and Cerianthidae (41 species, 76%). There is a clear prevalence in numbers of Cerianthidae species, and this can be explained by the large sizes and high visibility of many species described in this family (Stampar et al. 2016). There are two clear periods of comparatively high rates of formal species descriptions with a long break in between them (Fig. 3): a) the 'Carlgren/van Beneden/McMurrich period' (1890 to 1951), and b) the 'Molodtsova/Stampar period' (ongoing from 2001). During these two periods more than 75% of the valid Ceriantharia species were described.

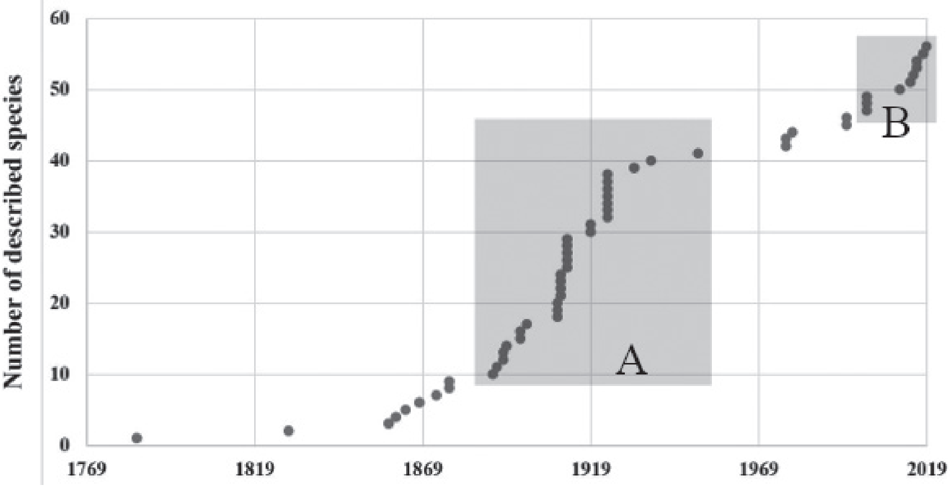

Figure 3. The cumulative number of Ceriantharian species descriptions per year. **A** Period Carlgren/van Beneden/McMurrich (1890 to 1951) and **B** Period Molodtsova/Stampar (2001 to present).

Checklist

Phylum Cnidaria Hatschek, 1888
Class Anthozoa Ehrenberg, 1834
Subclass Ceriantharia Perrier, 1893
Order Spirularia den Hartog, 1977

Number of valid taxa: two families, six genera, and 45 species

Family Cerianthidae Milne Edwards & Haime, 1851

Number of valid taxa: four genera and 41 species

Genus *Ceriantheomorphe* Carlgren, 1931

Table 1

Type species. *Ceriantheomorphe brasiliensis* by original designation (Carlgren 1931).

Number of valid species: 3

1 *Ceriantheomorphe ambonensis* (Kwietniewski, 1898)

http://zoobank.org/A5A81C1F-3180-4114-A624-E9F1CDA889B5

Cerianthus ambonensis Kwietniewski, 1898: 426; Pax 1910: 167; McMurrich 1910: 26–28 Carlgren 1912a: 44–47; Lopes et al. 2019: 127–148
(?) *Cerianthus sulcatus* McMurrich, 1910: 28–30
Ceriantheomorphe ambonensis: Carlgren 1931: 1

Type locality. Moluccas (Maluku) Islands, Indonesia, shallow waters.

Distribution. Only known from shallow water at the type locality.

Remarks. The original description made by Kwietniewski (1898) is very simple and based only on external characters. McMurrich (1910) obtained two specimens from the same area and conducted a more detailed anatomical study. Carlgren (1931), based on McMurrich's description, moved the species to the newly erected genus *Ceriantheomorphe*. There has been no other subsequent research performed on this species. This species is commercially exploited for the international aquarium trade (exported from Indonesia), perhaps owing to its vivid orange color (S. Stampar pers. obs.).

Type material. Not found in this study.

Table 1. Comparison of anatomical features of *Ceriantheomorphe* species (after Lopes et al. 2019).

	C. ambonensis	*C. brasiliensis*	*C. adelita*
Marginal tentacles	More than 100	Up to 392	Up to 352
Directive labial tentacle	Absent	Present	(?)
Arrangement of labial tentacles	(0)112.2112	(1)123.1324.3124.3124	(?)112.211
Actinopharynx	1/8 to 1/10 of gastric cavity	1/4–1/5 of gastric cavity	1/7 to 1/8 of gastric cavity
Oral disc	~ 4 cm	~5 cm	~3 cm
Siphonoglyph	Long, 6 mesenteries attached	Rather wide, 4 mesenteries attached	Long, 6 mesenteries attached
Directive mesenteries	>Actinopharynx	>Actinopharynx	>Actinopharynx
P2	Almost to aboral pole	To aboral pole	Almost to aboral pole
P3	Short, ≅ directives	Short, < directives	Short, > directives
M	± 2B	± 2B	± 2B
M3	± M2	=M2	± M2
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Present	Present
Craspedion tract at fertile mesenteries	2/4	2/5 – 3/5	2/5 – 3/5

2 *Ceriantheomorphe brasiliensis* (Mello-Leitão, 1919)

http://zoobank.org/6336C2A6-B8DB-4B0F-9137-3525DCE698D6

(?) *Cerianthus americanus*: Hertwig, 1882: 110 116

Cerianthus brasiliensis Mello-Leitão, 1919: 38–39

Ceriantheomorphe brasiliensis: Carlgren 1931: 2–6; Carlgren 1940: 6,11–12; Stampar et al. 2010: 205–209; Silveira and Morandini 2011: 3; Rodriguez et al. 2011: 52, 54–55; Spier et al. 2012: 1–3; Stampar et al. 2012: 5–6, 9; Stampar et al. 2014a: 2,5,8; Stampar et al. 2014b: 344, 347, 351, 353; and Stampar et al. 2015a: 3; González-Muñoz et al. 2016: 5, 9; Stampar et al. 2016: 64, 67, 68; Stampar and Morandini 2017: 690; Lopes et al. 2019: 127–148

(?) *Cerianthromorphe brasiliensis*: Hedgpeth 1954: 286

Type locality. Baía de Guanabara, Rio de Janeiro, Brazil**.**

Distribution. Brazil (Espírito Santo (20.5°S) to Rio Grande do Sul (33.7°S) states); Uruguay (35°S), and Gulf of Mexico (dubious record, 24–29°N), shallow waters (at < 40 m depth).

Remarks. This species was first described as *Cerianthus brasiliensis* by Mello-Leitão (1919) from Guanabara Bay, Rio de Janeiro, Brazil. This description is quite simple and based on only a few external morphological characters. Oskar Carlgren visited the Museu Nacional do Rio de Janeiro (MNRJ) at the time of description of the genus *Ceriantheomorphe* sometime between 1925 and 1929, but he was unable to find the type material designated by Mello-Leitão. However, the type material (MNRJ 100) of *Cerianthus brasiliensis* is available and, based on our examinations, every mesentery, except for the directives, is fertile. Thus, based on this, the species described by Mello-Leitão should be moved to the genus *Ceriantheomorphe*. Carlgren (1931) mentions that the species (with this name) as described by him in that publication may be a junior synonym of *C. brasiliensis* Mello-Leitão 1919, as Lopes et al. (2019) have shown. Hertwig (1882) recorded a specimen of *Cerianthus americanus* from the Uruguayan coast whose external shape appeared to be very similar to that of *Ceriantheomorphe brasiliensis*. However, that specimen was not available at the time of the present study and may be lost.

Type material. Museu Nacional do Rio de Janeiro – MNRJ 100 (Holotype).

3 *Ceriantheomorphe adelita* Lopes, Morandini & Stampar in Lopes et al., 2019
http://zoobank.org/702bdfdd-870c-43eb-b59a-05a994177d56

Ceriantheomorphe adelita Lopes et al., 2019: 127–148
Cerianthromorphe brasiliensis: Molodtsova 2009: 365–367
(?) *Cerianthromorphe brasiliensis*: Carlgren and Hedgpeth 1952: 148, 169–170; Hedgpeth 1954: 286; 290; Frey 1970: 309

Type locality. off Port Aransas, 32 km south off Corpus Christi, Texas, United States of America.

Distribution. Gulf of Mexico (Northern Mexico) to North Atlantic (North Carolina, United States of America), shallow waters.

Remarks. A very large species, which for many years was considered to be synonymous with *C. brasiliensis* even without biogeographic justification. Recently, Lopes et al. (2019) have indicated morphological differences that support the distinction between both species. Apparently, this is a species with very low incidence, since several sampling attempts have been unsuccessful (S. Stampar pers. obs.).

Type material. Smithsonian National Museum of Natural History NMNH 50015 (holotype).

Genus *Ceriantheopsis* Carlgren, 1912
Table 2

Type species. *Ceriantheopsis americana* by original designation (Carlgren 1912a)
Number of valid species: 4

4 *Ceriantheopsis americana* (Agassiz in Verrill, 1864)
http://zoobank.org/a5de3b9f-56d7-4f46-a5ff-56a01f2c132a

Cerianthus sp. Agassiz 1859: 24
Cerianthus americanus Agassiz in Verrill, 1864b: 32–33; Verrill 1864a: 56–57; Verrill 1872: 436; Hertwig 1882: 110,116; Andres 1883: 352; McMurrich 1887: 63; van Beneden 1897: 140; Haddon 1898: 401; Parker 1900: 756; Duerden 1902a: 329–

Table 2. Comparison of anatomical features of *Ceriantheopsis* species (after Stampar et al. 2016).

	C. americana	*C. nikitai*	*C. austroafricana*	*C. lineata*
Marginal tentacles	Up to 100–120	Up to 70	Up to 70	Up to 60
Directive labial tentacle	Present	Present	Present	Absent
Arrangement of labial tentacles	(2)413.4232.4312* (4)413.4231.4312.4312	(3)423.4232.4312.4312	(2)313.4343.4324.3124	4231.4231.4231.4231
Actinopharynx	1/12–1/8 of gastric cavity	1/5–1/4 of gastric cavity	1/10–1/8 of gastric cavity	1/6-1/5 of gastric cavity
Oral disc	0.7–1.0 cm	~0.6–0.7 cm	Wide, ~1.5 cm in preserved	1.0 – 1.5 cm in preserved
Siphonoglyph	Narrow, 4 mesenteries attached	Wide, 4 mesenteries attached	Wide, 4 mesenteries attached	Narrow, 2 mesenteries attached
Directive mesenteries	<Actinopharynx	~Actinopharynx	~Actinopharynx	<Actinopharynx
P2	To aboral pole	To aboral pole	To aboral pole	Almost to aboral pole
P3	=B	=B	=B	=B
M	>>B	<2B	>B	≥B
M3	≤M2	>M2	≤M2	<Half M2
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Not present	Present	Present
Craspedion tract at fertile mesenteries	6/7–8/9	3/5	6/7	~6/7-8/9
Cnido-glandular tract at B	<<b	=b	<b	<b
Craspedonemes of craspedion at fertile mesenteries	Sometimes present	Absent	Absent	Absent

330; Duerden 1902b: 301; Roule 1905: 89; McMurrich 1910a: 11,15–16,20; Hargitt 1912: 249; Mello-Leitão 1919: 36–38; van Beneden 1924: 91; Field 1949: 5–6, 18–21, 27; den Hartog 1977: 212; Pei 1998: 179–180

Ceriantheopsis americanus: Carlgren 1912a: 366; Carlgren 1912b: 19–26; Pax 1924: 118; Carlgren 1940: 6, 12–13; Leloup 1964: 257; Frey 1970: 309–311; Peteya 1973a: 301–316; Peteya 1973b: 1–10; Widersten 1976: 858; Shepard et al. 1986: 625–646; Kristensen et al. 1991: 590–591, 589–614; Sebens 1998: 13, 16, 21, 57; Holohan et al. 1998: 466–468; Molodtsova 2000: 14,17; Molodtsova et al. 2011: 2–3, 5–7; Reft and Daly 2012: 123–125, 127, 129; Mata et al. 2012: 602–603; Kayal et al. 2013: 3, 5–6, 10–11, 15; Stampar et al. 2014a: 2, 8

Cerianthiopsis americanus: Hedgpeth 1954: 286–290

Ceriantheopsis americana: Stampar et al. 2015b: 1–6; Stampar et al. 2016a: 69

Type locality. Off Charleston, South Carolina; Beaufort, North Carolina, United States of America (not specified).

Distribution. Atlantic coast of United States and Canada, Gulf of Mexico, and Caribbean Sea, at 2–250 m depth.

Remarks. This species is probably the most extensively studied among the Ceriantharia. There are appropriate descriptions of specimens (McMurrich 1910; Carlgren 1912a) and there is much biological information, especially related to ecological aspects (Shepard et al. 1986; Kristensen et al. 1991; Holohan et al. 1998). One important issue that still needs be studied is the possible occurrence of this species in the deep sea. Several photographic records, especially from ROV surveys below 400 m depth are available on the internet, but, to date, no such deep specimens have been collected for study.

Type material. Museum of Comparative Zoology (Harvard) – Invertebrate Zoology 243 and SCOR-1245 and Peabody Museum of Natural History (Yale) – YPM IZ 000977.CN (syntype).

5 *Ceriantheopsis austroafricanus* Molodtsova, Griffiths & Acuña, 2011

http://zoobank.org/5E824C53-474E-4822-B48E-EA47D6801DC0

Ceriantheopsis austroafricanus Molodtsova et al., 2011: 1–7; Stampar et al. 2015b: 1–3, 6

Type locality. Off Cape Town, South Africa.

Distribution. Only known from shallow waters at the type locality (8–15 m depth).

Remarks. This species was recently described and therefore little is known about it beyond a detailed morphological description. One of the most interesting features of the species is the wide range of colors (Molodtsova et al. 2011). This species occurs in waters around Cape Town. Interestingly, this species is found close to industrialized coastal development, such as marinas and ports (S. Stampar pers. obs.), which may have provided a special habitat.

Type material. Zoological Museum of Moscow State University – ZMMU No. Ec-105 (holotype).

6 *Ceriantheopsis lineata* Stampar, Scarabino, Pastorino & Morandini, 2015

http://zoobank.org/DD01594B-5E3E-4F92-9877-96AF05CCDE2C

Ceriantheopsis lineata Stampar et al., 2015c: 1475–1481

Type locality. off Quequén, Buenos Aires, Argentina.

Distribution. Warm temperate south-western Atlantic, from Argentina (Buenos Aires State) to Brazil, Laje de Santos (São Paulo State), at 5–130 m depth.

Remarks. This species was recently described, and little is known beyond a detailed morphological description. Similar to *Ceriantheopsis austroafricanus*, this species shows considerable variation in color pattern (Stampar et al. 2015b). The deepest record of the species is 130 m from a dredging expedition (Stampar et al. 2015b). However, it is possible that the species occurs at even greater depths.

Type material. Museu de Zoologia da Universidade de São Paulo – MZUSP 2686 (Holotype).

7 *Ceriantheopsis nikitai* Molodtsova, 2001

http://zoobank.org/References/F11F4732-5C5A-4A8D-BDDE-13D8888B11DC

Ceriantheopsis nikitai Molodtsova, 2001a: 773–780; Stampar et al. 2015c: 1475, 1480

Type locality. Benguela Upwelling System, Namibia.

Distribution. Only known from deep water at the type locality (145–240 m depth).

Remarks. This species was recently described and has not been the subject of any study since the original description of the species by Molodtsova (2001a). Recorded only from a restricted area in Namibia, this species occurs sympatrically with two other species, *Botrucnidifer shtokmani* and *Cerianthus malakhovi*. These three species were found in the same upwelling system, which suggests that they can also occur in deeper areas.

Type material. Zoological Museum of Moscow University – ZMMU UE-97 (Holotype).

Genus *Cerianthus* Delle Chiaje, 1841

Table 3

Type species. *Cerianthus membranaceus* (Spallanzani, 1784)

Number of valid species: 18

8 *Cerianthus andamanensis* Alcock, 1893

http://zoobank.org/0767B24E-372F-4A41-B206-BE26CF12FE37

Cerianthus andamanensis Alcock, 1893: 153; Carlgren 1896: 174; Pax 1910: 167; Molodtsova 2001b: 913

(?) *Cerianthus andamanensis*: Haldar 1981: 60–61

Type locality. off Port Blair, Andaman and Nicobar Islands, India.

Distribution. Only known from shallow water at the type locality.

Remarks. The species description is based on three specimens from Port Blair in the Andaman Sea (Alcock 1893); it is very simple with scant information on anatomy. The only two useful pieces of published information are related to the size of the preserved specimens (up to 10 cm in length), and the number of marginal tentacles (up to 160). The specimens observed by Alcock (1893) should be placed within the family Cerianthidae, but currently it is not possible to state that this species is truly part of the genus *Cerianthus*, and a systematic examination of this species is needed. The material recorded by Haldar

Table 3. Comparison of anatomical features of *Cerianthus* species.

Species	Directive mesenteries length	Directive labial tentacle	M-mesentery (M1) length	M-mesentery (M2) length	M-mesentery (m1) length	M-mesentery (m2) length	Mesenteries attached to siphonoglyph	Siphonoglyph shape	Number of marginal tentacles
C. andamanensis	–	–	Reach aboral pore	–	–	–	–	–	~160
C. bathymetricus	–	–	Reach aboral pore	1/2 of M-1	–	–	–	Wide?	28
C. filiformis	> stomodeum	Present	Reach aboral pore	6/8 of M-1	7/8 of M-1	5/8 of M-1	6	Wide?	~70
C. incertus	–	–	–	–	–	–	–	–	38-42
C. japonicus	> stomodeum	Present	Almost reach aboral pore	≅ M-1	3/4 of M-1	~1/2 of M-1	4?	Wide	65
C. lloydii	> stomodeum	Present	Almost reach aboral pore	Longer than M-1	1/5 of M-1	1/6 of M-1	4	Narrow	Up to 70
C. malakhovi	?		Half column (?)	> M-1	?	?	?	?	~160
C. medusula	?	?	?	?	?	?	?	?	Few
C. membranaceus	> stomodeum	Present	Almost reach aboral pore	≅M-1	≅P2	≅m-1	6	Narrow	140
C. mortenseni	>stomodeum	Present	Short, almost half of gastrovascular cavity	≅ M-1	3/4 of M-1	1/2 of M-1	8	Wide	125
C. punctatus	> stomodeum	Present	Almost reach aboral pore	=M-1	2/3 of M-1	1/4 of M-1	6	Rather wide	80-90
C. roulei	?	?	Long?	?	?	?	?	?	~40
C. stimpsonii	?	?	?	?	?	?	?	?	?
C. sulcatus	> stomodeum	Present	Reach aboral pore	≅M-1	?	?	?	Narrow	~180
C. taedus	> stomodeum	Present	Short?	Short	?	?	?	Narrow	55
C. valdiviae	≅stomodeum	Absent	Short?	=M-1	≅M-1	1/2 of M-1	4	Narrow	35
C. vas	?	?	?	?	?	?	?	?	?
C. vogti	> stomodeum	Present	(?)Almost reach aboral pore	(?)Longer than M-1	(?)1/5 of M-1	(?)1/6 of M-1	?	Narrow	30-40

(1981) is probably not the same species since the biogeographical region is different, but owing to the absence of a detailed description no definite conclusions can be drawn.

Type material. (?) Indian Museum.

9 *Cerianthus bathymetricus* Moseley, 1877

http://zoobank.org/6078abf1-2d50-4e1f-b956-2cee43bb5f87

Cerianthus bathymetricus Moseley, 1877: 302–305; Andres 1883: 350; van Beneden 1897: 142; Pax 1910: 167; Mello-Leitão 1919: 37; Molodtsova 2000: 14–15, 17, 19; Molodtsova 2001b: 913

Type locality. Deep sea, North Atlantic (35° 26'N 50° 53'W), at 5000 m depth.

Distribution. Only known from deep water at the type locality.

Remarks. This species is one of the smallest tube-dwelling anemone species known. The described specimens are only 2.5 cm long and lived in a very long membranous tube of more than 11 cm in length. The description is not detailed but provides some information on the anatomy, indicating a very long hyposulcus (especially in figure 17, Moseley 1877). Molodtsova (2001b) proposed that this species should be placed within the family Arachnactidae, however we are uncertain about this classification as some species of Cerianthidae have comparatively long hyposulcus regions, and the small size of this species may be misleading. Additionally, the description of the tube is much more consistent with the organization of Cerianthidae (see Stampar et al. 2015a). Thus, we choose to maintain this species as valid until additional studies say otherwise.

Type material. Not found in this study, but the original description provided a graphic representation.

10 *Cerianthus filiformis* Carlgren, 1924

http://zoobank.org/E466344E-55C1-4CE8-B84F-27BC677961F9

In part *Cerianthus orientalis* Verrill 1865: 151
Cerianthus sp. 1 Wassilieff 1908: 46
Cerianthus sp. 2 Wassilieff 1908: 46
Cerianthus filiformis Carlgren, 1924: 169–173; Uchida 1979: 195–197; Song 1986: 79–87; Song and Lee 1998: 239–240; Song 1998: 195–198; Pei 1998: 179–180; Song 2000: 324–326; Uchida and Soyama 2001: 127, 150, 152
Cerianthus misakiensis Nakamoto, 1923: 167

Type locality. Aburatsubo Bay, Miura, Japan.

Distribution. South Japan, South Korea, Korea (East China Sea), and China (Yellow Sea), at 1–50 m depth.

Remarks. There are some detailed descriptions about this species (e.g., Nakamoto 1923; Carlgren 1924). Uchida (1979) described the color variation of specimens from Japan (Kushimoto) and some ecological aspects. The same author also compared *C. filiformis* to other specimens described from the same area and concluded that all specimens belonged to the same species. This assumption includes the specimen from Okinose Bank, Sagami Bay (Kanagawa, Japan) described by Wassilieff as *C. orientalis* Verril, 1865. This specimen is deposited in the Zoologische Staatssammlung München (ZSM; 173/D65) and does not belong to the genus *Cerianthus* but to *Ceriantheomorphe* (S. Stampar pers. obs.). It is not very well preserved, but the overall organization of the mesenteries is quite consistent with that of *Ceriantheomorphe ambonensis* (Kwietniewski, 1898). The occurrence of *Ceriantheomorphe* in Japanese waters was also discussed by Molodtsova (2001b).

Type material. Lund Museum of Zoology – MZLU L930/3095b (Syntype).

11 *Cerianthus incertus* Carlgren, 1932

http://zoobank.org/8570871C-238B-47B6-A113-4FD870CEF0C5

Cerianthus danielsseni Levinsen, 1893: 398; Carlgren 1896: 174; Roule, 1904: 792; Kingsley 1904: 347; Roule 1905: 85–89; Pax 1910: 167; Carlgren 1912a: 5; Carlgren 1942: 71

Cerianthus incertus Carlgren, 1932: 255; Molodtsova 2000: 14–15; Molodtsova 2001b: 913; Molodtsova 2014: 100

Type locality. North Sea (not specified).

Distribution. Arctic Ocean, Norway, and Iceland, at 650–1185 m depth.

Remarks. *Cerianthus incertus* has a complicated taxonomic history and was originally described as *C. danielsseni* by Levinsen (1893) based only on its external morphology. Carlgren (1896) discussed this problem and, later, Roule (1905), based on specimens from nearby locations, described a new species using the same name. However, at this point, the name *C. danielsseni* became a homonym and was no longer available according to the rules of the International Commission on Zoological Nomenclature (ICZN). Thus, Carlgren (1932) suggested a new name (*Cerianthus incertus*) to solve both situations. Molodtsova (2014) postulated that *C. incertus* is a junior synonym of *C. vogti*, but there are no data available to confirm this hypothesis. Despite discussions on the past taxonomic confusion, this species is still understudied.

Type material. Not found in this study.

12 *Cerianthus japonicus* Carlgren, 1924

http://zoobank.org/116CDC46-02C7-4B61-B791-F1228F8AD3D3

Cerianthus japonicus Carlgren, 1924: 173–175, Uchida 1979: 185–194; Molodtsova 2000: 19; Molodtsova 2001b: 913

Type locality. Aburatsubo, Misaki (Sagami Bay), Japan.

Distribution. Sagami Bay and Miyazaki, Kyushu Island, Japan; North Hamgyong Province, North Korea, at 10–100 m depth.

Remarks. The original species description was based on two small specimens, one from North Korea (North Hamgyong Province) and the other one from Japan, Aburatsubo, Misaki (Sagami Bay). The description is quite adequate and presents the most important characteristics of the species. However, as noted by Molodtsova (2001b), differences between *C. japonicus* and *C. punctatus* Uchida, 1979 are very subtle. There are only two reliable characters that can be used to differentiate the two species: (1) the organization of the tentacular pseudocycles and (2) the number of mesenteries attached to the siphonoglyph. The first is a plastic character and intraspecific variation has been reported (Carlgren 1912a; Arai 1965), while the second seems to be consistent (Stampar et al. 2016). However, figure 4 by Carlgren (1924) does not allow verification if the third pair of mesenteries (P3) is in contact with the siphonoglyph or not. If the siphonoglyph format is the same as indicated by Uchida (1979), the P3 is probably also connected. Most data indicate that *C. punctatus* is synonymous to *C. japonicus*, which currently cannot be confirmed based on the available data.

Type material. Museum of Evolution- Evolutionsmuseet (Uppsala University – ZTY 2516) (Holotype).

13 *Cerianthus lloydii* Gosse, 1859

http://zoobank.org/F0DC99E3-1FB9-4729-9316-01535953DD3A

Edwardsia vestita Gosse, 1856a: 74–75

Cerianthus membranaceus Gosse, 1858: 419

Cerianthus lloydii Gosse, 1859: 50; Gosse 1860: 268–274; Fischer 1874: 201; M'Intosh 1875: 38–39; Robertson 1876: 25, 30; Koren and Danielssen 1877: 80; Andres 1883: 554; Hartlaub 1884: 203; Fischer 1887: 383–384, 432, 437; Carlgren 1893: 120–123, 133, 148; van Beneden 1897: 139–140, 142; Fowler 1897: 806; Haddon 1898: 401; Gravier 1902: 592; Gravier 1904: 259, 267, 276, 278, 280, 288; Roule 1904: 791–792; Roule 1905: 83–85; Walton 1908: 215, 225–226; Torrey and Kleeberger 1909: 117; Pax 1910: 166; McMurrich 1910: 10–11, 17–18; Carlgren 1912a: 11–18; Mello-Leitão 1919: 36, 39; Gravier 1922: 88–89; van Beneden 1924: 101–116, 126, 154; Pax 1928: 201, 234; Stephenson 1928: 83–84; Carlgren 1928: 255–263; Carlgren 1931: 10; Leloup 1931: 2, 3, 5–9; Carlgren 1932: 264–266; Müllegger 1938: 2, 12, 13; Carlgren 1940: 9, 10; Carlgren 1942: 69–71; Nyholm 1943: 95–140, 193–227; Dons 1945: 20; Carlgren 1945: 67–69, 71, 155; Teissier 1950: 33; Williams 1954: 52; Füller 1957: 31; Robins 1969: 339; Riemann-Zürneck 1969: 170, 199, 201, 210, 211, 225; Cutress 1961: 80; Laverack and Blackler 1974: 28; Manuel 1977: 484; den Hartog 1977: 233; Uchida 1979: 194; Manuel 1981: 64–66; Ates 1982: 80–83; Braber and Borghouts 1977: 16, 17; Eleftheriou and Basford 1983: 147–157; Ates 1985:

230–232; Chintiroglou and Koukouras 1991: 395; Harms 1993: 16; Molodtsova and Malakhov 1995a: 5–16; Molodtsova and Malakhov 1995b: 4–11; Ates 1997: 10, 18, 24, 25; Sebens 1998: 48; Blanco 1987: 198; Vafidis and Koukouras 1998: 123; Moore and Cameron 1999: 369–370; Molodtsova 2000: 3, 7, 12–13, 17; Molodtsova 2001a: 778; Molodtsova 2001b: 919; Molodtsova 2001c: 1035; Grebel'nyi 2001: 36; Uchida and Soyama 2001: 129, 150, 152; Molodtsova 2001d: 9, 10; Molodtsova 2003: 252; Molodtsova 2004a: 297; Molodtsova 2004b: 261; Wieking and Kröncke 2005: 395–396; Brown and Collier 2007: 207; Rehm and Rachor 2007: 130, 132; Schückel et al. 2010: 5–7, 9; Bolam et al. 2011: 2239, 2241; Strain et al. 2012: 63–65; Sciberras et al. 2013: 91, 93, 95; Peckett et al. 2014: 336; Coolen et al. 2015: 87

(?) *Cerianthus borealis* Danielssen, 1860: 251; Verrill 1873b: 405, 414; Danielssen 1888: 1–12; van Beneden 1924: 91, 120–127, 128–131

Cerianthus vermicularis Lütken, 1860: 199–200

Cerianthus lutkenii Andres, 1883: 353

Arachnactis bournei Fowler, 1897: 805–807 (larval stage)

Cereanthus lloydii Goette, 1897: 293

Cerianthus lloydii borealis Grieg, 1913: 142

Synarachnactis bournei Leloup, 1962: 2–4, 6–7 (larval stage)

Cerianthus septentrionalis van Beneden, 1924: 120: 126–131; Molodtsova 2001d: 9–10

(?) *Cerianthus* sp. Tarasov et al. 1990: 1–3; 6; 15, 17

(?) *Cerianthus lloydii*: Kussakin and Kostina 1996: 207; Çinar et al. 2014: 684

Type locality. Menai Strait, Irish Sea, United Kingdom.

Distribution. North Sea, Norwegian Sea, Barents Sea, Greenland Sea, Bay of Biscay, and (?) Sea of Okhotsk; (?) depths from 2 m to the deep sea,

Remarks. This species has been the subject of many studies. There have been several morphological descriptions (e.g., Gosse 1860; Carlgren 1912a; Molodtsova and Malakhov 1995a) and several aspects of its ecology and life cycle have been investigated (e.g., van Beneden 1924; Nyholm 1943; Molodtsova and Malakhov 1995b). However, two points still need further attention. The first is related to the distribution of the species, as the presence of some disjointed records in the Pacific Ocean raise the possibility of a disjunct distribution (e.g., more than one species contained in these records). However, the presence of larvae in plankton for long periods of time (Nyholm 1943) may explain the very large occurrence areas as already known for other Ceriantharia species (Stampar et al. 2015c). Braber and Borghouts (1977) reported the occurrence of this species from an estuary system (salinity around 16 psu), and Çinar et al. (2014) from the coast of Turkey, although the second record is questionable. The second point is related to the position of the species within the genus *Cerianthus*. Preliminary studies (unpublished) based on molecular data indicate that perhaps this species is more related to the genus *Ceriantheopsis* than to *Cerianthus*.

Type material. Not found in this study.

14 *Cerianthus malakhovi* Molodtsova, 2001

http://zoobank.org/830A9DD9-8EE9-4849-94EA-D89979D06926

Cerianthus malakhovi Molodtsova, 2001a: 909–913; Molodtsova 2001b: 913; Molodstova et al. 2011: 1

Type locality. Close to Torra Bay and Mowe Bay, Skeleton Coast Park, Namibia; at 300–350 m depth.

Distribution. Only known from deep water at the type locality.

Remarks. This species has been described in detail relatively recently based on five collected specimens. The original description, in Russian, contains no information on living animals because the material examined was already fixed at the time of diagnosis. This is a species that requires attention, as it can occur in deeper waters and may contain very important evolutionary information.

Type material. Zoological Museum of Moscow University, ZMMU EC-102 (Holotype).

15 *Cerianthus medusula* (Klunzinger, 1877)

http://zoobank.org/0D8AA956-7C46-4DCA-889E-32BCFC84F419

Paractis medusula Klunzinger, 1877: 71–72

Cerianthus medusula Andres, 1883: 353–354; Cerfontaine 1891a: 37–38; van Beneden 1897: 141; Mello-Leitão 1919: 36

(?) *Pachycerianthus maua*: Krempf 1905: 195

(?) *Pachycerianthus mana*: Fishelson 1970: 109

Type locality. Al-Qusair (Red Sea), Egypt.

Distribution. Only known from shallow water (at < 5 m depth) at the type locality.

Remarks. This is another species with only little available data, and these are quite contradictory. This species was described as a sea anemone (order Actiniaria) by Klunzinger (1877) based only on the external morphology. Andres (1883) described some aspects of the external morphology based on work by Klunzinger (1877) and indicated that this must be a species of family Cerianthidae. Cerfontaine (1891a) argued that this species may be the same as *C. oligopodus* (= *Arachanthus oligopodus*) found in Italy, and furthermore the specimen observed by Klunzinger (1877) was not in good condition. However, it is not possible to make more statements about this species due to the absence of material available from the region. On the other hand, the indication that this species is a member of the family Arachnactidae as stated by Cerfontaine (1891a) seems to be incorrect. The few characters present in the descriptions are not consistent with those of the Arachnactidae, but instead with those of the Cerianthidae. This is a species that requires additional sampling from the type locality for further examination, especially as some specimens identified as *Pachycerianthus maua* Carlgren, 1900 have been subsequently collected from the same region (Krempf 1905; Fishelson 1970).

Type material. Not found in this study, but the original description provided a graphic representation.

16 *Cerianthus membranaceus* (Gmelin, 1791)

http://zoobank.org/3AD7FFEB-56C0-49A3-9BDB-00A813327D90

Tubularie Spallanzani, 1784: 627–628
(?) *Tubularie*: Rapp 1829: 656–658
Tubularia membranosa Gmelin, 1791: 3836
Actinia cylindrica Renier, 1807: 23
Actinia vestita Renier, 1807: 23–24
Moschata rhododactyla Renier in de Blainville, 1830: 284; de Blainville 1834: 318;
Cereus cupreus Ilmoni, 1830: 698–699; Ilmoni 1831: 123
In part *Actinia elongata* Grube, 1840: 11–12; Sars 1857: 33
Cerianthus cornucopia Delle Chiaje, 1841: 136; Milne Edwards and Haime 1851: 14
Cerianthus breae Delle Chiaje, 1841: 136
Cerianthus actiniodeus Delle Chiaje, 1841: 136
Cerianthus membranaceus: Haime 1854: 352–389; Milne-Edwards 1857: 309; Sars 1857: 28–32; Agassiz 1863: 529; Fischer 1874: 200–203, 237–239; Fischer 1875: 184–185; Heider 1879: 204–254; Jourdan 1880: 16, 44–45, 103–117, 130–132, 152–153; Andres 1881: 331–332; Andres 1883: 347–349; Mark 1884: 42; Graeffe 1884: 340; Fischer 1887: 383–385, 405, 432, 435; Hertwig 1888: 54; Fischer 1889 252, 254–265; Hickson 1889: 8; Cerfontaine 1891a: 37; Cerfontaine 1891b: 133–141; Goette 1897: 292–316; van Beneden 1897: 54–56, 139, 142; Gravier 1902: 592; Child 1903a: 239–260; Child 1903b: 10; Child 1904a: 70–71; Child 1904b: 279–284; Gravier 1904: 259, 269, 276, 278, 280; Carlgren 1906: 77–78; van Beneden 1924: 18, 28, 59, 30–68, 70, 73, 77, 85, 92, 94, 104, 108, 135–144, 163–164, 175; Carlgren 1927: 443; Menon 1927: 31–32; Torelli 1932: 2–15; Müllegger 1938: 2, 12; Pax and Müller 1955:110; Leloup 1960:1–3; Pax and Müller 1962: 107–110; Leloup 1962: 3–4, 6–7; Schmidt 1972: 427, 429, 431, 433; Schmidt 1974: 535, 537, 547; den Hartog 1977: 233, 235; Uchida 1979: 194; Ates 1982: 80–83; Tur and Godall 1982: 178, 180–182; Gili 1982: 120, 125–126; Ates 1985: 230; Morri et al. 1991: 37; Chintiroglou et al. 1995: 362; Vafidis and Koukouras 1998: 119–120, 123; Molodtsova 2000: 14, 17; Ocaña et al. 2000a: 57; Molodtsova 2001b: 913; Molodtsova 2004: 261; Wiedenmann et al. 2004: 270, 272–274, 276; Calado 2006: 391; Nienhaus et al. 2006: 12942–12943; Casellato et al. 2007: 127, 129; Cosentino et al. 2011: 409–411, 413–414; Lo Iacono et al. 2012: 466–467; Rastorgueff et al. 2015: 142, 148; Stampar et al. 2015b: 2167
(?) *Edwardsia vestita* Gosse, 1856a: 74–75; Gosse 1856b: 220; Milne-Edwards 1857: 286; Gray 1867: 240
(?) *Cerianthus membranaceus*: Gosse 1858: 419; Heller 1868: 20, 79
Cerianthus cylindricus Milne-Edwards, 1857: 309; Heller 1868: 20, 79
Saccanthus purpurescens Milne-Edwards, 1857: 310

Cerianthis membranaceus: Sars 1857: 28–32
(?) *Cerianthus lloydii* Gosse, 1859: 419; Çinar et al. 2014: 684
Cerianthus membranaceus nigricans Andres, 1881: 332
Cerianthus membranaceus violaceus Andres, 1881: 332
Cerianthus membranaceus viridis Andres, 1881: 332
Cerianthus membranaceus roseus Andres, 1881: 332
Cerianthus nans Andres, 1881: 333
Saccanthus purpurascens Andres, 1883: 351
Saccanthus purpurensis van Beneden, 1897: 142
Pachycerianthus multiplicatus: Çinar et al. 2014: 684

Type locality. Mediterranean Sea, Italy (not specified).

Distribution. Mediterranean Sea (Italian coast), shallow waters.

Remarks. This is one of the most well-known cerianthid species, but at the same time there are many questions about the taxonomic consistency of past works. This was the first species of Ceriantharia described (type locality Italy); however, this has caused many records from the Mediterranean Sea being incorrectly attributed to this species. For example, Pax (1908) argued that *C.* (*Saccanthus*) *maderensis* (= *Isarachnanthus maderensis*) Johnson, 1861 is synonym of *C. membranaceus* based on the two species' original descriptions. However, the descriptions presented and discussed by Johnson (1861) and Pax (1908) are incompatible with *C. membranaceus* and more likely describe a species of the family Arachnactidae, perhaps a member of the genus *Isarachnanthus*. In addition, *I. maderensis* is very common in Madeira and the Azores (Stampar et al. 2012; Stampar and Morandini 2017). Haque (1977) recorded *C. membranaceus* from Bangladesh and Pakistan, but these records are biogeographically incongruent and probably these specimens from the Indian Ocean are another species. In short, *C. membranaceus* is a species that requires a comprehensive review of all its records, especially for the presence of cryptic species, and to assess if the different morphotypes reported truly belong to just one species or to a species complex.

Type material. Not found in this study.

17 (?) *Cerianthus mortenseni* Carlgren, 1924

http://zoobank.org/3AA339E2-4BFC-424A-997A-BBEA7EB45041

Cerianthus mortenseni Carlgren, 1924: 175–182, 195; Molodtsova 2001b: 773

Type locality. Paniquian Island, Mindoro, Philippines.

Distribution. Only known from shallow water at the type locality.

Remarks. This is a very intriguing species as the two specimens described in the original description are very different in shape. The organization of the mesenteries is not coincident on both sides of the body, indicating a considerable difference in the development of mesenteries (Carlgren 1924). This sort of large variation is not commonly reported in tube-dwelling anemones. The mesentery organization and associated structures indicate a strong correlation of these specimens with the genera *Cerianthus* and *Pachycerianthus*. Thus, this species may be important in the ongoing discussion about the validity of the genus *Pachycerianthus* (Torelli, 1961). Unfortunately, these are the only two specimens collected from the type locality (Philippines). Other specimens examined from this area (S. Stampar pers. obs.) are not similar to the specimens described by Carlgren (1924).

Type material. Department of Zoology, University of Stockholm, Sweden (holotype) (?).

18 *Cerianthus punctatus* Uchida, 1979

http://zoobank.org/DBEE9A26-932A-4F64-B0D5-12BF79BA5E33

Cerianthus punctatus Uchida, 1979: 189–195; Molodtsova 2000: 19; Uchida and Soyama 2001: 129, 150, 152; Molodtsova 2001b: 913

Type locality. Suruga Bay (Numazu), Japan.

Distribution. Only known from shallow water at the type locality.

Remarks. The available information on this species is amongst the most complete from before the advent of detailed descriptions in the 2000s. Uchida (1979) gives a complete comparison of several characters with most species of the genus *Cerianthus*. However, besides morphological data there is still no other information about this species (e.g., reproduction).

Type material. Saibura Marine Park Research Station (lost?), but the original description provided a graphic representation.

19 *Cerianthus roulei* Carlgren, 1912

http://zoobank.org/8180341D-C667-45AF-9A80-B85DB5C6B2CD

Cerianthus lloydii Gosse, 1859: 50; Roule 1904: 791–792; Roule 1905: 83–85; van Beneden 1924: 111–116

Cerianthus roulei Carlgren, 1912a: 3–5; Carlgren 1932: 255–256; Carlgren 1942: 71; Molodtsova 2001b: 913

Type locality. close to Svalbard, Norway, Greenland Sea.

Distribution. Svalbard, Norway, Greenland Sea; depth unknown.

Remarks. This species has a very deficient description and is represented by very few museum specimens for comparison. The description of *C. lloydii* by Roule (1905) (see synonymy list) may fit a range of species (e.g., *Cerianthus lloydii*, *Ceriantheopsis americana*) and thus it is not possible to discuss it based on these data. The type locality is difficult to reach, and it may be very problematic to obtain additional specimens due to the absence of precise locality data and because material is likely to be from great depths up to 5000 m (Ritzmann et al. 2004). Therefore, the validity of this species remains uncertain.

Type material. Not found in this study.

20 (?) *Cerianthus stimpsonii* Verrill, 1868

http://zoobank.org/555D3481-FEF5-4615-9C3F-DE58BB8B4EE8

Cerianthus stimpsonii Verrill, 1868: 317–318; Verrill 1870: 102; Andres 1883: 351–352; van Beneden 1897: 140; Pax 1910: 167; Mello-Leitão 1919: 36; Molodtsova 2001b: 913

Type locality. Port Lloyd, Bonin Islands (Ogasawara Islands), Japan.

Distribution. Only known from shallow water (18 m depth) at the type locality.

Remarks. Based on the description by Verrill (1868), this species probably belongs to the family Arachnactidae, particularly due to the description of a soft tube (see Stampar et al. 2015b). The few external characters presented are only consistent with those of the family Arachnactidae. Unfortunately, there are no specimens from the Ogasawara Islands deposited in museums, and further discussions on this point depends on finding some material that can be correlated with the type material or else new collections for the designation of a neotype.

Type material. Not found in this study.

21 *Cerianthus sulcatus* Kwietniewski, 1898

http://zoobank.org/98D51C07-651B-4476-8409-BE60BA39C86A

Cerianthus sulcatus Kwietniewski, 1898: 427; Pax 1910: 167; Carlgren 1912a: 44–47; Uchida 1979: 194; Molodtsova 2001b: 919

(?) *Cerianthus sulcatus*: McMurrich 1910: 28–30

Type locality. Raha, Ambon, Moluccas, Indonesia.

Distribution. Only known from shallow water at the type locality.

Remarks. This species was described by Kwietniewski (1898) based on a 4 cm long and 2.5 cm wide specimen with 90 tentacles in each tentacle series (marginal and labial) and three cycles each. However, these are the only characteristics indicated. McMurrich (1910a) gave a description of a specimen collected from near the type locality. However, the description is incomplete and presents some differences compared to original description. Thus, currently, we cannot confirm if this species is valid or not.

Type material. Not found in this study.

22 *Cerianthus taedus* McMurrich, 1910

http://zoobank.org/DBA7107E-9E29-43D3-8345-822BB1D77067

Cerianthus taedus McMurrich, 1910: 30–31; Carlgren 1912a: 44–47; van Soest 1979: 117; Pei 1998: 181

Type locality. Makassar Strait, Central Sulawesi, Indonesia.

Distribution. Only known from deep water (at 724 m depth) at the type locality.

Remarks. This species was described based on only one damaged specimen, which was 6 cm long, with 55 marginal and labial tentacles arranged in two and four cycles, respectively. The organization of the mesenteries was not described in detail by McMurrich (1910), who simply indicated the alternation of fertile and sterile mesenteries. There are several observations of different morphotypes that are not formally associated with any other name described from this or related areas. As there are no other species described for this region with this morphotype, it is probably a valid species, but it is not possible to certainly state that this species belongs to *Cerianthus*.

Type material. Possibly lost (Zoological Museum of Amsterdam, now Naturalis Biodiversity Center, Leiden).

23 *Cerianthus valdiviae* Carlgren, 1912

http://zoobank.org/15818B70-049E-4801-AFB0-A1D1E69FCA4A

Cerianthus valdiviae Carlgren, 1912a: 44–47; Carlgren 1923: 245–252; Uchida 1979: 193; Molodtsova 2001b: 929

Type locality. Between Keeling and south Sumatra, Indian Ocean.

Distribution. Only known from deep water (at 5000 m depth) at the type locality.

Remarks. This species was initially described in a table by Carlgren (1912a). However, the same author redescribed this species in 1923 in more detail. This is a species from the deep sea; however, the detailed description allows confirmation that this species belongs to *Cerianthus*. This is another example of a species that needs further study, as it may present very different characters compared to species from shallow waters.

Type material. Not found in this study.

24 *Cerianthus vas* McMurrich, 1893

http://zoobank.org/c01102cc-ec9d-474a-968e-82b0bbe5686f

Cerianthus vas McMurrich, 1893: 202–203, 206; Carlgren 1896:174; Haddon 1898: 401; Torrey and Kleeberger 1909: 115 -116; Pax 1910: 167; Arai 1965: 205

Type locality. Cedros Island, Mexico (Pacific coast).

Distribution. Only known from shallow to deep water (at 80 m depth) at the type locality.

Remarks. This is a doubtful species, as the original description is very incomplete, and some characters are incongruent. Torrey and Kleeberger (1909) comment that *Cerianthus vas* is a very problematic species, but they did not discuss the problems in detail. This species may actually be valid, but due to the absence of materials from the same depth and location, it is not possible to further discuss this.

Type material. Not found in this study, but the original description provided a graphic representation.

25 *Cerianthus vogti* Danielssen, 1890

http://zoobank.org/3B09DBC0-6D5E-4371-AAD7-94F8DAA4DABC

Cerianthus vogti Danielssen, 1890: 137–142; Carlgren 1895: 284; Roule 1905: 89; Pax 1910: 167; Carlgren 1912a: 18–21; Mello-Leitão 1919: 36–38; Carlgren 1932: 255; Carlgren 1942: 69, 71; Jensen 1992: 75–80; Molodtsova 2000: 15,17; Molodtsova 2001b: 919

Cerianthus abyssorum Danielssen, 1890: 143; Carlgren 1895: 284; van Beneden 1897: 140; Roule 1905: 89; Pax 1910: 167; Mello-Leitão 1919: 36

Type locality. Norwegian Sea (not specified).

Distribution. Only known from deep water (at 900–1400 m depth) at the type locality.

Remarks. This species is well known, even though it is a species from deeper areas. The description by Danielssen (1890) is incomplete as it presents few characters related to the organization of the mesenteries. Nevertheless, it is quite detailed in various other aspects. Carlgren (1912a) presents a slightly more complete description with more comprehensive information on the organization of the mesenteries and a comparison with *C. lloydii*. Jensen (1992) presents environmental and biological data about the species, especially on the occurrence of branching and fairly long tubes (tube system).

Type material. Not found in this study.

Genus *Pachycerianthus* Roule, 1904

Table 4

Type species. *Pachycerianthus multiplicatus* Carlgren, 1912a (proposed by Kelly and Keegan 2000)

Number of valid species: 16

26 *Pachycerianthus aestuarii* (Torrey & Kleeburger, 1909)

http://zoobank.org/3DEBCB69-32C3-4CDD-8F03-AFBD67DFDBB8

Cerianthus aestuarii: Child, 1908: 27–53; Torrey and Kleeburger 1909: 115–119, 121, 123; Pax 1910: 167; Pei 1998: 181

Pachycerianthus aestuari: McMurrich, 1910: 11; Arai 1965: 205, 210; Arai 1971: 1680; Carter 1995: 6

Pachycerianthus aestuarii: Carlgren 1912a: 44–47; Stampar et al. 2014b: 345, 350, 352

Type locality. Mission Bay, East Pacific, California, United States of America.

Distribution. East Pacific, California, USA, shallow waters.

Remarks. This species was described by Torrey and Kleeburger (1909) based on specimens obtained from Mission Bay, California. This description is not very detailed but relevant information about its morphology is available. Child (1908) described some information on the movements and regeneration of *P.* (*Cerianthus*) *aestuarii* and morphological adaptations in relation to the environment. Carlgren (1912a) moved the species to genus *Pachycerianthus* based on the original description. Arai (1965) described a new species of the same genus, *P. torreyi*, from a nearby area and claimed that this was not the same species as described by Torrey and Kleeburger (1909). This species was considered a synonym of *P. fimbriatus* by Arai (1971), which occurs in the same area as *P. aestuarii*.

Type material. Not found in this study, but the original description provided a graphic representation.

27 *Pachycerianthus borealis* (Verrill, 1873)

http://zoobank.org/73181FBE-06D8-416C-8C79-C94AF7FB94E7

Cerianthus borealis: Danielssen 1860: 251 (senior homonym); Verrill 1873b: 5,14; Verrill 1873a: 349, 350, 368, 391; Verrill 1873c: 440–441; Verrill 1874: 413; Harger and Smith 1876: 54; Verrill 1879: 15; Andres 1883: 352; Verrill 1885: 534; Danielssen 1888 1–12; McMurrich 1893: 204; van Beneden 1897: 140 -142; Parker 1900: 757; Kingsley 1904: 345–359; Torrey and Kleeburger 1909: 119, 125; McMurrich 1910a: 167; Pax 1910: 167; Carlgren 1912a: 44–47; Mello-Leitão 1919: 36; 37; Verrill 1922: 134–136; van Beneden 1924: 91, 120–127, 128–131; MacGinitie 1955: 61, 75, 84, 85, 97, 122; Widersten 1976: 857, 858; Shepard et al. 1986: 625–646; Sebens 1998: 13, 16, 21, 57; Molodtsova 2001d: 9; Molodtsova 2004b: 261

Cerianthus verrillii McMurrich, 1910: 10–11

Pachycerianthus borealis: Molodtsova 2000: 15, 17; Molodtsova 2001b: 9; Stampar et al. 2014b: 344–345, 350, 352–353

Type locality. Georges Bank, Massachusetts, United States/Nova Scotia, Canada (not specified).

Distribution. Northwestern Atlantic (Arctic Sea to North Carolina, USA), at depths of 10–500 m.

Remarks. This species was described by Verrill (1873b) based on external morphology but he did not give many details. Danielssen (1888) gave a very detailed description, including various characters concerning the internal anatomy. A century later, Shepard et al. (1986) presented a study on ecological aspects of tube-dwelling anemones from the Northwest Atlantic and included some information about *Pachycerianthus* (*Cerianthus*) *borealis*. Molodtsova (2001b), in her discussion of the genus *Cerianthus*, showed that *Cerianthus borealis* should be part of the genus *Pachycerianthus*. This species occurs at lower temperatures and apparently resists considerable variations in salinity (S. Stampar pers. obs.).

Table 4. Comparison of anatomical features of *Pachycerianthus* species (after Stampar et al. 2015).

Species	Directive mesenteries length	Directive labial tentacle	M-mesentery (M1) length	M-mesentery (M2) length	M-mesentery (m1) length	M-mesentery (m2) length	Mesenteries attached to siphonoglyph	Siphonoglyph shape	Number of marginal tentacles
P. aestuari	> stomodeum	?	Reach aboral pore	≅ M-1	1/5 of M-1	= m-1	16	Wide	30–34
P. benedeni	< stomodeum	?	Reach aboral pore	?	?	?	6?	Wide?	~125
P. borealis	> stomodeum	?	Reach aboral pore	= M-1	3/4 of M-1	~1/3 of M-1	8	Wide	139–155
P. curacaoensis	> stomodeum	Absent	Reach aboral pore	1/2 of M-1	1/4 of M-1	2/3 of m-1	4	Short and narrow	74–105
P. delwynae	> stomodeum	Present	Almost reach aboral pore	Larger than M-1	1/3 of M-1	1/2 of M-1	6	Narrow	89–114
P. dohrni	?		Half column (?)	> M-1	?	?	?	?	~160
P. fimbriatus	> stomodeum	Present	Reach aboral pore	3/4 of M-1	1/3 of M-1	1/3 of M-1	8	Wide and long	<60
P. insignis	< stomodeum	Present	Almost reach aboral pore	≅M-1	≅M-1	≅M-2	8	?	~100
P. johnsoni	< stomodeum	?	Reach aboral pore	≅3/4 of M-1	3/4 of M-1	1/2 of M-1	8	Wide	~108
P. longistriatus	> stomodeum	Present	Reach aboral pore	=M-1	1/3 of M-1	1/4 of M-1	6	Wide	138–140
P. magnus	> stomodeum	Present	Almost reach aboral pore	3/4 of M-1	1/3 of M-1	1/2 of M-1	6	Short and narrow	~120
P. maua	< stomodeum	Absent	Reach aboral pore	1/4 of M-1?	1/3 of M-1?	1/3 of M-1?	6	Narrow	~150
P. monostichus	> stomodeum	Present	Reach aboral pore	≅M-1	1/2 of M-1	≅m-1	8	Narrow and long	~47
P. multiplicatus	> stomodeum	Absent	Reach aboral pore	=M-1	1/3 of M-1	1/3 of M-1	6	Narrow	175
P. nobilis	?	?	?	?	?	?	?	?	160–170
P. schlenzae	> stomodeum	Present	Reach aboral pore	3/4 of M-1	1/2 of M-1	1/3 of M-1	6	Long and narrow	60–85
P. solitarius	> stomodeum	Present	Reach aboral pore	≅ M-1	1/4 of M-1	1/5 of M-1	6	Narrow	~64

Type material. Peabody Museum of Natural History (Yale – YPM 9830, 9831, 9832 (Syntype).

28 *Pachycerianthus curacaoensis* den Hartog, 1977

http://zoobank.org/9599F783-723C-4B15-9949-3C80F5AB8B98

Pachycerianthus curacaoensis den Hartog, 1977: 215–221, 237; Carter 1995: 6; Molodtsova 2000: 15, 17; Stampar et al. 2014b: 344, 345, 350, 353

Type locality. Curaçao, Dutch Caribbean.

Distribution. Caribbean Sea (Curaçao), at 65–75 m depth.

Remarks. This species was described by den Hartog (1977) based on specimens from Curaçao. The description of this species is fairly detailed and includes a wide range of biological and morphological information. This is the only species of this genus in the Caribbean Sea and it shows no morphological similarity to congeners described from the Pacific Ocean. On the other hand, this species shares some characters with *P. schlenzae,* which was described from the South Atlantic (Stampar et al. 2014b). Thus, the evolutionary correlation of these two species is of biogeographical relevance.

Type material. Naturalis Biodiversity Center (former Rijksmuseum van Natuurlijke Historie, Leiden – RMNH.COEL.11359 (holotype).

29 *Pachycerianthus delwynae* Carter, 1995

http://zoobank.org/96DDF06E-467C-47ED-9DB1-96E8085BC67A

Pachycerianthus delwynae Carter, 1995: 2–3; Molodtsova 2007: 133; Stampar et al. 2014b: 350, 352

Type locality. off Port Jackson, Sydney harbor, Australia.

Distribution. Sydney harbor, Australia, at 5–15 m depth.

Remarks. This is one of two species of this genus described from Australia by Carter (1995), the other one being *P. longistriathus*. They co-occur in the same bay and therefore doubts about the consistency of the two taxonomic species still exist. The morphological differences between the two species appear consistent, but intraspecific variation is quite significant and thus a more thorough evaluation of the morphological characters and the inclusion of molecular data may change this view.

Type material. Australian Museum; AMG15399 (holotype).

30 *Pachycerianthus dohrni* (van Beneden, 1924)

http://zoobank.org/3C1075B6-988C-4FB5-8855-FD4CC5DCA9D0

Cerianthus membranaceus viridis Andres, 1881: 332

Cerianthus membranaceus Andres, 1883: 347–349

Cerianthus dohrni: Lo Bianco 1909: 552; Pax 1910: 166; van Beneden 1924: 24, 30, 32, 33, 45, 60, 63, 65–89, 92, 94

In part *Cerianthus viridis* Torelli, 1932: 1–15

Pachycerianthus dohrni: Carlgren 1940: 15; Arai 1971: 1679; Carter 1995: 6; Vafidis and Koukouras 1998: 122–123; Stampar et al. 2014b: 350, 352

Type locality. Naples, Tyrrhenian Sea, Italy.

Distribution. Tyrrhenian Sea, Italy and Aegean Sea, Greece, shallow waters.

Remarks. This species was initially described from the Italian coast (Naples region) as a variation of *Cerianthus membranaceus* (Andres 1881). However, Lo Bianco (1909) recognized distinct differences from the material identified as *C. membranaceus* and suggested a new name, *Cerianthus dohrni*, but without giving a description. Subsequently, van Beneden (1924) gave a very detailed morphological description of the species with some observations from specimens in aquaria. Some years later, Torelli (1932) described *Cerianthus viridis* based on specimens with a morphology clearly related to that of *Cerianthus dohrni*. Carlgren (1940) relocated *C. dohrni* to the genus *Pachycerianthus*. This is one of the largest species of tube-dwelling anemones in the world with a length of more than 40 cm, which is comparable to the lengths of *Ceriantheomorphe brasiliensis* and *Cerianthus membranaceus*.

Type material. Not designated (several specimens mentioned, which can be considered syntypes).

31 *Pachycerianthus fimbriatus* McMurrich, 1910

http://zoobank.org/A1F21314-9AFC-42C8-A5DE-1A70BB00D3AE

(?) *Cerianthus elongatus* Kwietniewski, 1898: 426–427; Pax 1910: 167

Pachycerianthus fimbriatus McMurrich, 1910: 35–38; Carlgren 1912a: 44–47; Arai 1971: 1677–1680; Arai 1972: 311–317; Arai and Walder 1973: 1086–1088, 1090; Arai and Karakashian 1973: 719–720, 723–724; Tiffon and Hugon 1977: 289–290; Uchida 1979: 188; Carter 1995: 6; Fautin 1998: 135; Arai 1985: 47–48; Pirtle et al. 2012: 1896, 1905–1906; Stampar et al. 2014b: 350, 352

Pachycerianthus plicatus Carlgren, 1924: 182–186, 195; den Hartog 1997: 352; Arai 1971: 1677; 1680

(?) *Pachycerianthus torreyi* Arai, 1965: 205–210; Arai 1971: 1677; 1680

Type locality. Cebu, Philippines.

Distribution. Sulu Sea and Celebes Sea, Philippines, and Indonesia, (?) Pacific Coast of US and Canada; shallow waters.

Remarks. This species forms part of a taxonomic problem. The description of *P. fimbriatus* was based on a study of 15 specimens collected mainly from the Celebes Sea, Philippines, by McMurrich (1910). In the same study, McMurrich argued that

Cerianthus elongatus was the same as the new species *P. fimbriatus*, and considered Kwietniewski's (1898) description as incomplete and invalid. McMurrich (1910) also argued that *Cerianthus nobilis* described by Haddon and Shackleton (1893), based on specimens from North Australia, could also be the same species, but specimens were not available for comparison. Later, Arai (1965) described a new species from the Pacific Coast of North America, *P. torreyi*. The same author in 1971 recognized that this species was highly correlated with McMurrich's *P. fimbriatus* from the Celebes Sea. Thus, Arai (1971) considered *P. torreyi* to be a junior synonym of *P. fimbriatus*. However, the geographical distribution is disjunct by 14,000 km, and it is likely that a more detailed study with the inclusion of molecular data will present different results. In our opinion, *P. torreyi* should be a valid species.

Type material. The provenance data of a specimen in the Natural History Museum at London, NHMUK 1889.11.25.64, is coherent with the locality and dates in the original description, but it is impossible to make an exact connection between the materials.

32 *Pachycerianthus insignis* Carlgren, 1951

http://zoobank.org/046E54F7-B238-4BD9-8E51-0EFA1FD54917

Pachycerianthus insignis Carlgren, 1951: 435–436; Arai 1965: 205, 210; Arai 1971: 1679; Carter 1995: 6; Stampar et al. 2014b: 350, 352

Type locality. El Mogote, Baja California, Mexico.

Distribution. Gulf of California, Mexico; shallow waters.

Remarks. Although this species occurs in an area with a long history of marine research, it is still little known, and the only study focused on this species is the original description by Carlgren (1951). The species description is based only on one individual and therefore knowledge is quite limited and morphological variation is not known to date. Thus, this species still lacks taxonomic confirmation as well as other studies.

Type material. Smithsonian National Museum of Natural History – USNM 49454 (Holotype).

33 *Pachycerianthus johnsoni* (Torrey & Kleeburger, 1909)

http://zoobank.org/789ED1B7-5FEF-49D4-937E-4B20740A295E

Cerianthus johnsoni Torrey and Kleeburger, 1909: 116, 119, 123–125; Pax 1910: 167; Pei 1998: 181

Pachycerianthus johnsoni: McMurrich 1910: 11; Carlgren 1912a: 44–47; Arai 1965: 205, 210; Arai 1971: 1679; 1680; Carter 1995: 6; Stampar et al. 2014b: 350, 352

Type locality. Los Angeles, East Pacific, United States of America.

Distribution. Only known from shallow water at the type locality.

Remarks. This is another species described from the United States' Pacific Coast by Torrey and Kleeburger (1909) with a relatively good amount of detail; like *P. insignis*, there have been no more subsequent detailed or comparative studies. Arai (1971) has been the only author that has mentioned the morphological characters of this species after the original description, but even this characterization was based on the characters listed in the original description. The taxonomic status of this species is doubtful.

Type material. Not found in this study, but the original description provided a graphic representation.

34 *Pachycerianthus longistriatus* Carter, 1995

http://zoobank.org/96D33C91-AA78-42A2-918D-C9CB9B6B3EB8

Pachycerianthus longistriatus Carter, 1995: 3–5; Stampar et al. 2014b: 350, 352

Type locality. off Port Jackson, Sydney harbor, Australia.

Distribution. Sydney Harbor, Australia; 5–10 m depth.

Remarks. As mentioned for *P. delwynae*, the taxonomic status between the two Australian species, *P. delwynae* and *P. longistriatus*, is not clear. Both were described from a very restricted area and the morphological variation between them is very subtle. There is a need for a more detailed study approach to understand the differences between these two currently valid species.

Type material. Australian Museum – AM G15402 (Holotype).

35 *Pachycerianthus magnus* (Nakamoto, 1919)

http://zoobank.org/909B29CC-61CA-4766-A000-73FB6FFAFB18

Cerianthus magnus Nakamoto, 1919: 118–120
Pachycerianthus magnus: Uchida 1979: 186–189; Carter 1995: 6; Uchida and Soyama 2001: 125, 151, 152; Molodtsova 2004b: 261; Stampar et al. 2014a: 2; Stampar et al. 2014c: 350, 352; Stampar et al. 2019: 1–9

Type locality. south of Jogashima, Sagami Bay, Miura, Kanagawa, Japan (at 1100 m depth).

Distribution. Japan and China, shallow to deep waters.

Remarks. The description of *Cerianthus magnus* by Nakamoto (1919) is quite adequate, but still very simple. Nevertheless, the author presented a scheme of the mesenteries, and two photos of preserved and dissected material, which allows an adequate comparison with other species. Uchida (1979) moved this species to the genus *Pachycerianthus* and performed a very detailed redescription of the species based on specimens from Sagami Bay, Japan. This species occurs in an area with several other species of Ceriantharia but is apparently consistent with regard to its taxonomy. The co-occurrence of these species in Sagami Bay may be relevant in an evolutionary context with a focus on environmental niche differentiation among Ceriantharia species.

Type material. Not found in this study, but the original description provided a graphic representation.

36 *Pachycerianthus maua* (Carlgren, 1900)

http://zoobank.org/7797F482-1430-400F-ABD3-7FB2E511A132

Cerianthus maua Carlgren, 1900: 27–29; Krempf 1905: 195; Pax 1909: 413; Pax 1910: 167; Schmidt 1972: 427, 433; Emig et al. 1972: 304–307

Cerianthus mana Fishelson 1970: 109

Pachycerianthus maua: Carlgren 1912b: 389–391; Arai 1971: 1680; Carter 1995: 5; Stampar et al. 2014b: 350, 352

Type locality. Mkokotoni, Zanzibar, Tanzania.

Distribution. Indian Ocean (Mozambique, Madagascar, and Tanzania) and Aden Gulf (Djibouti) and Red Sea (Egypt and Saudi Arabia), shallow waters.

Remarks. This species was described by Carlgren (1900), who subsequently moved this species to the genus *Pachycerianthus* and added some comments on its morphology (Carlgren 1912b). Krempf (1905) recorded two specimens from Djibouti, but he did not study anatomical characteristics. Much later, Fishelson (1970) recorded a great number of specimens from Eilat, Israel. However, again, the author failed to mention any anatomical characters of the specimens, and the figure of the presented specimen is quite inconsistent with the description of Carlgren (1900) or with specimens analyzed from Mozambique (S. Stampar pers. obs.). Thus, the identification of the Red Sea specimens may be misleading, and these Red Sea specimens could be classified either as another species already known to the region (perhaps *Cerianthus medusula*) or as an undescribed species.

Type material. Not found in this study, but the original description provided a graphic representation.

37 *Pachycerianthus monostichus* McMurrich, 1910

http://zoobank.org/CDDC2972-281C-488C-84C4-BD5D468ADFA1

Pachycerianthus monostichus McMurrich, 1910: 38–39; Carlgren 1912a: 44–47; Arai 1971: 1680; van Soest 1979: 118; Carter 1995: 6; den Hartog 1997: 352; Stampar et al. 2014b: 350 352

Type locality. Ambon, Maluku, Indonesia.

Distribution. Only known from shallow water at the type locality.

Remarks. This species was described by McMurrich (1910) based on two specimens from Ambon Island, Indonesia. The information presented by the author is quite suitable for characterization of the species, especially as the mesentery organization is quite conspicuous. No further relevant information on this species is available to date.

Type material. Not found in this study, but the original description provided a graphic representation.

38 *Pachycerianthus multiplicatus* Carlgren, 1912

http://zoobank.org/1D9265CA-F705-4693-B955-D17D0A63500A

Cerianthus membranaceus: Lütken 1889: 362

Cerianthus danielssen: Levinsen 1893: 397; Carlgren 1896: 174

Pachycerianthus multiplicatus Carlgren, 1912a: 5–11; Carlgren 1931: 8–9; Carlgren 1940: 9–12; Carlgren 1942: 70–71; Carlgren 1945: 68–70; Schmidt 1972: 427, 432–433; Arai 1971: 1689; Keegan and Könnecker 1973: 257 Mariscal et al. 1977: 395; Manuel 1981: 64, 67; Picton 1985: 485; McFarlane 1988: 365–370; Carter 1995: 6; Molodtsova 2000: 12, 15, 17; Jonsson et al. 2001: 189–195; Stampar et al. 2014b: 350, 352

(?) *Pachycerianthus multiplicatus*: Çinar et al. 2014: 684

Type locality. Two areas are mentioned – Kattegat Strait and Trondheim, Norway (not specified)

Distribution. North, Inner, Celtic, Irish and Norwegian Seas, Gulf of Biscay, at < 130 m depth.

Remarks. Levinsen (1893) described this species as *Cerianthus danielssen*, however, this description was incomplete and did not meet the minimum characterization requirements for a ceriantid species. Thus, Carlgren (1912a) proposed the new name *P. multiplicatus*, while giving a detailed description of this species. Carlgren (1912b) included several records in the region as well as some biological aspects. Nyholm (1943) gave a detailed study of the life cycle of the species, including information on reproductive seasons and also on larval development (a modified planula). This is a very interesting species for ecological studies, as several reports have mentioned clusters of individuals in different regions (e.g., Jonsson et al. 2001). There is still doubt about the true distribution of the species as individuals recorded from the coast of France and Spain have never been studied in detail.

Type material. (?) Lund Museum of Zoology (MZLU) - 6570 (syntype), but not formally designated in description.

39 *Pachycerianthus nobilis* (Haddon & Shackleton, 1893)

http://zoobank.org/7EE6D6AD-FAF0-447C-A609-D2D03A083096

Cerianthus nobilis Haddon and Shackleton, 1893: 116, 118; Carlgren 1896: 174; Haddon 1898: 400–401; Pax 1910: 167

Pachycerianthus nobilis: Molodtsova 2000: 19; Molodtsova 2007: 133; Stampar et al. 2014b: 350, 352

Type locality. Thursday Island, Queensland, Australia.

Distribution. Queensland and Northern Territory, Australia, New Caledonia, shallow waters.

Remarks. A large species originally described from northeastern Australia as *Cerianthus nobilis*. This description is very simple and was based only on external characters and there have been no further studies based on specimens from this area. Molodtsova (2000, 2007) correctly suggest that this species does not belong to the genus *Cerianthus*, but to the genus *Pachycerianthus*. The relation with two species described by Carter (1995) (*P. delwynae* and *P. longistriatus*) is completely unknown, however, there is the possibility that all three species are, in fact, a single one, based on their overlapping morphological characters.

Type material. Museum of Zoology (University of Cambridge) – I.33575.A-B (holotype).

40 *Pachycerianthus schlenzae* Stampar, Morandini & Silveira, 2014

http://zoobank.org/7D2022C6-CE8E-4FC4-B54D-39ED0006FA7F

Pachycerianthus sp. Vieira and Stampar 2014: 365, 367–368, 370–371
Pachycerianthus schlenzae Stampar et al., 2014b: 343–354

Type locality. off Guarapari, Espírito Santo state, Brazil.

Distribution. Brazil, from Bahia to Espírito Santo states (Abrolhos Bank and Royal Charlotte Bank), at 5–10 m depth.

Remarks. This species was recently described based on a study of several specimens from the central area of the Brazilian coast, where it is an endemic occurring along a coastline of approximately 500 km length. Some aspects of external morphology are similar to those of *P. curacaoensis* and may reflect a correlated evolutionary history between the two species. Although Stampar et al. (2014b) presented some biological information mainly related to the reproduction seasons, little is known about the ecology and biology of this species. The species is endangered as its range suffers from high levels of anthropogenic pressure (Miranda and Marques, 2016), which could result in the loss of its habitat.

Type material. Museu de Zoologia, Universidade de São Paulo (MZSP) – 1949 (Holotype).

41 *Pachycerianthus solitarius* (Rapp, 1829)

http://zoobank.org/DDC053BF-7A9C-4CB8-9126-FE701530AB39

Tubularia solitaria Rapp, 1829a: 656–658; Rapp 1829b: 48–49

(?) *Cereus cupreus* Ilmoni, 1830: 689–699; Ilmoni 1831: 123
Cerianthus brerae Delle Chiaje, 1841: 136
Edwardsia vestita Forbes, 1843: 42; Milne-Edwards 1857: 286
Cerianthus membranaceus: Sars 1857: 28–32; Heller 1868: 20, 79
Cerianthus solitarius: Andres 1881: 332; Andres 1883: 345–346; Fischer 1887: 384–385, 432, 437; Fischer 1889: 254, 264, 265; Faurot 1895: 221; van Beneden 1897: 138; Child 1903a: 239–260; Child 1903b: 8–10; Child 1904a: 70–71; Child 1904b: 266–284; Gravier 1904: 283; Rioja and Martin 1906: 280; Cerfontaine 1909: 699–700; McMurrich 1910: 17–18; Pax 1910: 166; Mello-Leitão 1919: 35–36, 39; van Beneden 1924: 29, 89–96; Torelli 1961: 17–28
Pachycerianthus solitarius: Carlgren 1912a: 367–387; Carlgren 1912b: 44–47; Carlgren 1927: 443; Panikkar 1936: 259; Pax and Müller 1962: 110; Torelli 1963: 175–177; Naumov 1968: 73; Arai 1971: 1680; Uchida 1979: 188; Williams 1981: 350; Ates 1985: 230–231; Carter 1995: 6; Molotsova 2003: 250, 252–253; Çinar et al. 2014: 684
(?) *Pachycerianthus solitarius*: Kisseleva 1975: 1595–1596; Wirtz et al. 2003: 115, 116
Cerianthus bicyclus Torelli, 1961: 17–28

Type locality. off Languedoc coast, France.

Distribution. Mediterranean Sea, Azores, and (?) Black Sea; shallow waters.

Remarks. After *Cerianthus membranaceus*, this was the second species to be formally described in Ceriantharia. It was first described as an unclassified polyp with some similarities with Hydrozoa and Anthozoa (Rapp 1829a). Later, it was only characterized as a Ceriantharia by Sars (1857). This species was widely studied by Child (1903a, 1903b, 1904a, 1904b) in a series of experimental studies related to asexual reproduction, behavior, and regeneration of polyps. Carlgren (1912b) presented a detailed redescription of this species and moved it to the genus *Pachycerianthus*. He described several abnormalities of the species' anatomy (Carlgren 1912a), which were attributed to asexual reproduction events that are uncommon in Ceriantharia. After this, several authors reported this species from various regions, including the Black Sea (Kiseleva 1975). If *P. solitarius* occurs in the Black Sea, it would show a great tolerance to brackish water. Therefore, specimens recorded in the Black Sea may not be of the same species that inhabits the Mediterranean Sea. However, there are no available specimens for comparison. Wirtz et al. (2003) recorded this species in the Azores, however a more detailed study is needed to understand if this species occurs outside the Mediterranean Sea, or whether the Azores specimens belong to *P. solitarius*.

Type material. Not found in this study.

Family Botrucnidiferidae Carlgren, 1912

Number of valid taxa: two genera and four species.

Genus *Botruanthus* McMurrich, 1910

Table 5

Type species. *Botruanthus benedeni* (Torrey & Kleeberger, 1909)

Number of valid species: 2

42 *Botruanthus benedeni* (Torrey & Kleeberger, 1909)

http://zoobank.org/B663D1F1-44EB-4EBC-8644-729518D0104A

Pachycerianthus benedeni Roule, 1904: 708–710

Cerianthus benedeni: Torrey and Kleeberger 1909: 115, 119, 120–123, 125; Pax 1910: 167;

Botryanthus benedeni: McMurrich 1910: 11; Torelli 1932: 9

Botruanthus benedeni: Carlgren 1912a: 44–47; Leloup 1932: 17; Carlgren 1951: 431, 433–435; Arai 1965: 205; den Hartog 1977: 211, 233, 236–237; Molodtsova 2001c: 1027, 1033–1035; Fautin et al. 2007: 551–552, 567–569; Stampar et al. 2016b: 1; 5

Type locality. San Diego Bay, California, United States of America.

Distribution. California (United States of America), Baja California (Mexico) and Galapagos Islands (Ecuador), shallow waters.

Remarks. This species was described based on a study of a single specimen. This species (and genus) is characterized by possessing wart-like structures (cnidorages) organized in bunches (botrucnids) in the mesenterial filaments. Except for these structures, the anatomy is very similar to species of the genus *Pachycerianthus*. The holotype is not available, and we therefore here designate a neotype collected from the same region by Charles Cutress in 1955 (NMNH 49400). This specimen was studied by Stampar et al. (2017) (erroneously referred to as "holotype") and its characters are consistent with those in the original description. Because of its importance as type species of the genus *Botruanthus*, the neotype designation for this species is justified. This is a poorly studied genus and there is no biological or ecological information about this species.

Type material. Smithsonian National Museum of Natural History (USNM) – 49400 (neotype).

43 *Botruanthus mexicanus* Stampar, González-Muñoz & Morandini, 2017

http://zoobank.org/61DE065D-E0EB-4BE4-A283-E7EADFCD7262

Botruanthus mexicanus Stampar et al., 2017: 113–118

Type locality. off Veracruz, Mexico.

Table 5. Comparison of anatomical features of *Botruanthus* species (after Stampar et al. 2016a).

	B. benedeni	*B. mexicanus*
Marginal tentacles	Up to 90–100	Up to 40–60
Directive labial tentacle	Present	Present
Arrangement of labial tentacles	(1)321.3213.3213	(2)314.2314.2314.2314
Actinopharynx	1/3 – 1/4 of gastric cavity	1/5–1/4 of gastric cavity
Oral disc	1.1–1.3 cm	0.5–0.7 cm
Siphonoglyph	Broad, 8 mesenteries attached	Narrow, 2 mesenteries attached
Directive mesenteries	>Actinopharynx (= size of Actinopharynx)	> Actinopharynx
P2	Long, almost to aboral pole (> 2/3 of gastric cavity)	Short (<1/3 of gastric cavity)
P3	Short (1/3 of P2)	Short (~P2)
M1	To aboral pore	Almost to aboral pore
M3	Almost to aboral pore	Short, 1/2 of M1
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Present
Craspedion tract at fertile mesenteries	5/7–8/9	8/9
Cnido-glandular tract at B	< ½	3/4
Craspedonemes of craspedion at fertile mesenteries	Sometimes present	Sometimes present
Botrucnidae	Rare in m and B, absent in M and b mesenteries	Very abundant (4-5 groups) in M and m, absent in B and b mesenteries

Distribution. Gulf of Mexico, intertidal to shallow waters.

Remarks. This species was recently described by specimens from the intertidal zone in reefs of Central Mexico in the Gulf of Mexico. Morphological characterization is quite easy, as the number of anatomical characters allow its distinction in relation to *B. benedeni*. There have been no studies on ecological or biological aspects of this species.

Type material. Museu de Zoologia da Universidade de São Paulo; MZUSP 002757 (Holotype).

Genus *Botrucnidifer* Carlgren, 1912

Table 6

Type species. *Botrucnidifer norvegicus* Carlgren, 1912

Number of valid species: two

44 *Botrucnidifer norvegicus* Carlgren, 1912

http://zoobank.org/5D96E928-EB37-4362-ADD0-F20293438F44

Botrucnidifer novergicus Carlgren, 1912a: 30–34; Carlgren 1931: 10; Leloup 1932: 16–18; Carlgren 1940: 6,10,14–15; Carlgren 1942: 70–71; Carlgren 1945: 72;

Table 6. Comparison of anatomical features of *Botrucnidifer* species.

	B. novergicus	*B. shtokmani*
Marginal tentacles	Up to 17	72
Directive labial tentacle	Present	Absent
Arrangement of labial tentacles	(1)431.3231.3231	(0)230.2024.3123.3142
Actinopharynx	1/4 – 1/5 of gastric cavity	1/3 of gastric cavity
Oral disc	0.3 cm	1.5 cm
Siphonoglyph	Narrow, 2 mesenteries attached	Narrow, 4 mesenteries attached
Directive mesenteries	>Actinopharynx	= Actinopharynx
P2	Long, almost to aboral pole (> 4/5 of gastric cavity)	Regular (<2/3 of gastric cavity)
P3	Long (2/3 of P2)	Short, 1/2 of P2
M1	Almost to aboral pore	= P2
M3	Almost to aboral pore (3/4 of M1)	Long, 3/4 of P2
Cnido-glandular tract at fertile mesenteries of first quartets	Present	Present
Craspedion tract at fertile mesenteries	¾	1/2 – 3/4
Cnido-glandular tract at B	Present	Present
Botrucnidae	Only in M mesenteries	Only in B/b mesenteries

Nair 1949: 245; den Hartog 1977:136; Molodtsova 2000: 14–17; Molodtsova 2001c: 1027, 1033–1036; Molodtsova 2004a: 292–293, 295–296; Stampar et al. 2016c: 2,4; Ceriello et al. 2019: 2017–2020

Type locality. Trondheimfjord**,** Trondheim, Norway.

Distribution. Norwegian Sea, at 50–700 m depth.

Remarks. This species was described by Carlgren (1912a) based on specimens from Trondheim Fjord, Norway. These are small ceriantharians (up to 4 cm long) with an expansion of the cnidoglandular tract and some botrucnidae (= cnidoragae) at the end of some mesenteries. Although the description is fairly comprehensive, knowledge of this species is limited. Other authors cite only some of the species characteristics or have reported occurrences in areas that look similar (e.g., Molodtsova 2004a). Recently, Ceriello et al. (2019) reported on the coloniality of this species, which is a newly discovered trait among Ceriantharia. This species is important in the discussion on the homology of morphological characters, particularly in relation to mesenterial structures.

Type material. Lund Museum of Zoology (MZLU) – L898/3051 and Marine invertebrate collection Norwegian University of Science and Technology University Museum (NTNU) – 40499 (syntype).

45 *Botrucnidifer shtokmani* Molodtsova, 2001

http://zoobank.org/2B2E3575-21EB-4B85-80AA-817B45BB89A1

Botrucnidifer shtokmani Molodtsova, 2001a: 773; Molodtsova 2001c: 1027–1036; Molodtsova et al. 2011: 1

Type locality. off Namibia coast (southeast Atlantic), at 130–350 m depth.

Distribution. Only known from deep water at the type locality.

Remarks. This species was described based on dredged specimens from off the Namibian coast. This is the second species of this genus that has been sampled beyond conventional SCUBA diving depths. The description of this species (in Russian) is very detailed and addresses all the necessary characters. As discussed by Molodtsova (2001c) some larval forms of this family are recognized from this area, however the link between larval and adult stages is only possible based on molecular or developmental approaches (Nyholm 1943; Stampar et al. 2015c).

Type material. Zoological Museum of Moscow University – ZMMU EC-100 (holotype).

Order Penicillaria den Hartog, 1977

Number of valid taxa: one family, two genera, and nine species

Family Arachnactidae McMurrich, 1910

Number of valid taxa: two genera, and nine species

Genus *Arachnanthus* Carlgren, 1912

Table 7

Type species. *Arachnanthus oligopodus* (Cerfontaine, 1891)

Number of valid species: Five

46 *Arachnanthus australiae* Carlgren, 1937

http://zoobank.org/249FDE31-6249-45B8-8930-D87A827BC87B

Arachnanthus australiae Carlgren, 1937: 177–180; den Hartog 1977: 235; Fautin et al. 2007: 570; Stampar et al. 2018: 3,8

Type locality. Low Isles, Queensland, Australia.

Distribution. Queensland, Australia, shallow waters.

Remarks. Carlgren (1937) described this species from northeastern Australia and this is the only study so far on this species. Although the description is adequate, it does not include detailed information. In general, the Australian coast is vastly understudied regarding Ceriantharia species diversity. The taxonomic status of *A. australiae* in relation to *Arachnanthus bockii* remains to be studied in detail.

Table 7. Comparison of anatomical features of *Arachnanthus* species (after Stampar et al. 2018).

	A. australiae	*A. bockii*	*A. oligopodus*	*A. sarsii*	*A. lilith*
Marginal tentacles	Up to 40	Up to 30	~20	Up to 35	Up to 24
Arrangement of labial tentacles	(0)1.11.11.11.11	(0)1.11.11.11.11(?)	(0)1.11.11.11.11	(0)1.11.11.11.11	(0)3.12.31.23.23.12
Length of actinopharynx	~2/3 of gastric cavity	~1/2 of gastric cavity	~1/2 of gastric cavity	~1/2 of gastric cavity	>1/2 of gastric cavity
Hyposulcus	~1/2 size of stomodeum	~1/2 size of stomodeum	~2X size of stomodeum	< size of stomodeum	= size of stomodeum
Oral disc diameter	~0.7 cm	–	–	~1 cm	0.5 cm
Mesentery attachment to actinopharynx	Broad, 12 mesenteries attached	Broad, 12 mesenteries attached	Narrow, 4 mesenteries attached	Broad, 6 mesenteries attached	Broad, 8 mesenteries attached
Directive mesenteries	= length of Actinopharynx	< length of Actinopharynx	> length of Actinopharynx	< length of Actinopharynx	< length of Actinopharynx
P(C)2	Short, 1/2 of gastric cavity	Very short, 1/4 of gastric cavity	Short, 1/2 of gastric cavity	Long, 3/4 of gastric cavity	Long, 6/7 of gastric cavity, almost to aboral pole
P(C)3	Very short, <1/4 of gastric cavity	Very short, <1/4 of gastric cavity	Short, ~1/2 of gastric cavity	Short, ~1/3 of gastric cavity	Short, 1/3 of gastric cavity
M1	Almost to aboral pore	Almost to aboral pore	To aboral pore	Almost to aboral pore	To aboral pore
M3	4/5 of gastric cavity	Almost to aboral pore	1/5 of gastric cavity	Almost to aboral pore	3/4 of gastric cavity
Cnido-glandular tract of fertile mesenteries	Present (short?)	Present (short?)	Present	Present	Present
Cnido-glandular tract of B	Present (short?)	Present (short?)	Present (short?)	Present (short)	Present (short)
Acontioids	Only in M1, M2 and M3	Only in M1, M2 and M3	Only in M1	Only in M1, M2 and M3	Only in M3 and M4

Type material. Natural History Museum (London); NHMUK – 1954.6.25.47 (holotype).

47 *Arachnanthus bockii* Carlgren, 1924

http://zoobank.org/357544F3-9111-420C-B6AD-B9A446BB9451

Arachnanthus bockii Carlgren, 1924: 193–195; den Hartog 1977: 235

Type locality. Viti Levu, Fiji.

Distribution. Only known from shallow water at the type locality.

Remarks. This is another species with little information, except for the morphological description. There are some characters in Carlgren's (1924) description that allows distinction of this species in comparison to *Arachnanthus australiae*, however, the reduced number of specimens may be a problem to understand the intraspecific variation of these characters.

Type material. Not found in this study, but the original description provided a graphic representation.

48 *Arachnanthus oligopodus* (Cerfontaine, 1891)

http://zoobank.org/7B2B79CA-DC0A-4E14-9ED0-06F2AB20C245

Cerianthus oligopodus Cerfontaine, 1891a: 32–38; Carlgren 1895: 284; van Beneden 1897:140; Gravier 1904: 286; Cerfontaine 1909: 653–707; McMurrich 1910a: 165; Pax 1910: 166; Mello-Leitão 1919: 36, 39; van Beneden 1924: 12, 20, 30, 45, 92, 97, 98; Torelli 1932:12; Torelli 1961: 17–28

Pachycerianthus oligopodus: McMurrich 1910b: 11–13

Arachnanthus oligopodus: Carlgren 1912a: 367–388; Carlgren 1912b: 44–47; Panikkar 1947: 243; Leloup 1960: 2; den Hartog 1977: 235; Vafidis and Koukouras 1998: 123–124; Molodtsova 2003: 253; Çinar et al. 2014: 677, 683, 687, 688; Rastorgueff et al. 2015: 142, 148

Type locality. Italian Coast, Mediterranean Sea (not specified in detail).

Distribution. Mediterranean Sea, shallow waters and caves.

Remarks. *Arachnanthus oligopodus* was initially described as a species of the genus *Cerianthus* by Cerfontaine (1891a), and was moved to the genus *Arachnanthus* by Carlgren (1912b). This is a very common species in several areas of the Mediterranean Sea, especially on the Italian Coast (Carlgren 1924; Torelli 1961). This species has a number of descriptions with appropriate levels of detail (e.g., Cerfontaine 1909; Carlgren 1912a). However, knowledge of the species is still incipient. Biological aspects, especially on the life cycle, are still quite unknown.

Type material. Not found in this study.

49 *Arachnanthus lilith* Stampar & El Didi in Stampar et al. 2018

http://zoobank.org/fc381c67-9db8-4280-9c9c-00dbd04f7d56

Arachnanthus lilith Stampar and El Didi in Stampar et al. 2018: 1–7

Type locality. island near Jaz'air Sila, Saudi Arabia.

Distribution. Red Sea, shallow waters.

Remarks. This species was recently described from shallow Saudi Arabian waters of the Red Sea. Morphological characterization was based on internal anatomy and there have been no studies on ecological or biological aspects of this species yet.

Type material. Florida Museum of Natural History – FLMNH UF9168 (holotype).

50 *Arachnanthus sarsi* Carlgren, 1912

http://zoobank.org/04EE6C07-87AA-4137-8391-D6FE93024EFB

Arachnanthus sarsi Carlgren, 1912a: 27–30; Carlgren 1942: 70–71; Nair 1949: 243; Picton and Manuel 1985: 343–349; Picton 1985: 485–486; Molodtsova 2000: 15, 17; Molodtsova 2003: 251; Stampar et al. 2015c: 2164

Arachnanthus sarsii: Carlgren 1931: 9–10; Carlgren 1940: 6, 11, 13, 15

Type locality. Röberg Indalbay, Trondheim, Norway.

Distribution. North Sea, at 10–200 m depth.

Remarks. This species is rather common in some areas of Great Britain and Scotland and there are two detailed descriptions; the original (Carlgren 1912b) and a redescription (Picton and Manuel 1985). The life cycle has been inferred from the occurrence of larvae named as *Arachnactis albida* (Picton and Manuel 1985), but further study is needed to understand the relationship in detail. Not much is known about ecological aspects of this species and this should be a very interesting field of study.

Type material. Swedish Museum of Natural History (Naturhistoriska riksmuseet) – NRM 134778 (Holotype).

Genus *Isarachnanthus* Carlgren, 1924

Table 8

Type species. *Isarachnanthus maderensis* (Johnson, 1861)

Number of valid species: 4

51 *Isarachnanthus bandanensis* Carlgren, 1924

http://zoobank.org/66c30a7f-149e-4c92-8a8d-c7a63fe71194

Isarachnanthus bandanensis Carlgren, 1924: 187–190, 195; Cutress 1977: 145; den Hartog 1977: 235; Cutress and Arneson 1987: 54, 56–58; den Hartog 1997: 352; Stampar et al. 2012: 1–2, 5–9.

Type locality. Neira, Banda Island, Indonesia.

Distribution. Indonesia, French Polynesia, and Hawaii (USA), shallow waters.

Remarks. This species was described based on two specimens from the Banda Islands, Indonesia. The diagram of mesenteries, part of cnidome, and tentacle organization are present in the original description, however, there are some evident similarities in relation to *Isarachnanthus panamensis*. Furthermore, unpublished molecular data indicate similarity between these two species and studies on this clade should be prioritized.

Type material. Zoological Museum of Amsterdam (now Naturalis Biodiversity Center, Leiden) – (ZMA.COEL.000209 – Lectotype/ ZMA.COEL.000210 – Paralectotype).

52 *Isarachnanthus maderensis* (Johnson, 1861)

http://zoobank.org/B6923781-7CEE-4F15-89C6-A35765626176

Saccanthus maderensis Johnson, 1861: 305–306; Andres 1883: 346
Cerianthus maderensis: Pax 1908: 262–263;
In part *Cerianthus membranaceus* Pax 1908: 464–465, 497–498
Arachnanthus nocturnus: Ocaña et al. 2000b: 107; Wirtz et al. 2003: 114–116
Isarachnanthus cruzi Brito, 1986: 174–181
? *Cerianthus* sp. Torelli 1963: 714–715
Isarachnanthus maderensis: Molodtsova 2003: 249–253; Stampar et al. 2012: 1–9; Stampar and Morandini 2017: 689–693

Type locality. Madeira Island, Portugal**.**

Distribution. Madeira Island (Portugal), Ascension Island, Rocas Atoll (Brazil), Caribbean Sea, (?) Mediterranean Sea; at 2–30 m depth.

Remarks. This species was described by Johnson (1861) from Madeira Island. However, the first detailed morphological characterization was presented by Brito (1986) (as *I. cruzi*). The delimitation of this species is quite complicated, as according to Stampar et al. (2012) only molecular data or morphometric data of the cnidome can be used to compare to other species of the genus. The distribution of this species is quite wide, from oceanic islands of the South Atlantic to the Caribbean Sea and the Mediterranean Sea (Stampar and Morandini 2017).

Type material. Not found in this study.

53 *Isarachnanthus nocturnus* (den Hartog, 1977)

http://zoobank.org/07411A5F-9150-4FDD-9080-565F5C4A8D00

Cerianthus natans: Verrill 1901: 47
Ceriantheopsis sp. Pax 1924: 94, 118–120
Arachnanthus nocturnus den Hartog, 1977: 221–230; Cairns et al. 1986: 192–193; Uchida and Soyama 2001: 142, 150, 152 Wirtz et al. 2003: 115–116;
Isarachnanthus nocturnus: Molodtsova 2000: 15,17; Molodtsova 2003: 251–252; Stampar et al. 2012: 1–9
Isarachnanthus sp. Rodriguez et al. 2011: 51; 52, 54
Tessera gemmaria Goy, 1979: 288–289; Rodriguez et al. 2011: 51–55; Stampar et al. 2015c: 2162

Type locality. Piscadera Bay, Curaçao, Dutch Caribbean.

Table 8. Comparison of anatomical features of *Isarachnanthus* species.

	I. bandanensis	*I. maderensis*	*I. nocturnus*	*I. panamensis*
Marginal tentacles	Up to 40	Up to 42	Up to 60	Up to 32
Arrangement of labial tentacles	(3)413.4242.4312.4312	(1)1.11.11.11.11	(1)2.12.12.12.12	(2)431.4231.4231
Length of actinopharynx	~1/4 of gastric cavity	~2/5 of gastric cavity	~2/5 of gastric cavity	~1/2 to 1/3 of gastric cavity
Hyposulcus	~2/3 size of stomodeum	= size of stomodeum	= size of stomodeum	= size of stomodeum
Oral disc diameter	~2cm	2 cm	3.5 cm	~0.5 cm
Mesentery attached to siphonoglyph	Broad, 18 mesenteries attached	Broad, 10 mesenteries attached	Broad, 12-14 mesenteries attached	Broad, 16 mesenteries attached
Directive mesenteries	= length of Actinopharynx	> length of Actinopharynx	> length of Actinopharynx	>length of Actinopharynx
P(C)2	Long, 3/4 of gastric cavity	Short, 1/3 of gastric cavity	Short, 1/3 of gastric cavity	Long, 3/4 of gastric cavity
P(C)3	Very short, <1/8 of gastric cavity	Very short, ~1/6 of gastric cavity	Very short, ~1/5 of gastric cavity	Short, ~1/5 of gastric cavity
M1	Almost to aboral pore	Almost to aboral pore	Almost to aboral pore	Reach aboral pore
M3	Almost to aboral pore	Almost to aboral pore	Almost to aboral pore	Reach aboral pore
Cnido-glandular tract of fertile mesenteries	Present (short?)	Present	Present	Present (short?)
Cnido-glandular tract of B	Present (short?)	Present (short)	Present (short)	Present (short?)
Acontioids	Only in M1- M4	Only in M1-M6	M1-M3 (sometimes in M4 and M5)	Only in M1- M5 or absent

Distribution. Caribbean Sea, South Atlantic (Argentina; Brazil), at 1–20 m depth.

Remarks. This species was described by den Hartog (1977) based on specimens from Curaçao. The specific epithet is related to the nocturnal behavior of this species. This is the most studied species of the genus, as the larval development has been described and the taxonomy has been reviewed with molecular data (Stampar et al. 2012, 2015c). Molodtsova (2003) argued that this species is only a synonym of *Isarachnanthus maderensis*, however, based on molecular and micrometric data (Stampar et al. 2012) it has been shown that these two species are distinct.

Type material. Naturalis Biodiversity Center, Leiden (former Rijksmuseum van Natuurlijke Historie) – RMNH.COEL.11364 (Holotype).

54 *Isarachnanthus panamensis* Carlgren, 1924

http://zoobank.org/CB322F62-0E21-4157-9107-4279DA1E16A9

Isarachnanthus panamensis Carlgren, 1924: 190–193, 195; Carlgren 1940: 6, 11, 13–14; Molodtsova 2003: 251; Stampar et al. 2012: 1–2

Type locality. Taboga, Panama (Pacific coast).

Distribution. Only known from shallow water at the type locality

Remarks. This species was described from the Panama coast based on three specimens. The description is also detailed, including two mesentery diagrams. Thus, variation in mesenterial organization is quite evident, especially in relation to the size of directive mesenteries. As discussed above, regarding *Isarachnanthus bandanensis*, these two species are very similar in terms of both morphological and molecular data and further studies are needed.

Type material. Zoological Museum of Amsterdam (now Naturalis Biodiversity Center, Leiden) – ZMA.COEL .000211) (holotype).

Key to species

* Species with limited information on their anatomy, therefore key must be used with caution.

1a Ceriantharia with mesenteries organized in doublets (Spirularia) **2**

1b Ceriantharia with mesenteries organized in quartets (Penicillaria) **16**

2a Ceriantharia with cnidorage (botrucnidae).. **3**

2b Ceriantharia without cnidorage (botrucnidae) **6**

3a Cnidorage on appendages united as botrucnidae... **4**

3b Cnidorage over mesenteries.. **5**

4a P-mesenteries (P2) and M-mesenteries (M3) long, almost to aboral pore...... .... ***Botruanthus benedeni* (Torrey & Kleeburger, 1909)**

4b P-mesenteries (P2) and M-mesenteries (M3) short, 1/2 to 1/3 of gastric cavity... ...... ***Botruanthus mexicanus* Stampar, González-Muñoz & Morandini, 2016**

5a Directive mesenteries much longer than hyposulcus .... ***Botrucnidifer novergicus* Carlgren, 1912**

5b Directive mesenteries shorter or equal than hyposulcus................................ .... ***Botrucnidifer shtokmani* Molodtsova, 2001**

6a Ceriantharia with all mesenteries except directives fertile **7**

6b Ceriantharia with second couple of protomesenteries (P) short and sterile.... **8**

6c Ceriantharia with second couple of protomesenteries (P) long and fertile, mesenteries in quartets m, B, M, b... **11**

6d Ceriantharia with second couple of protomesenteries (P) long and fertile, mesenteries in quartets M, B, m, b... **12**

7a Directive mesenteries of the same length as protomesenteries 3 (P3)............ .... ***Ceriantheomorphe brasiliensis* (Mello-Leitão, 1919)**

7b Directive mesenteries shorter than protomesenteries 3 (P3) .... ***Ceriantheomorphe ambonensis* (Kwietniewski, 1898)**

7c Directive mesenteries longer than protomesenteries 3 (P3)... ***Ceriantheomorphe adelita* Lopes, Morandini & Stampar in Lopes et al., 2019**

8a Number of marginal tentacles – less than 90.. **9**

8b Number of marginal tentacles – more than 115 .... **10**

9a Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and 6 mesenteries attached to siphonoglyph .... **_Pachycerianthus schlenzae_ Stampar, Silveira & Morandini, 2014**

9b Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and more than 90 marginal tentacles .... **_Pachycerianthus johnsoni_ (Torrey & Kleeburger, 1909)**

9c Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and less than 70 marginal tentacles .... **_Pachycerianthus fimbriatus_ (Kwietniewski, 1898)**

9d Metamesenteries 2 (M2) longer than half of metamesenteries 1 (M1) and 4 mesenteries attached to siphonoglyph .... **_Pachycerianthus curacaoensis_ den Hartog, 1977**

9e Metamesenteries 2 (M2) longer than metamesenteries 1 (M1), 6 mesenteries attached to siphonoglyph and directive labial tentacle present.. **_Pachycerianthus delwynae_ Carter, 1995**

9f Metamesenteries 2 (M2) longer than Metamesenteries 1 (M1) and 16 mesenteries attached to siphonoglyph .... **_Pachycerianthus aestuarii_ (Torrey & Kleeburger, 1909)**

9g Metamesenteries 2 (M2) and metamesenteries 1 (m1) longer than metamesenteries 1 (M1) and 8 mesenteries attached to siphonoglyph .... **_Pachycerianthus insignis_ Carlgren, 1951**

9h Metamesenteries 2 (M2) and metamesenteries 2 (m2) longer than metamesenteries 1 (M1) and 8 mesenteries attached to siphonoglyph .... **_Pachycerianthus monostichus_ McMurrich, 1910**

9i Metamesenteries 1 (m1) longer than ¼ of Metamesenteries 1 (M1) and 6 mesenteries attached to siphonoglyph .... **_Pachycerianthus solitarius_ van Beneden, 1924**

10a Metamesenteries 2 (M2) longer than metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than than ¾ of M1 .... **_Pachycerianthus borealis_ Kingsley, 1904**

10b Metamesenteries 2 (M2) longer than metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1, labial directive tentacle present .... **_Pachycerianthus longistriatus_ Carter, 1995**

10c Metamesenteries 2 (M2) longer than ¾ of metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1 .... **_Pachycerianthus magnus_ Uchida, 1979**

10d Metamesenteries 2 (M2) longer than 1/4 of metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1 .... **_Pachycerianthus maua_ Carlgren, 1900**

10e Metamesenteries 2 (M2) longer than metamesenteries 1 (M1) and metamesenteries 1 (m1) longer than 1/3 of M1, labial directive tentacle absent.. **_Pachycerianthus multiplicatus_ Carlgren, 1912**

10f Polyp with more than 160 tentacles from Australia .... ***Pachyceranthus nobilis*** **(Haddon & Shackleton, 1894)**

10g Polyp with more than 160 tentacles from Mediterranean Sea .... ***Pachyceranthus dohrni*** **van Beneden, 1924**

11a Polyp with up to 60 marginal tentacles and directive labial tentacle absent .... ***Ceriantheopsis lineata*** **Stampar, Scarabino, Pastorino & Morandini, 2015**

11b Polyp with up to 70 marginal tentacles and cnido-glandular tract at fertile mesenteries present .... ***Ceriantheopsis austroafricana*** **Molodtsova, Griffiths & Acuña, 2011**

11c Polyp with up to 70 marginal tentacles and cnido-glandular tract at fertile mesenteries absent .... ***Ceriantheopsis nikitai*** **Molodtsova, 2001**

11d Polyp with more than 90 marginal tentacles and short directive mesenteries. .... ***Ceriantheopsis americana*** **(Agassiz in Verrill, 1864)**

12a Polyp from India (shallow waters) with more than 150 marginal tentacles .... ***Ceriantheus andamanensis*** **Alcock, 1893***

12b Polyp from India (deep sea ~ 5000 m) with up to 40 marginal tentacles and directive labial tentacle absent .... ***Ceriantheus valdiviae*** **Carlgren, 1912***

12c Polyp from North Atlantic (deep sea ~ 5000 m) with up to 30 marginal tentacles .... ***Ceriantheus bathymetricus*** **Moseley, 1877***

12d Polyp from Red Sea (shallow waters) with up to 20 marginal tentacles .... ***Ceriantheus medusula*** **(Klunzinger, 1877)***

12e Description with information about mesentery organization and tentacle distribution **13**

13a Species from Pacific Ocean **14**

13b Species from Atlantic Ocean **15**

14a Protomesenteries 2 (P2) short, sterile and metamesenteries 1 (M1) reach or almost reach the aboral pore, marginal/ labial tentacles in 4 pseudocycles .... ***Ceriantheus (?) mortenseni*** **Carlgren, 1924**

14b Polyp from Japan, Korea or China, marginal tentacles in 4 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 3 .... ***Ceriantheus filiformis*** **Carlgren, 1924**

14c Polyp from Japan, marginal tentacles in 3 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 2 .... ***Ceriantheus japonicus*** **Carlgren, 1924**

14d Polyp from Japan, marginal tentacles in 4 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 2 .... ***Ceriantheus punctatus*** **Uchida, 1979**

14e Polyp from Indonesia, marginal tentacles in 4 pseudocycles and directive in position 2, labial tentacles in 4 pseudocycles and directive in position 2 .... ***Ceriantheus sulcatus*** **Kwietniewski, 1898**

14f Polyp from Indonesia, marginal tentacles in 2 pseudocycles and directive in position 1, labial tentacles in 4 pseudocycles and directive in position 2 .... ***Ceriantheus taedus*** **McMurrich, 1910**

15a Polyp from North Sea/North Atlantic, directive labial tentacle absent, 4 mesenteries attached to siphonoglyph .... ***Cerianthus lloydii* Gosse, 1859**

15b Polyp from Mediterranean Sea and Central Atlantic, directive labial tentacle present, 6 mesenteries attached to siphonoglyph .... ***Cerianthus membranaceus* (Gmelin, 1791)**

15c Polyp from Norwegian Sea, directive labial tentacle present, 4 mesenteries attached to siphonoglyph .... ***Cerianthus vogti* Danielssen, 1890**

15d Polyp from Namibia, mesenteries type M and m and P2 are almost of the same size .... ***Cerianthus malakhovi* Molodtsova, 2001**

16a Directive labial tentacle present **17**

16b Directive labial tentacle absent **18**

17a Polyp from Atlantic Ocean, microbasic P-mastigophore absent in column.... .... ***Isarachnanthus nocturnus* (den Hartog, 1977)**

17b Polyp from Atlantic Ocean, microbasic P-mastigophore present in column... .... ***Isarachnanthus maderensis* (Johnson, 1861)**

17c Polyp from Pacific Ocean, directive labial tentacle in position 2................... .... ***Isarachnanthus panamensis* Carlgren, 1924**

17d Polyp from Pacific Ocean, directive labial tentacle in position 3................... .... ***Isarachnanthus bandanensis* Carlgren, 1924**

18a Polyp with 6 mesenteries attached to actinopharynx, protomesenteries 2 (P2) long (3/4 of gastric cavity) .... ***Arachnanthus sarsi* Carlgren, 1912**

18b Polyp with 4 mesenteries attached to actinopharynx, protomesenteries 2 (P2) short (1/2 of gastric cavity) .... ***Arachnanthus oligopodus* (Cerfontaine, 1891)**

18c Polyp with 12 mesenteries attached to actinopharynx, protomesenteries 2 (P2) very short (1/4 of gastric cavity) .... ***Arachnanthus bockii* Carlgren, 1924**

18d Polyp with 12 mesenteries attached to actinopharynx, protomesenteries 2 (P2) short (1/2 of gastric cavity) .... ***Arachnanthus australiae* Carlgren, 1937**

18e Polyp with 8 mesenteries attached to actinopharynx, protomesenteries 2 (P2) long (almost to aboral pole) .... ***Arachnanthus lilith* Stampar & El Didi in Stampar et al. 2018**

The species *Cerianthus incertus*, *Cerianthus roulei*, *Cerianthus vas* and *Cerianthus stimpsonii* are not included in key due to absence of characters.

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Taxonomic note on *Trichelix horrida* (Pfeiffer, 1863) from Laos, with a type catalogue of *Moellendorffia*, *Trichelix*, and *Moellendorffiella* (Heterobranchia, Camaenidae)

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Abstract

Land snail surveys conducted in northern Laos between 2013 and 2014 have led to the discovery of a living population of *Trichelix horrida* (Pfeiffer, 1863). This species has never been recorded from specimens other than the types, and its distribution and anatomy have remained essentially unknown. The genitalia and radula morphology are documented here for the first time and employed to re-assess the systematic position of this species: the unique morphological characters of *T. horrida* are a penis similar in length to the vagina, a small and triangular penial verge, gametolytic organs extending as far as the albumen gland, head wart present, and unicuspid triangular radula teeth. The type locality of this species was believed to be from "Lao Mountains, Camboja," and is restricted herein to be Luang Phrabang Province, northern Laos. The assignment of species to either of three genera, *Trichelix* Ancey, 1887, *Moellendorffia* Ancey, 1887, and *Moellendorffiella* Pilsbry, 1905, based solely on information provided in their original descriptions is difficult. The type specimens of all nominal species presently placed in either of these three genera are examined and illustrated herein. Comparison with the primary type specimens will assist future revisions aiming to resolve the systematics of these taxa. In addition, we transfer *Moellendorffia faberiana* (Möllendorff, 1888) to the genus *Moellendorffiella*.

Keywords
Biodiversity, Indochina, Japan, land snail, limestone, systematics, type specimen

Introduction

The land snail genus *Trichelix* Ancey, 1887 has a wide distribution from southeastern China to the northern parts of Laos and Vietnam, Taiwan, and the central Ryukyu Islands of Japan (Schileyko 2003). Originally, *Trichelix* was described as a monotypic genus for the type species *Helix horrida* Pfeiffer, 1863. The flattened to sunken spire, elevated parietal callus, aperture with denticles, external furrows on the outer wall of the last whorl, and the hirsute shell microsculpture confer a very distinctive morphology to the shell of this species (Ancey 1887; Pilsbry 1890, 1895, 1901, 1905; Yen 1939; Zilch 1960). The early taxonomic work was restricted to the description of shell morphology, and Pilsbry (1905) treated *Trichelix* as a subgenus of *Moellendorffia* Ancey, 1887 due to a similar shell and apertural morphology. Five additional species have since been assigned to this taxon (Pilsbry 1905). Subsequently, Habe (1957), Minato (1971, 1980, 2011), and Azuma (1982) described the genital anatomy of the species from the eastern Asian islands. Schileyko (2003) revised the genus based on published information about species other than the type species. Schileyko (2003) found differences in the genital anatomy of species, which may be indicative of a distinct lineages, but he hesitated to propose this conclusion because the anatomy of the type species was still unknown. Later, examination of the genital anatomy and shell morphology of *Moellendorffia eastlakeana* (Möllendorff, 1882) from Vietnam has suggested a possibly close relationship between *Moellendorffia* and *Trichelix* (Panha et al. 2010). Recently, Minato (2011) reviewed the genus and followed Pilsbry's (1905) classification by recognizing *Trichelix* as a subgenus; Minato (2011) examined the genital anatomy of Taiwanese species. These reports appear to be the only published literature on the systematics of *Trichelix*.

Helix horrida Pfeiffer, 1863 was established based on three specimens from the collection of H. Cuming, and these syntypes were collected by H. Mouhot. The type locality was stated to be "Lao Mountains, Camboja," without any other precise locality information. Localities recorded by Mouhot were usually tentative and based on a broad geographical scale. This has rendered it difficult to infer the type localities of many species that were described based on material collected by Mouhot, including fish (Kottelat and Tan 2018), reptiles and amphibians (Stuart et al. 2006), and land snails (Sutcharit et al. 2019). Similarly, the type locality of *Helix horrida* Pfeiffer, 1863 is rather vague, and with no later records of this species available. The distribution of this species has remained essentially unknown to this day. The field surveys performed during 2013 and 2014 in the northern part of Laos contained a records of *Helix horrida* Pfeiffer, 1863 and comparisons with the type material confirm its identity.

Here, we report on the examination of examples of *T. horrida* (Pfeiffer, 1863) collected from northern Laos. The type locality is discussed, and a correction is proposed in accordance with the guidelines of ICZN (1999). In addition, the primary type specimens of all recognized taxa belonging to the genera *Moellendorffia*, *Trichelix*, and *Moellendorffiella* Pilsbry, 1905 are included for comparisons and because the species identification could not have been possible without comparison with the type specimens.

Materials and methods

Shells and living specimens were collected in a limestone forest in Luang Phrabang Province, northern Laos. The live specimens were photographed, euthanized (AVMA 2013), and then transferred to 70% (v/v) ethanol for fixation and preservation. The genitalia of three specimens were dissected and examined under a stereomicroscope. Drawings were made with a camera lucida. Radulae were extracted, soaked in 10% (w/v) NaOH, and then examined under scanning electron microscopy (SEM; JEOL, JSM-6610 LV). The formulae and morphology of radula were observed, recorded, and described. Adult shells were used to measure the shell height and shell width, and to count the number of whorls. The voucher specimens are now deposited in the Chulalongkorn University Museum of Zoology (CUMZ) and in the collection at the National University of Laos.

Anatomical conventions and abbreviations: In the descriptions of the genitalia, the following abbreviations are used, as defined by Habe (1957), Schileyko (2003), and Panha et al. (2010). The term 'proximal' refers to the region closest to the genital orifice, while 'distal' refers to the region furthest away from the genital orifice. Abbreviations: ag, albumen gland; at, atrium; e, epiphallus; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; hw, head wart; ov, oviduct; p, penis; pp, penial pilaster; pr, penial retractor muscle; pv, penial verge; v, vagina; vd, vas deferens; vp, vaginal pilaster.

Institutional abbreviations

ANSP	Academy of Natural Sciences of Drexel University, Philadelphia
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN	Muséum National d'Histoire Naturelle, Paris
NHM	Natural History Museum, London
NHMW	Naturhistorisches Museum, Vienna
NIGPAS	Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, Nanjing
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main
ZMB	Museum für Naturkunde, Berlin
ZMNH AIMS	Zhejiang Museum of Natural History, Hangzhou

Photo credits

Photos of the type specimens from the Molluscs Collection (IM) of MNHN are credited to the museum taken under the project E-RECOLNAT: ANR-11-INBS-0004 and MNHN/Philippe Maestrati, or as otherwise stated.

Systematics

Family Camaenidae

Genus *Trichelix* Ancey, 1887

Trichelix Ancey 1887: 64. Schileyko 2003: 1513.
Helix (*Trihelix*): Pilsbry 1890: 9 (incorrect subsequent spelling). Pilsbry 1895: 289.
Moellendorffia (*Trihelix* [sic]): Pilsbry 1905: 65.
Moellendorffia (*Trichelix*): Zilch 1960: 612.

Type species. *Helix horrida* Pfeiffer, 1863; by original designation.

Description. Shell small to medium-sized, flattened to concave, rather thin, umbilicate, and corneous to brownish. Spire shrunken; embryonic shell nearly smooth; following whorls granulated and with short to long periostracal hairs arranged in oblique rows along the lines of growth. Last whorl rounded and descending anteriorly. Aperture ventral or subvertical; trigonal or subcircular; with strong or weak barriers inside the aperture at upper periphery and below periphery, and externally marked with strong to weak longitudinal furrows. Peristome expanded and continuous or discontinuous; parietal callus thin or thickened and little elevated.

Genitalia typical of camaenids, without either dart apparatus or accessory glands. Penis and epiphallus long, penial verge present, and flagellum short. Internal wall of penis and vagina with longitudinal pilasters.

Radular teeth arranged in V-shaped rows; central and lateral teeth triangular.

Remarks. The genus is currently comprised of six nominal species (Schileyko 2003; Minato 2011). Two species occur in northern Laos and southern China (Fig. 3), viz. *T. horrida* and *T. biscalpta* (Heude, 1885), and one has been recorded from Taiwan, viz. *T. hiraseana* (Pilsbry, 1905). Three species occur on the Amami Islands, Central Ryukyu Islands, Japan, viz. *T. eucharista* (Pilsbry, 1901), *T. diminuta* (Pilsbry & Hirase, 1905) and *T. tokunoensis* (Pilsbry & Hirase, 1905).

Trichelix horrida (Pfeiffer, 1863)

Figures 1, 2, 7B

Helix horrida Pfeiffer 1863["1862"]: 272, pl. 36, fig. 15. Type locality: "Lao Mountains, Camboja" [probably in northern Laos around Luang Phrabang area, Laos]. Pfeiffer 1868a: 395. Pfeiffer 1868b: 399, 400, pl. 92, figs 17–19. Pfeiffer and Kobelt 1880: 579, pl. 170, figs 8–10.
Helix (*Trihelix*) *horrida*: Ancey 1887: 64. Pilsbry 1890: 9, pl. 1, figs 9–11.
Helix (*Moellendorffia*) *horrida*: Pilsbry 1895: 290.
Moellendorffia (*Trichelix*) *horrida*: Zilch 1960: 612. Inkhavilay et al. 2019: 105, figs 53f, 54a, 58h.
Moellendorffia horrida: Richardson 1985: 185.

Type material. Three specimens originating from H. Cuming's collection with the original label stating the taxon name and collection location in Pfeiffer's handwriting are present in the malacological collection of the NHMUK. Of these specimens, the one most closely matching the measurements given in the original description is here designated as the lectotype NHMUK 20200202/1 (Fig. 7B) to stabilize the name. The other two shells from the same lot become paralectotypes NHMUK 20200202/2 to 20200202/3.

Trichelix horrida was originally described based on specimens collected by H. Mouhot, with "Lao Mountain, Camboja" as the published type locality. Our survey following Mouhot's itinerary in the south-western part of Cambodia yielded no specimens that could be identified in this genus. This record type locality seems to be imprecise. On the other hand, our survey in the northern part of Laos, where Mouhot had visited Luang Phrabang in 1861, recorded populations of this species in Muang Ngoi about 90 km north of Luang Phrabang City. Therefore, we restricted the known distribution and propose Luang Phrabang Province, Laos as the correct type locality for this species.

Material examined. Moist evergreen forest on limestone hills between Ban Pha Toke and Ban Nong Ian, Muang Ngoi (Town), Ngoi District, Luang Phrabang Province, Laos (20°32'31.2"N, 102°38'56.3"E): CUMZ 5248 (eight specimens in ethanol; Fig. 1A), CUMZ 5249 (five shells; Fig. 1B), CUMZ 5250 (one shell).

Measurement. From 10 specimens analyzed; shell height ranged from 12.4–14.7 mm (mean 13.5 ± 1.0); shell width ranged from 20.8–23.9 mm (mean 22.0 ± 1.2); and whorl count ranged from 6–6⅛ whorls.

Shell. Shell medium-sized, dextral, slightly thin, translucent, depressed globose, biconcave shaped (dorsoventrally concave), and deeply umbilicate. Whorls 5–6, slightly convex, and increasing regularly; suture depressed, spire concave, looking like umbilicus. Embryonic shell large with very fine growth lines. Following whorl with corneous to brownish periostracum; upper surface with long hairs arranged in oblique rows; lower surface with slightly shorter hairs and few hairs around umbilicus. In worn specimens, shell surface possesses rough rows of tubercles running obliquely and descending, relatively smooth around umbilicus. Last whorl well rounded and little convex below periphery. Last whorl descending about ¼ whorl from aperture, and constriction occurs close to apertural lip. Aperture ear-shaped and opened subventrally; lip margin pale corneous, little thickened, and continuously expanded. External furrow aligns with internal apertural lamella or fold. Upper periphery marked with two furrows arranged spirally and correspond with palatal lamella and fold; below periphery with one furrow close to lip aligned with basal lamella. Parietal callus thickened, elevated, emarginated, and obtusely projecting inward. Umbilicus wide, but narrower than apex side which is cascade-shouldered.

Genitalia. Atrium (at) short; penis (p) long; proximally with penial verge and enlarged fold at penial verge base; distally similar in length as proximally and somewhat slender tube. Epiphallus (e) slightly enlarged and almost the same length as penis. Flagellum (fl) very short and small. Vas deferens (vd) a small tube, follows vagina and penis, and connects distally on epiphallus and free oviduct. Penial retractor muscle (pr) slightly thickened and long (Fig. 2A).

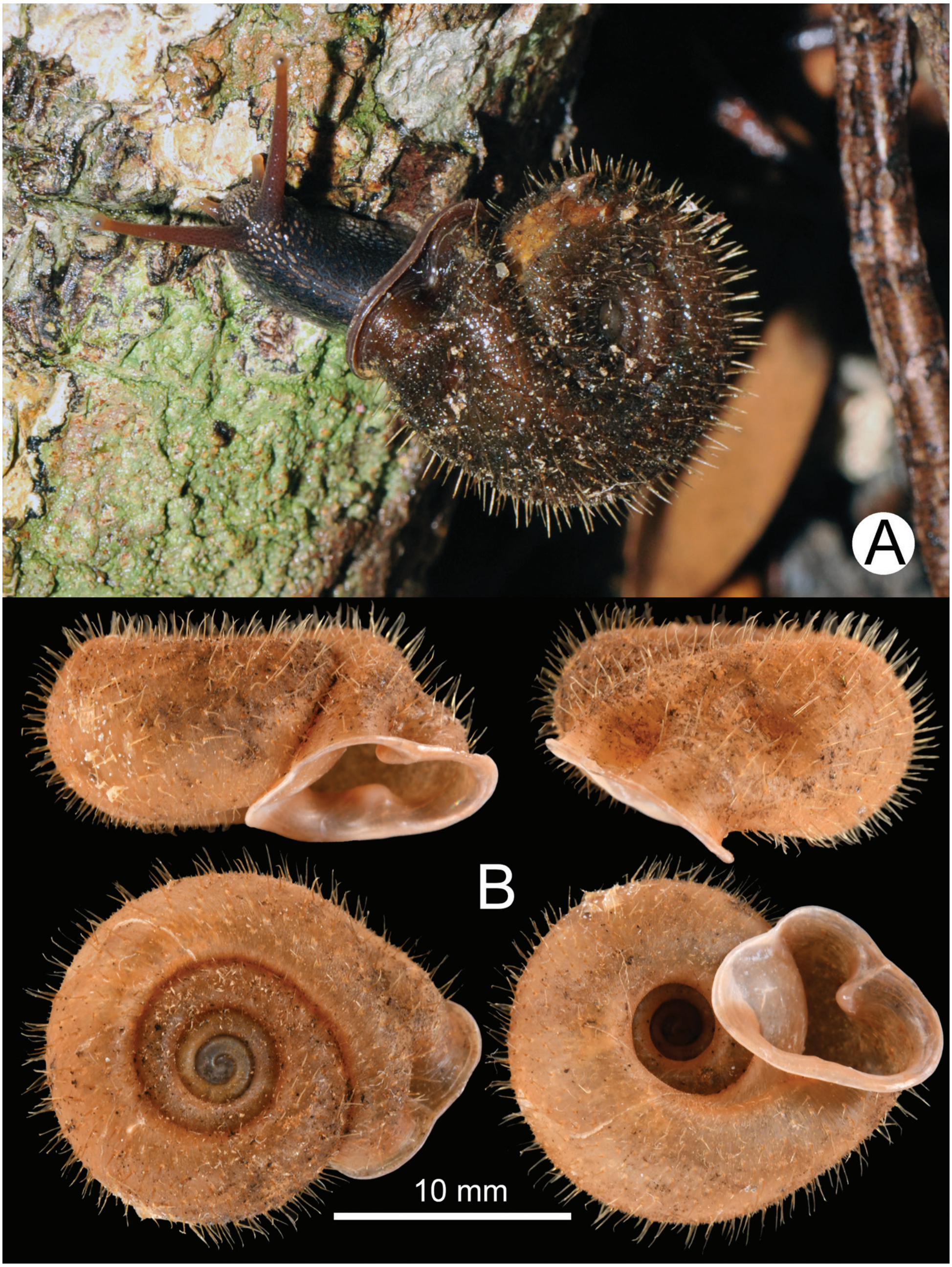

Figure 1. Living snail and shell **A** specimen CUMZ 5248 **B** specimen CUMZ 5249.

Internal wall of penis ribbed by a series of swollen longitudinal penial pilasters (pp). Smooth pilasters line introverts penial chamber and encircles penial verge tip. Penial verge (pv) small, short conic with smooth surface (Fig. 2B).

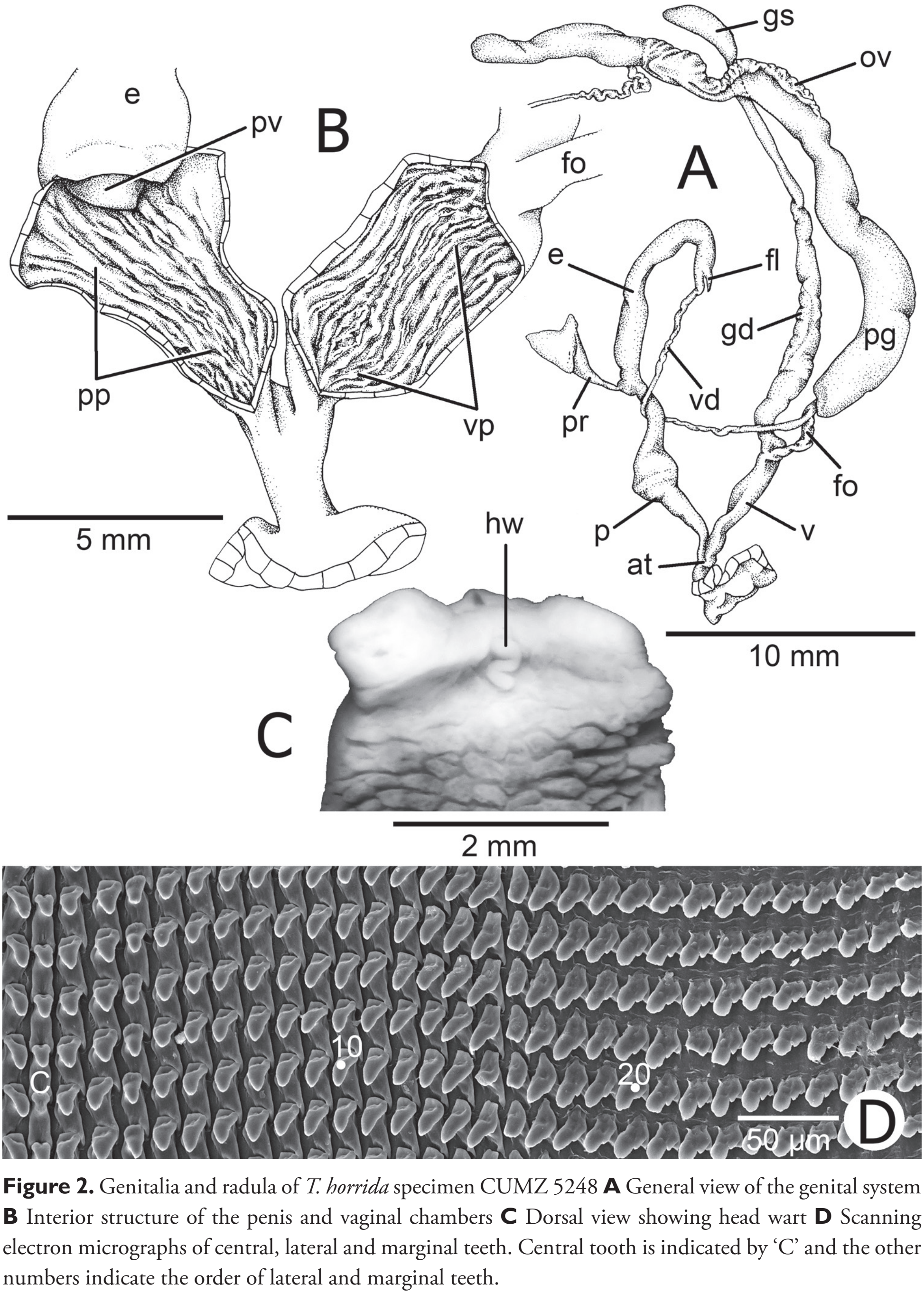

Figure 2. Genitalia and radula of *T. horrida* specimen CUMZ 5248 **A** General view of the genital system **B** Interior structure of the penis and vaginal chambers **C** Dorsal view showing head wart **D** Scanning electron micrographs of central, lateral and marginal teeth. Central tooth is indicated by 'C' and the other numbers indicate the order of lateral and marginal teeth.

Vagina (v) of similar length to proximal penis and held in position by series of muscles attached to foot floor. Gametolytic organ (duct and sac) long, cylindrical, and extending as far as albumen gland. Gametolytic duct (gd) as wide as gametolytic sac (gs) for most of its length but narrows before reaching gametolytic sac. Free oviduct (fo) short, about half of vagina length; oviduct (ov) small. Prostate gland (pg) and oviduct (ov) developed; hermaphroditic duct long and convoluted tube; albumen gland solid and tongue shape (Fig. 2A).

Internal wall of vagina possesses several longitudinal vaginal pilasters (vp). Pilasters with smooth surface and line entire vaginal chamber (Fig. 2B).

Animal. Live animal covered with blackish-brown reticulated skin and dorsally with whitish stripe in middle of the body. A small curved head wart (hw) is located between the posterior tentacles (Fig. 2C). Foot narrow and long; mantle edge greyish; tentacles brownish, and lower tentacles pale brown. Mantle cavity possesses blackish pigmentation. Live snails possess short to long periostracal hairs, which mostly disappear in worn shells or old snails.

Radula. Teeth arranged in anteriorly pointed, V-shaped rows; each row contains about 75 (37-(18–20)-1-(18–20)-38) teeth. Central tooth unicuspid, triangular with blunt cusp. Lateral teeth unicuspid, triangular with blunt tip, gradually taller laterally and little inclined to central tooth. Marginal teeth starting around tooth numbers 18 to 20 outwards from lateral teeth. Tricuspid or bicuspid marginal teeth, endocone usually absent; mesocone large, broad and with curved to blunt cusp; ectocone slightly large, pointed head and located at base of the teeth. Outer marginal teeth rather small; mesocone and ectocone indistinguishable, with undulated cusp (Fig. 2D).

Distribution. *Trichelix horrida* was previously known only from the type locality ("Lao Mountain, Cambojia" [Cambodia or Laos]). The specimens examined herein were collected from limestone karst in Muang Ngoi Town, about 90 km north of Luang Phrabang City.

Our sampling locality was characterized by monsoonal karst landforms with high humidity. The snails occurred in tropical moist deciduous forest. There was heavy rain before our visit in August 2014. The snails were active, crawling or sitting on moist rotten logs among the limestone outcrops.

Remarks. *Trichelix horrida* is distinctly different in shell morphology from all other *Moellendorffia* species by having a concave spire, rounded last whorl, and two furrows arranged spirally on the upper periphery (Table 1). In contrast, *Moellendorffia* species tend to have flattened to elevated spires, rounded to shouldered last whorls, and two furrows arranged vertically on the periphery. *Trichelix horrida* differs from the other congeners in having two short furrows on the last whorl and an elevated parietal callus (Fig. 7B), while *T. biscalpta* and *T. hiraseana* tend to have a long furrow on the last whorl and unelevated parietal callus (Figs 6C, 7A). In addition, *T. hiraseana* has a relatively long, drumstick-shaped flagellum, while the type species has a very short protrusion (see Minato 2011 for a comparison). In addition, *Chloritis bifoveata* (Benson, 1850) from Myanmar and Thailand, *C. diplochone* Möllendorff, 1898 from Laos and Thailand, and *C. vinhensis* Thach & Huber, 2018 from Vietnam differ from *T. horrida* by having a thin parietal callus, with a shell constriction occurring about half a whorl from the aperture (absent in *C. vinhensis*), and without apertural dentition (Sutcharit and Panha 2010; Páll-Gergely and Neubert 2019; Páll-Gergely et al. 2020).

Table 1. Comparison of *Trichelix* (continental and eastern Asian islands species) and the related genera *Moellendorffia* and *Moellendorffiella*.

Characters	***Moellendorffia*** **Ancey, 1887**	***Trichelix*** **Ancey, 1887**		***Moellendorffiella*** **Pilsbry, 1905**
		Continental group	**Central Ryukyu group**	
Shell shape	low conic to convex	concave	concave	flat
Last whorl	round or angular	round	round	shouldered or strong shouldered keel
Periostracal hair	short to long	short to long	short	absent
Furrow on upper periphery and alignment on last whorl	–	one or two / spiral alignment	–	–
Furrow on periphery and alignment on last whorl	two / vertical alignment	–	–	one/ spiral alignment
Furrow below periphery	one and strong	one and strong	absent or very weak	one and strong
Parietal callus	long elevated with nodule	short elevated with nodule	thin with cords	thin
Distribution (Fig. 3)	Southern China and Indochina	Central China, Indochina and Taiwan	Restricted to the Central Ryukyu Islands, Japan	Central China
Suggested nominal species (**bold** = type species)	*blaisei*, *deflexa*, *dengi*, *depressispira*, *eastlakeana*, *hensaniensis*, *loxotata*, *messageri*, *sculpticoncha*, *spurca*, ***trisinuata***	*biscalpta*, *hiraseana*, ***horrida***	*diminuta*, *eucharista*, *tokunoensis*	***erdmanni***, *faberiana*

Discussion

The newly collected material from Laos presents valuable additional information for the taxonomic position of *Trichelix* and its congeners. The relationship of *Trichelix* with *Moellendorffia* and *Moellendorffiella* has been suggested based on shell and genital anatomy characters (Panha et al. 2010). The shrunken spire and one or two furrows located on the upper periphery are the unique characteristics of *Trichelix*. At present, *Trichelix* s.l. has a wide distribution across Indochina to Taiwan, southern China, and the Central Ryukyu Islands of Japan (Fig. 3).

The genus *Trichelix* s.l. appears to be a heteromorphic assemblage, as noted by Schileyko (2003), based on both shell and genital anatomy characters. The genus comprises the continental group and the Central Ryukyu group. The continental group includes three nominal species from northern Laos (the type species), Taiwan (*T. hiraseana*), and southern China (*T. biscalpta*). They all have prominent palatal lamellae arranged spirally on upper periphery, strong columellar lamella, and vagina almost the same length as penis. The Central Ryukyu group contains three nominal species: *T. eucharista*, *T. tokunoensis*, and *T. diminuta*; they lack the parietal lamella

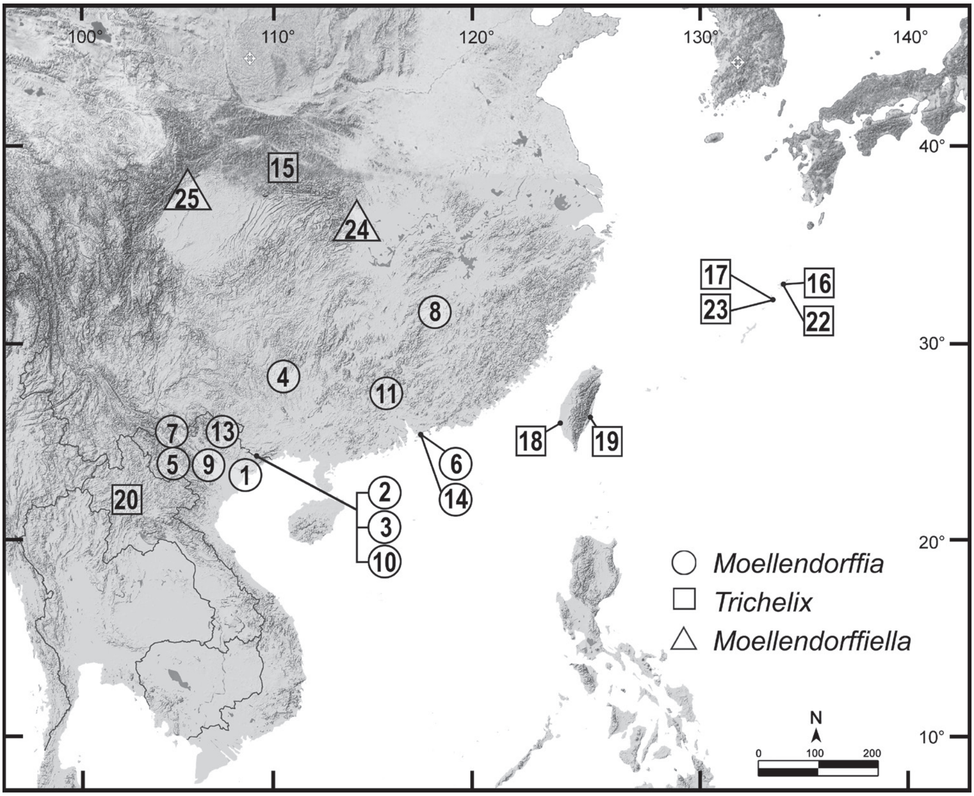

Figure 3. Approximate geographical position of the type locality of all nominal species of the genera *Moellendorffia* (circle), *Trichelix* (square), and *Moellendorffiella* (triangle). The numbers indicated correspond to the nominal species listed in the catalogue of the type specimen.

and have a very weak or absent columellar lamella, and the vagina is relatively longer than the penis (Habe 1957; Minato 1971, 1980, 2011; Schileyko 2003). The unique genital characters of *T. eucharista* are: penis about half of vagina length and vagina with constrictions; *T. tokunoensis* possesses two penial retractor muscles, a very small epiphallus and penis about one-third of the vagina length; *T. diminuta* has the penis about half of the vagina length and the gametolytic duct bears constrictions (Habe 1957; Minato 1971, 1980, 2011; Schileyko 2003). These unique and distinct genital characters are likely to be apomorphic traits and would be the main reproductive barrier among these species. It is very likely that the three species inhabiting the Central Ryukyu Islands of Japan do not belong to the same genus as the continental and Taiwanese species. However, with so few synapomorphic traits among these Central Ryukyu Islands species, the confidence in defining distinct lineages remains low. Therefore, we refrain from describing a genus without additional evidence from molecular analyses.

Catalogue of type specimens of *Moellendorffia*, *Trichelix*, and *Moellendorffiella*

In the following catalogue list, the primary type specimens (i.e., holotype, lectotype, and syntype/s) along with secondary type specimens (paratype/s and paralectotype/s) of *Moellendorffia*, *Trichelix*, and *Moellendorffiella* species are provided. The species-group names are arranged by alphabetical order. The references for the usage of each taxon name have been comprehensively provided by Richardson (1985), Zilch (1966), and Minato (2011). The name in the original combination is given with the bibliographic information or the original description. The type locality is given, and if possible, the modern name and/or regional names of the type locality are provided in square brackets. The current taxonomic status includes the generic placement, whether a valid name or synonym. If necessary, remarks are given on the status of type specimens, authorships, availability of name, notes on the type locality, and other useful comments.

Alphabetical list of the taxa

I. Genus *Moellendorffia* Ancey, 1887

Moellendorffia Ancey 1887: 64. Zilch 1960: 611, 612. Schileyko 2003: 1514, 1515.
Proctostoma Mabille 1887b: 102.
Moellendorffia (*Moellendorffia*): Pilsbry 1905: 65. Zilch 1960: 612. Zilch 1966: 210.

Type species. *Helix trisinuata* Martens, 1867; by original designation.

Diagnosis. Shell flattened to globose-conic, and umbilicate. Periostracum thick and covered with short to long hairs. Last whorl rounded to shoulder and descending anteriorly. Aperture trigonal or squarish, entirely free from preceding whorl; with barriers inside, and externally marked with furrows. Parietal wall elevated to form prominent nodule; one or two palatal lamellae (two lamellae arranged vertically); one columellar lamella.

Remarks. The genus *Moellendorffia* can be distinguished from *Trichelix* s.l. in having low conical to elevated spire, one or two furrows (arranged vertically) on periphery and elevated parietal callus, while *Trichelix* s.l. has a concave spire. In addition, the continental-*Trichelix* have one or two furrows (arranged spirally) on the upper periphery and little elevated parietal callus, and the Central Ryukyu-*Trichelix* performs very weak or absent furrows, and a thin parietal callus.

1. *blaisei* Dautzenberg & Fischer, 1905

Moellendorffia blaisei Dautzenberg and Fischer 1905: 99, 100, pl. 3, figs 17–19. Type locality: Ile Krieu, Tonkin [Krieu Island, Ha Long Provincial, Quang Ninh Province, Vietnam]. Schileyko 2011: 43.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Syntype MNHN-IM-2000-1843 (one shell, Fig. 4A).

2. *callitricha* (Bavay & Dautzenberg, 1899)

Helix (*Moellendorffia*) *callitricha* Bavay and Dautzenberg 1899: 35, 36, pl. 1, fig. 6. Type locality: That-Khé [That Khe Town, Trang Dinh District, Lang Son Province, Vietnam].
Moellendorffia callitricha: Richardson 1985: 183.

Current taxonomic status. *Moellendorffia*. Synonym of *Moellendorffia eastlakeana* (see Panha et al. 2010).

Type specimens. Syntype MNHN-IM-2000-2006 (one shell, Fig. 4B).

3. *deflexa* Möllendorff, 1901

Moellendorffia spurca deflexa Möllendorff 1901: 74. Type locality: Masongebirge [Mau Son Mountains, Lang Son Province, Vietnam].
Moellendorffia (*Moellendorffia*) *spurca deflexa*: Zilch 1966: 210, pl. 6, fig. 54.
Moellendorffia spurca deflexa: Richardson 1985: 186. Schileyko 2011: 44.

Current taxonomic status. *Moellendorffia spurca*. Accepted subspecies.

Type specimens. Lectotype SMF 27260a (Fig. 4C) and paralectotype SMF 27260b (one shell) from Manson Gebirge, Tonkin.

Remarks. The lectotype was designated in Zilch (1966: 210).

4. *dengi* Yang, Fan, Qiao & He, 2012

Moellendorffia dengi Yang et al. 2012: 32, fig. 1. Type locality: Leye Country, Guangxi Province, China.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Holotype ZMHN AIMS 1693 (Fig. 4D) and paratypes unnumbered (three shells).

5. *depressispira* (Bavay & Dautzenberg, 1909)

Helix (*Moellendorffia*) *depressispira* Bavay and Dautzenberg 1909b: 244. Type locality: Pac-Kha [Pa Kha in Long Luong Commune, Van Ho District, Son La Province, Vietnam]. Bavay and Dautzenberg 1909a: 197, 198, pl. 8, figs 10–12.
Moellendorffia depressispira: Richardson 1985: 183. Schileyko 2011: 44.

Figure 4. A *Moellendorffia blaisei*, syntype MNHN-IM-2000-1843 **B** *Moellendorffia callitricha*, syntype MNHN-IM-2000-2006 **C** *Moellendorffia spurca deflexa*, lectotype SMF 27260a **D** *Moellendorffia dengi*, holotype ZMHN AIMS 1693 **E** *Moellendorffia depressispira*, syntype MNHN-IM-2000-34941 **F** *Moellendorffia eastlakeana*, lectotype SMF 8328/1. Photo: J He (**D**).

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Syntype MNHN-IM-2000-34941 (one shell, Fig. 4E).

6. *eastlakeana* (Möllendorff, 1882)

Helix eastlakeana Möllendorff 1882: 185. Type locality: Guang-dung [Guangdong, China].

Moellendorffia (*Moellendorffia*) *eastlakeana*: Zilch 1966: 210, pl. 6, fig. 52.
Moellendorffia eastlakeana: Richardson 1985: 184. Panha et al. 2010: 21–24, figs 1–10. Schileyko 2011: 44.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Lectotype SMF 8328/1 (Fig. 4F) and paralectotype SMF 8329 (one juvenile) from Tai-mo-Shan, Guong-dong.

Remarks. The lectotype was designated in Zilch (1966: 210).

7. *exasperata* (Bavay & Dautzenberg, 1909)

Helix (Moellendorffia) loxotata var. *exasperata* Bavay and Dautzenberg 1909a: 196, pl. 8, figs 13, 14. Type locality: Nat-Son, Muong-Hum [probably in the area of Lao Cai Province, Vietnam].
Moellendorffia loxotata exasperata: Schileyko 2011: 44.

Current taxonomic status. *Moellendorffia loxotata*. Accepted subspecies.

Type specimens. Syntype MNHN-IM-2000-34940 (one shell, Fig. 5A).

8. *hensaniensis* (Gredler, 1885)

Helix (*Polygyra*) *hensaniensis* Gredler 1885: 4. Type locality: Heng-shan-hsien, Hunan, China. Gredler 1887: 283, pl. 11, figs 1–3.
Moellendorffia (*Moellendorffia*) *hensaniensis*: Zilch 1966: 210.
Moellendorffia hensaniensis: Zilch 1974: 194. Richardson 1985: 185.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Lectotype NHMW 15795 (Fig. 5B) and paralectotype SMF 50076/1 (one shell, Fig. 5C) from Hensan, China.

Remarks. The lectotype was designated in Zilch (1974: 194) and illustrated for the first time in this study.

9. *loxotata* (Mabille, 1887)

Helix loxotata Mabille 1887a: 5. Type locality: Tonkin.
Proctostoma loxotatum: Mabille 1887b: 102–104, pl. 1, figs 1–3.
Moellendorffia loxotata: Richardson 1985: 185.
Moellendorffia loxotata loxotata: Schileyko 2011: 44.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Syntype MNHN-IM-2000-2071 (one shell, Fig. 5D).

10. *messageri* (Bavay & Dautzenberg, 1899)

Helix (*Moellendorffia*) *messageri* Bavay & Dautzenberg, 1899: 33–35, pl. 1, fig. 5. Type locality: entre Lang-Son et That-Khé [That Khe Town, Trang Dinh District, Lang Son Province, Vietnam].

Moellendorffia messageri: Richardson 1985: 185, 186. Schileyko 2011: 44.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Syntype MNHN-IM-2000-1939 (one shell, Fig. 5E).

11. *sculpticoncha* (Zilch, 1951)

Helix (*Polygyra*) *trisinuata* var. *sculptilis* Möllendorff 1884: 310, 311, pl. 7, fig. 4 [non Bland 1858: 279]. Type locality: Lo-fou-shan, Guang-dung [Guangdong, China].

Moellendorffia trisinuata sculpticoncha Zilch 1951: 86 [nomen novum for *Helix* (*Polygyra*) *trisinuata* var. *sculptilis* Möllendorff, 1884]. Zilch 1966: 211, pl. 6, fig. 53. Richardson 1985: 186.

Current taxonomic status. *Moellendorffia trisinuata sculpticoncha*. Accepted subspecies (Zilch 1966).

Type specimens. Lectotype SMF 8331/1 (Fig. 5F) and paralectotypes SMF 8332/3 (three shells), SMF 27142/4 (four shells) from Lo-fou-shan, Guang-dung, China.

Remarks. The lectotype was designated in Zilch (1966: 211).

12. *sculptilis* Möllendorff, 1884

Remarks. see under “*sculpticoncha*”.

13. *spurca* (Bavay & Dautzenberg, 1899)

Helix (*Moellendorffia*) *spurca* Bavay and Dautzenberg 1899: 31–33, pl. 1, fig. 4. Type locality: environ de Bac-Kau [Bac Quang, Than Uyen District, Lai Chau Province, Vietnam].

Moellendorffia spurca: Richardson 1985: 186.

Moellendorffia spurca spurca: Schileyko 2011: 44.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Syntype MNHN-IM-2000-1992 (one shell, Fig. 6A).

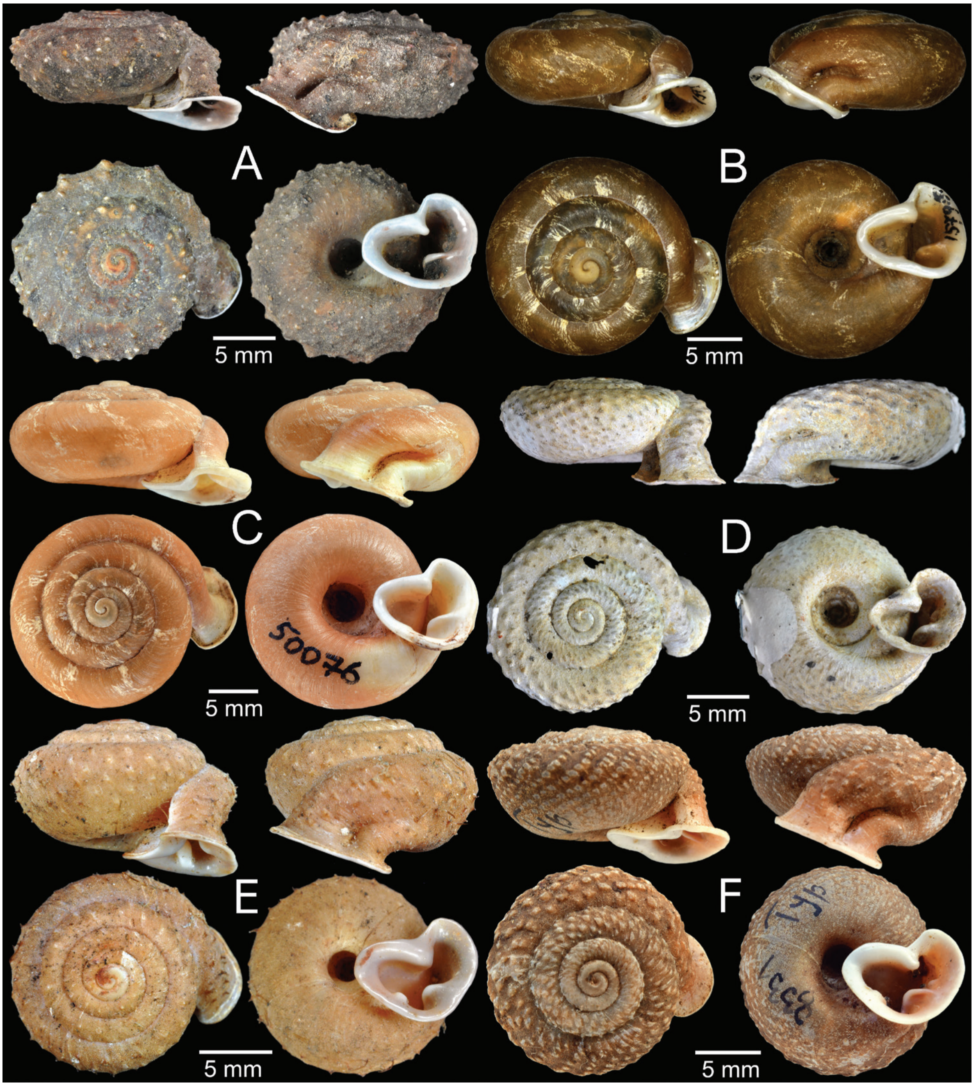

Figure 5. A *Moellendorffia loxotata exasperata*, syntype MNHN-IM-2000-34940 **B, C** *Moellendorffia hensaniensis* **B** lectotype NHMW 15795 and **C** paralectotype SMF 50076/1 **D** *Moellendorffia loxotata*, syntype MNHN-IM-2000-2071 **E** *Moellendorffia messageri*, syntype MNHN-IM-2000-1939 **F** *Moellendorffia trisinuata sculpticoncha*, lectotype SMF 8331/1. Photo: S Schnedl (**B**).

14. *trisinuata* (Martens, 1867)

Helix trisinuata Martens 1867: 50, 51. Type locality: Hongkong [Hong Kong].
Moellendorffia (*Moellendorffia*) *trisinuata trisinuata*: Zilch 1966: 210, 211.
Moellendorffia trisinuata: Richardson 1985: 186.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Syntype ZMB 7620 (one shell, Fig. 6B) from Hongkong.

II. Genus *Trichelix* Ancey, 1887

Type species. *Helix horrida* Pfeiffer, 1863; by original designation.

Diagnosis. Shell flattened to concave, spire shrunken and umbilicate. Periostracum covered with short hairs. Last whorl well rounded and descending anteriorly. Aperture subcircular, without barrier or with barriers inside, and externally marked with furrows. Parietal callus thin, with cord at margin or a little elevated to form nodule; two palatal lamellae arranged spirally; one columellar lamella.

Remarks. The genus *Trichelix* s.l. can be distinguished from *Moellendorffiella* by having concave spire, and short to long periostracal hairs, while *Moellendorffiella* have flat spire and without periostracal hair. The Central Ryukyu-*Trichelix* have a thin parietal callus with cord and very weak furrows below the periphery, and the continental-*Trichelix* have an elevated parietal callus with a nodule, and there are one or two furrows (arranged spirally) on the upper periphery. In comparison, *Moellendorffiella* has a thin parietal callus and one furrow on periphery.

15. *biscalpta* (Heude, 1885)

Helix biscalpta Heude 1885: 113, pl. 29, fig. 10. Type locality: Tchen-k'eou [Chengkou, Chongqing, China].
Moellendorffia biscalpta: Richardson 1985: 183.
Moellendorffia (*Trichelix*) *biscalpta*: Minato 2011: 25, fig. 3h.

Current taxonomic status. *Trichelix*. Valid species.

Type specimens. Syntype MCZ 167125 (two shells, Fig. 6C).

Remarks. The original description does not clearly state how many specimens were available to the author, and a unique name-bearing type was not explicitly designated. Heude's (1885) original description included a single illustration and one set of shell measurements. Johnson (1973: 17) used the term "paratypes" for a lot of two shells from the MCZ collection, but this does not constitute a valid holotype designation (ICZN 1999: Articles 73.1.1 and 73.2 and Recommendation 73F). The MCZ museum registration book states "Cotype"; these are also considered to be syntypes.

16. *diminuta* (Pilsbry & Hirase, 1905)

Moellendorffia eucharistus diminuta Pilsbry and Hirase 1905: 710. Type locality: Koniya, Oshima, Osumi [Koniya-Setouchi, Oshima District, Kagoshima Prefecture, Japan].
Moellendorffia diminuta: Baker 1963: 245.

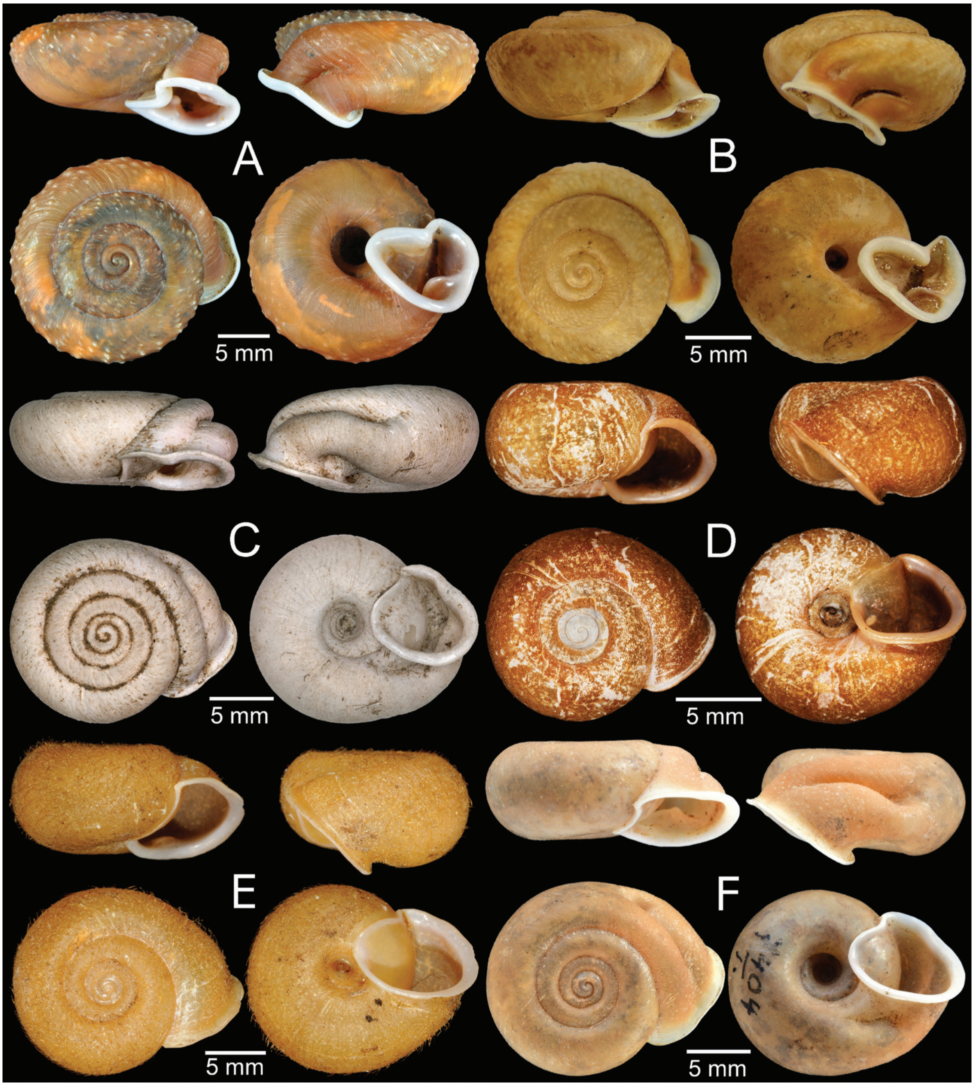

Figure 6. A *Moellendorffia spurca*, syntype MNHN-IM-2000-1992 **B** *Moellendorffia trisinuata*, syntype ZMB 7620 **C** *Trichelix biscalpta*, syntype MCZ 167125 **D** *Trichelix diminuta*, lectotype ANSP 90049 **E** *Trichelix eucharista*, lectotype ANSP 81221 **F** *Trichelix hiraseana*, lectotype SMF 7404/1 of *Stegodera helleri*. Photo: AJ Baldinger (**C**).

Moellendorffia eucharistus diminuta: Richardson 1985: 184.

Moellendorffia (*Trichelix*) *diminuta*: Minato 1971: 36–38, figs 2, 10–12. Minato 1980: 190, fig. 2. Minato 2011: 28, fig. 5c–f.

Current taxonomic status. *Trichelix*. Valid species.

Type specimens. Lectotype ANSP 90049 (Fig. 6D) and paralectotypes ANSP 452028 (three shells).

Remarks. The lectotype was designated by Baker (1963: 245).

17. ***eucharista*** **(Pilsbry, 1901)**

Chloritis eucharistus Pilsbry 1901: 347, 348. Type locality: Oshima [Oshima District, Kagoshima Prefecture, Japan].
Moellendorffia (*Trichelix*) *eucharistus*: Habe 1957: 8, 9, pl. 1, figs 3–8. Minato 1971: 36, figs 1, 7–9. Minato 1980: 190, fig. 1. Minato 2011: 26, 28, figs 2a, b, 5a, b.
Moellendorffia eucharista: Richardson 1985: 184.
Trichelix eucharistis: Schileyko 2003: fig. 1950b, c. (incorrect subsequent spelling)

Current taxonomic status. *Trichelix*. Valid species.

Type specimens. Lectotype ANSP 81221 (one shell, Fig. 6E) from Oshima, Osumi.

Remark. The lectotype was designated in Baker (1963: 245). In the original publication, the type locality was recorded as "Oshima" (=Island) which cannot be precisely located. The original label accompanying the lectotype states "Oshima, Osumi" (= historical name of Kagoshima). Habe (1957) examined the radula and genital anatomy based on a specimen from Amami Oshima, Kagoshima. Therefore, the type locality of this species is probably in the area of the Amami Islands, Kagoshima Prefecture.

18. ***helleri*** **(Rolle, 1911)**

Stegodera (*Trichelix*) *helleri* Rolle 1911: 31, 32. Type locality: Toyenmongai auf Formosa [Dong-yuan-men-jie, Tainan City, Taiwan]. Zilch 1966: 211, pl. 6, fig. 57.
Moellendorffia hiraseana helleri: Richardson 1985: 185.

Current taxonomic status. *Trichelix*. Synonym of *Trichelix hiraseana* (see Zilch 1966).

Type specimens. Lectotype SMF 7404/1 (Fig. 6F) and paralectotypes SMF 156134/4 (four shells) from Toyenmongai, Formosa. Possible paralectotype NHMUK 20040594 (four shells).

Remarks. Zilch (1966) assumed the SMF 7404 ex. H. Rolle as the holotype. However, there was no unique name-bearing type fixed in the original publication. Hwang (2014: 25) subsequently designated SMF 7404 as the lectotype.

19. ***hiraseana*** **Pilsbry, 1905**

Moellendorffia (*Trichelix*) *hiraseana* Pilsbry 1905: 66, 67, pl. 2, figs 4–6. Type locality: Hotawa, Taiwan. Zilch 1966: 211. Minato 2011: 25, figs 3g, 5h.
Moellendorffia hiraseana: Richardson 1985: 185.

Current taxonomic status. *Trichelix*. Valid species.

Type specimens. Lectotype ANSP 89999 (Fig. 7A).

Remarks. Pilsbry (1905) clearly stated that there were two specimens in his lot. The lectotype was designated in Baker (1963: 245).

20. ***horrida*** **(Pfeiffer, 1863)**

Helix horrida Pfeiffer 1863[“1862”]: 272, pl. 36, fig. 15. Type locality: Lao Mountain, Camboja [Cambodia or Laos].
Moellendorffia horrida: Richardson 1985: 285. Inkhavilay et al. 2019: 105, figs 53f, 54a, 58h.

Current taxonomic status. *Trichelix*. Valid species.

Type specimens. Lectotype NHMUK 20200202/1 ex. Cuming coll. (Fig. 7B), present designation, and paralectotypes NHMUK 20200202/2 to 20200202/3 ex. Cuming coll. (two shells).

21. ***malangensis*** **(Bullen, 1905)**

Chloritis malangensis Bullen 1905: 192, pl. 11, fig. 2. Type locality: Malang, Java [error]. Gude 1907: 228.
Moellendorffia eucharista malangensis: Richardson 1985: 184.

Current taxonomic status. *Trichelix*. Synonym of *Trichelix eucharista* (see Gude 1907: 228).

Type specimens. Syntypes NHMUK 19991540 (two shells, Fig. 7C).

Remarks. Ancey (1906: 128) stated that specimens sent by Mr Rouyer were often with doubtful or inaccurate locality records, where *C. malangensis* Bullen, 1905 was described based on Mr Rouyer’s collection. The type locality was mentioned as “Malang Java,” which is erroneous and should be ignored (Ancey 1906; Gude 1907). Ancey (1906: 128) also noticed this species was similar to *Moellendorffia eucharista* (Pilsbry, 1901) and does not occur in Java. Gude (1907: 228) compared the type specimen of *C. malangensis* with the *Moellendorffia eucharista* (Pilsbry, 1901) from Japan and found no differences in any of the shell characters.

22. ***oshimana*** **(Gude, 1901)**

Chloritis oshimana Gude 1901: 157, 158, figs 1–4. Type locality: Oshima, Loo-Choo Isles [Amami Islands, Kagoshima Prefecture]. Minato 2011: 26.
Moellendorffia eucharista oshimana: Richardson 1985: 184.

Current taxonomic status. *Trichelix*. Synonym of *Trichelix eucharista* (see Minato 2011: 26).

Type specimens. Syntype NHMUK 1922.8.29.83 (one shell, Fig. 7D).

Remark. Gude (1901: 158) noted that the collection locality was from Oshima, Osumi Province. The type locality of this species is probably in the area of the Amami Islands of Kagoshima.

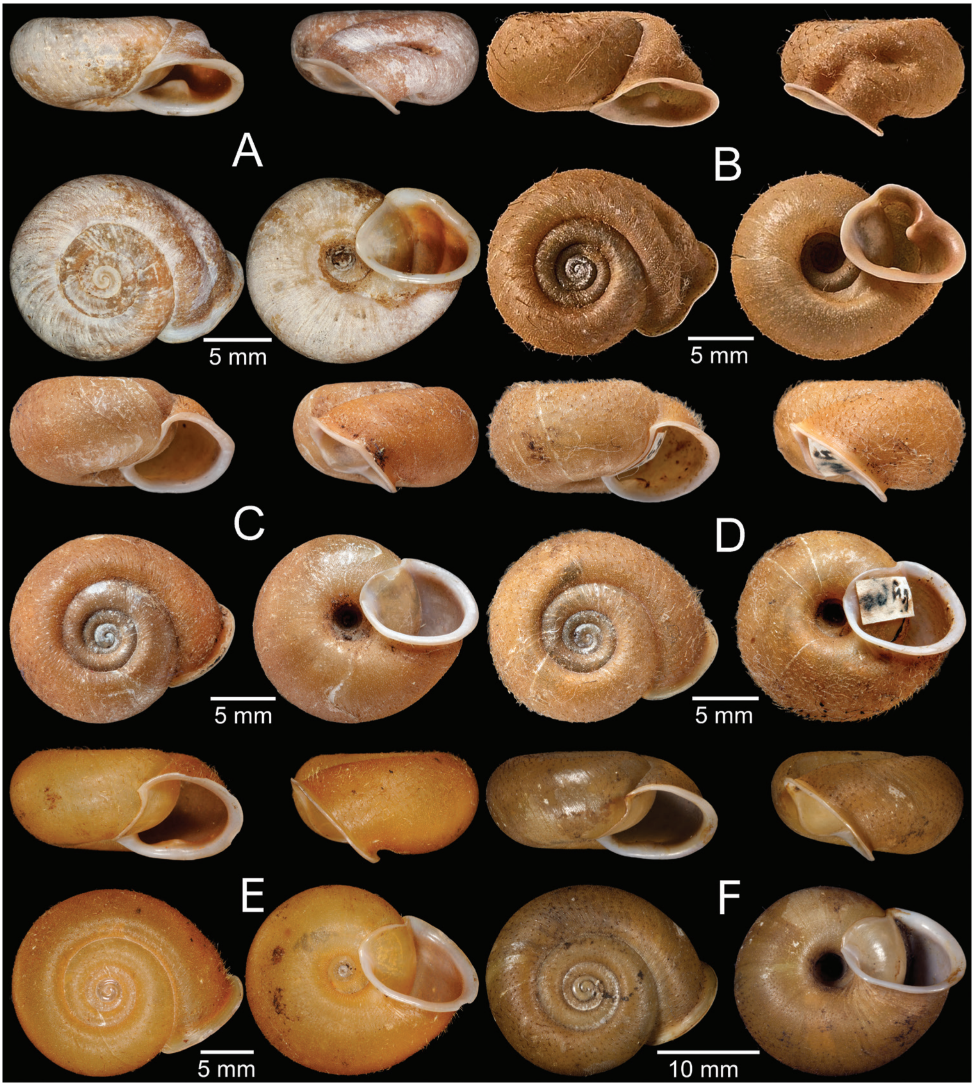

Figure 7. A *Trichelix hiraseana*, lectotype ANSP 89999 **B** *Trichelix horrida*, lectotype NHMUK 20200202/1 **C** *Trichelix eucharista*, syntype NHMUK 19991540 of *Chloritis malangensis* **D** *Trichelix oshimana*, syntype NHMUK 1922.8.29.83 **E, F** *Trichelix tokunoensis* **E** lectotype ANSP 87680 and **F** paralectotype ANSP 90048.

23. *tokunoensis* (Pilsbry & Hirase, 1905)

Moellendorffia eucharistus tokunoensis Pilsbry and Hirase 1905: 710. Type locality: Tokunoshima, Osumi [Tokunoshima Island, Oshima District, Kagoshima Prefecture, Japan].

Moellendorffia tokunoensis: Baker 1963: 247.

Moellendorffia eucharista tokunoensis: Richardson 1985:184, 185.

Moellendorffia (*Trichelix*) *tokunoensis*: Minato 1971: 38, 39, figs 3, 4–6. Minato 1980: 190–192, fig. 3. Minato 2011: 28, 29, fig. 5g.

Current taxonomic status. *Trichelix*. Valid species.

Type specimens. Lectotype ANSP 87680 (Fig. 7E) and paralectotypes ANSP 90048 (two shells, Fig. 7F), ANSP 460394 (one shell) from Tokunoshima, Osumi.

Remarks. The original description did not clearly state how many specimens were available to Pilsbry, although he stated "Types No. 90,048, A. N. S. Phila., from No. 1,207 of Mr. Hirase's collection." Later, Baker (1963: 247) designated the ANSP 87680 ex. Hirase no. 1207 lot as the lectotype. This designation is still valid unless there is evidence that ANSP 87680 lot did not form part of the type series (ICZN 1999: Articles 72.1 and 74.2).

III. Genus *Moellendorffiella* Pilsbry, 1905

Moellendorffia (*Moellendorffiella*) Pilsbry 1905: 65. Zilch 1960: 612. Zilch 1966: 211.
Moellendorffiella: Schileyko 2003: 1513.

Type species. *Helix* (*Moellendorffia*) *erdmanni* Schmacker & Boettger, 1894; monotypy.

Diagnosis. Shell flattened and umbilicate. Periostracum thin, corneous. Last whorl shouldered and descending anteriorly. Aperture subcircular with barriers inside and externally marked with furrows. Parietal callus thin; one palatal lamella; one columellar lamella.

Remarks. The genus *Moellendorffiella* differs from *Moellendorffia* in having one furrow on periphery, parietal callus thin, and without periostracal hair. While, *Moellendorffia* has one or two furrows on periphery, parietal callus elevated with nodule and short to long periostracal hairs.

24. *erdmanni* (Schmacker & Boettger, 1894)

Helix (*Moellendorffia*) *erdmanni* Schmacker and Boettger 1894: 173, 174, pl. 9, fig. 8. Type locality: China.
Moellendorffia (*Moellendorffiella*) *erdmanni*: Zilch 1966: 211, pl. 6, fig. 55.
Moellendorffia erdmanni: Richardson 1985: 184.
Moellendorffiella erdmanni: Schileyko 2003: 1513, fig. 1951.

Current taxonomic status. *Moellendorffiella*. Valid species.

Type specimens. Lectotype SMF 8333/1 (Fig. 8A) and paralectotype SMF 8334 (one shell) from Chang-yang, Hupei, China.

Remarks. The lectotype was designated in Zilch (1966: 211).

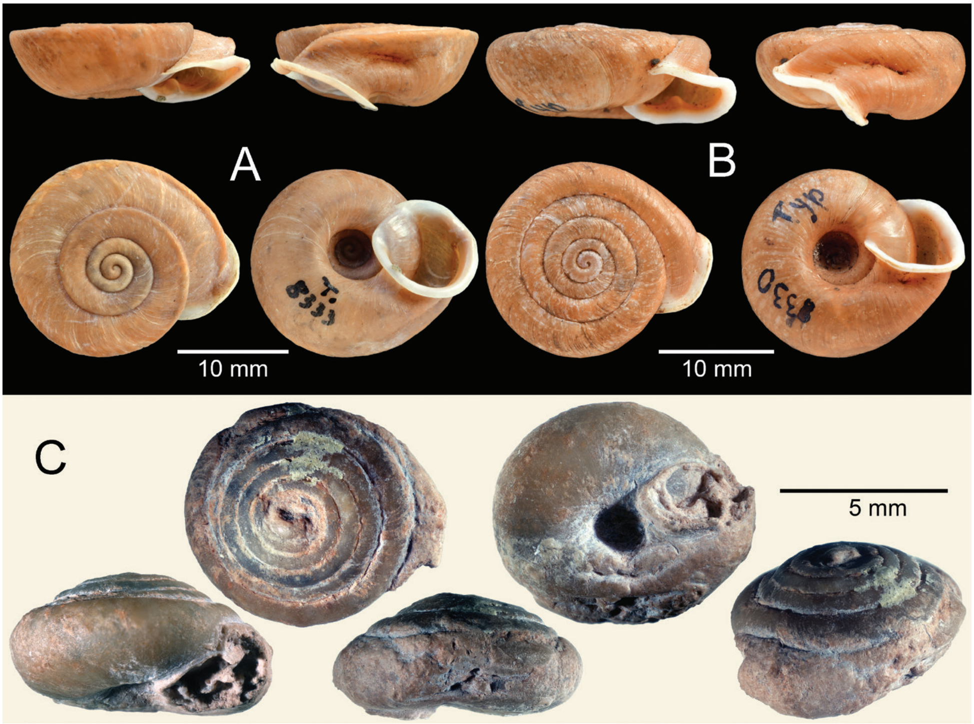

Figure 8. A *Moellendorffiella erdmanni*, lectotype SMF 8333/1 **B** *Moellendorffiella faberiana*, holotype SMF 8330/1 **C** *Moellendorffia* ? *polygyrella*, holotype NIGPAS 36428. Photo: T Yü (**C**).

25. *faberiana* (Möllendorff, 1888) comb. nov.

Helix faberiana Möllendorff 1888: 39, 40. Type locality: Omi, Sytshuan, 1000 m. alt. [in the area of Sichuan, China].
Moellendorffia (*Trichelix*) *faberiana*: Zilch 1966: 211, pl. 6, fig. 56.
Moellendorffia faberiana: Richardson 1985: 185.

Current taxonomic status. *Moellendorffiella*. Valid species.

Type specimens. Holotype SMF 8330/1 (Fig. 8B) and paratype SMF unnumbered (one juvenile in the same holotype lot) from Berg Omi, Szechwan, China.

Remarks. The distinguishing characters are depressed conic spire, aperture with elevated parietal callus, furrows on periphery and below periphery. Therefore, we move this species to the genus *Moellendorffiella*.

Species inquirenda

mariae (Nobre, 1909)

Stegodera (*Moellendorffia*) *mariae* Nobre 1909: 79. Type locality: Lucira, dist. de Benguella [Lucira Communes, Namibe Province, Angola].

Moellendorffia mariae: Richardson 1985: 185.

Current taxonomic status. Not a member of *Moellendorffia*, *Trichelix*, or *Moellendorffiella*.

Type specimens. The type specimen could not be located.

Remarks. This nominal species was described by Nobre (1909) based on material collected from Angola on the west coast of Africa. Based on the shell morphology, Nobre (1909) attributed this taxon to the Southeast Asian endemic genus *Stegodera* (*Moellendorffia*). Later, Richardson (1985) placed this species under the genus *Moellendorffia*. However, the record of *Moellendorffia* on the east coast of Africa (Ethiopian Realm) are far outside of the known range of the genus. Thus, further study and anatomical examination are needed to relocate this nominal species into the suitable nominal genus, very probably a *Sculptaria* Pfeiffer, 1855 (Sculptariidae).

polygyrella Yü, 1982

Moellendorffia ? *polygyrella* Yü in Yü et al. 1982: 19, 20, pl. 5, figs 10–14. Type locality: Late Cretaceous and Early Tertiary red series of Xuaneheng, Langxi and Nanling, Southern Anhui.

Current taxonomic status. *Moellendorffia*. Valid species.

Type specimens. Holotype NIGPAS 36428 (one shell: Fig. 8C) from Xuancheng, Luojing, Anhui, China.

Remarks. The species was described based on one specimen. The holotype has a relatively small shell (shell width 8 mm) compared to other recent congeners. This species possesses a smooth shell surface and a narrow umbilicus. The outer surface of the last whorl probably has one spiral furrow on the periphery and two spiral furrows below the periphery. These characters suggest the possibility that it is closely related to the genus *Traumatophora* Ancey, 1887 (see Wu 2019 for a comparison).

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RESEARCH ARTICLE

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Two new genera and eight new species of jumping spiders (Araneae, Salticidae) from Xishuangbanna, Yunnan, China

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Abstract

Two new genera and eight new species of jumping spiders from Xishuangbanna Tropical Botanical Garden (XTBG) are diagnosed, described, and illustrated. The new genera are *Dendroicius* **gen. nov.** (type species *D. hotaruae* **sp. nov.** (♂♀)) and *Megaeupoa* **gen. nov.** (type species *M. yanfengi* **sp. nov.** (♂♀)). The new species are *Colyttus yiwui* **sp. nov.** (♂♀), *Euophrys xuyei* **sp. nov.** (♂♀), *Foliabitus weihangi* **sp. nov.** (♂♀), *Nigorella mengla* **sp. nov.** (♂♀), *Onomastus chenae* **sp. nov.** (♂♀), and *Synagelides platnicki* **sp. nov.** (♂♀). A new combination is proposed: *Megaeupoa gravelyi* (Caleb, 2018), **comb. nov.**, ex *Brettus* Thorell, 1895. Two new synonyms have been proposed: *Irura prima* (Żabka, 1985), **syn. nov.** with *Irura mandarina* Simon, 1903; *Evarcha digitata* Peng & Li, 2002, **syn. nov.** with *Ptocasius montiformis* Song, 1991.

Keywords

All Species Inventory, taxonomy, tropical rainforest, XTBG

Introduction

Salticidae Blackwall, 1841, or jumping spiders, is the largest spider family, with 6183 species in 646 genera worldwide (WSC 2020). Of the 5078 species of spiders described from China, 526 are jumping spiders (Li 2020a). This paper describes two new genera and eight new species of jumping spiders from Xishuangbanna Tropical Botanical Garden (XTBG), Yunnan, southwestern China.

Xishuangbanna Tropical Botanical Garden is located on Hulu Island in Menglun Township, Mengla County. XTBG is separated from the mainland by the Luosuo River, a tributary of the Mekong River (known as the Lancang River in China). XTBG's 11.25 square kilometers includes a 2.50 square kilometer patch of well-preserved primary tropical rainforest, the main research area of our "All Species Inventory" on XTBG spiders for the past 20 years.

Until now, the Xishuangbanna spider checklist included 782 species in 46 families (Li 2020a). The species diversity from XTBG is greater than the number of species found in thoroughly studied regions, such as the United Kingdom, Norway, and Denmark (Nentwig et al. 2020). From our long-term study, we expect to find more spider species from XTBG.

Materials and methods

Specimens were collected by fogging in XTBG. All specimens were preserved in 100% ethanol. Epigynes were cleared in trypsin enzyme solution to dissolve non-chitinous tissues. Specimens were examined under a LEICA M205C stereomicroscope. Photomicroscope images were taken with an Olympus C7070 zoom digital camera (7.1 megapixels). Photos were stacked with Helicon Focus (version 6.7.1) or Zerene Stacker (version 1.04) and processed in Adobe Photoshop CC 2018. All measurements are in millimeters. Eye sizes are measured as the maximum diameter from either the dorsal or frontal view. Leg measurements are given as follows: total length (femur, patella+tibia, metatarsus, tarsus); however, in *Synagelides platnicki* sp. nov., because of the long patella, we use (femur, patella, tibia, metatarsus, tarsus). All specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing, China.

Abbreviations used in the text and figures:

AER	anterior eye row	**C**	conductor
AERW	anterior eye row width	**CD**	copulatory duct
AG	accessory gland	**CO**	copulatory opening
AL	abdomen length	**Cy**	cymbium
ALE	anterior lateral eye	**dEA**	dorsal embolic apophysis
AME	anterior median eye	**DH**	distal hematodocha
AW	abdomen width	**DTA**	dorsal tibial apophysis
BH	basal hematodocha	**E**	embolus

EFL	eye field length	**PME**	posterior median eye
EO	embolic opening	**PS**	primary spermathecae
ED	embolic disc	**PTA**	posterior terminal apophysis
EP	embolic part	**RSDL**	retrolateral sperm duct loop
ES	embolic sheath	**RTA**	retrolateral tibial apophysis
FD	fertilization duct	**rMA**	retrolateral median apophysis
iTA	inferior terminal apophysis	**S**	spermathecae
LE	lamella of embolus	**SP**	spur on mesal branch of conductor
lTA	lateral terminal apophysis		
M	membrane	**Sp**	spine
MA	median apophysis	**SD**	sperm duct
mDTA	mesal branch of DTA	**SS**	secondary spermathecae
MH	median hematodocha	**ST**	subtegulum
MS	median septum	**T**	tegulum
MTP	membranous tegular peak	**TA**	terminal apophysis
PA	patellar apophysis	**TL**	tegular lobe
PER	posterior eye row	**TS**	tegular sclerite
PERW	posterior eye row width	**VTB**	ventral tibial bump
PLE	posterior lateral eye	**W**	window

Taxonomy

Family Salticidae Blackwall, 1841

Genus *Colyttus* Thorell, 1891

Type species. *Colyttus bilineatus* Thorell, 1891.

Colyttus yiwui sp. nov.

http://zoobank.org/022B0848-4F66-4B45-83D1-17E9AFDD2316
Figures 1, 2

Type material. ***Holotype*** ♂(IZCAS-Ar40379), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 27.IX.2017, Zhigang Chen leg. ***Paratypes*** 7♂3♀(IZCAS-Ar40380–Ar40389), same data as holotype.

Etymology. This species is named after Mr. Yiwu Zhu, who has helped us greatly with this research; noun (name) in genitive case.

Diagnosis. The males of *Colyttus yiwui* sp. nov. are similar to *C. proszynskii* Caleb, Chatterjee, Tyagi, Kundu & Kumar, 2018 by having a similarly-shaped embolus. However, *C. zhui* sp. nov. can be distinguished by the well-developed tegular lobe (vs. less well-developed in *C. proszynskii*), the ratio of the length of the embolus to the width of the embolic disc 1:1 (vs. 2:1 in *C. proszynskii*), the curved embolic tip (vs. straight in *C. proszynskii*) and the blunt lamella of the embolus (vs. pointed in *C. proszynskii*).

Description. Male (Figs 1, 2C, E, G). Total length 6.76. Carapace 3.36 long, 2.72 wide. Abdomen 3.40 long, 1.85 wide. Clypeus 0.05 high. Eye sizes and inter-distances: AME 0.67, ALE 0.45, PLE 0.43, AERW 2.21, PERW 2.12, EFL 1.44. Legs: I 6.93 (2.45 + 2.66 + 1.22 + 0.60), II 5.55 (1.63 + 2.15 + 1.22 + 0.55), III 5.81 (1.80 + 1.95 + 1.46 + 0.60), IV 6.04 (1.90 + 2.05 + 1.49 + 0.60). Carapace yellow-brown with black edge, eye region dark brown, with black rings around eyes. Fovea longitudinal, situated between PLEs. Clypeus black, covered with white setae. Chelicerae dark brown with two promarginal teeth and one retromarginal fissident tooth with two cusps. Endites, labium and sternum brown. Leg I black, other legs pale yellow except femora with black pattern. Abdomen elongated oval, dorsum with two pairs of muscle depressions medially, irregular yellow stripe across entire surface and bifurcated posteriorly, covered with brown setae and sparse, long setae; venter brown. Spinnerets brown.

Palp (Fig. 1A–C): Tibia stocky, slightly wider than long, with relatively long RTA; cymbium longer than wide; bulb approximately as long as wide; lamella of embolus blunt, embolus long, connected to embolic disc, embolic tip curved.

Female (Fig. 2A, B, D, F, H). Total length 4.82. Carapace 2.04 long, 1.63 wide. Abdomen 2.78 long, 1.61 wide. Clypeus 0.12 high. Eye sizes and inter-distances: AME

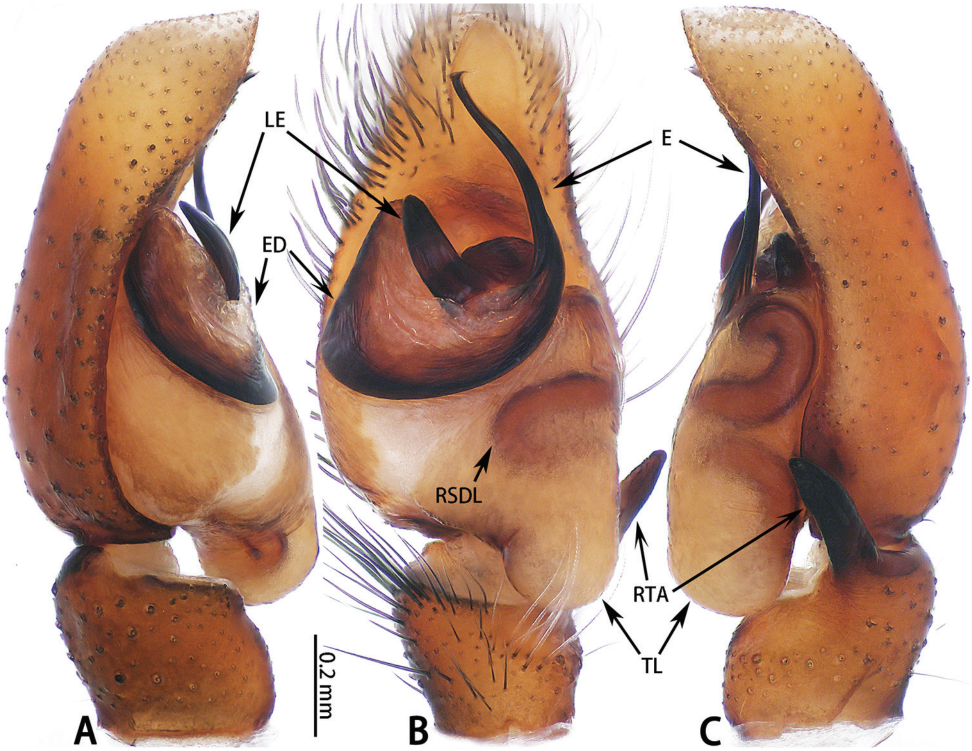

Figure 1. Palp of *Colyttus yiwui* sp. nov., male holotype. **A** prolateral **B** ventral **C** retrolateral.

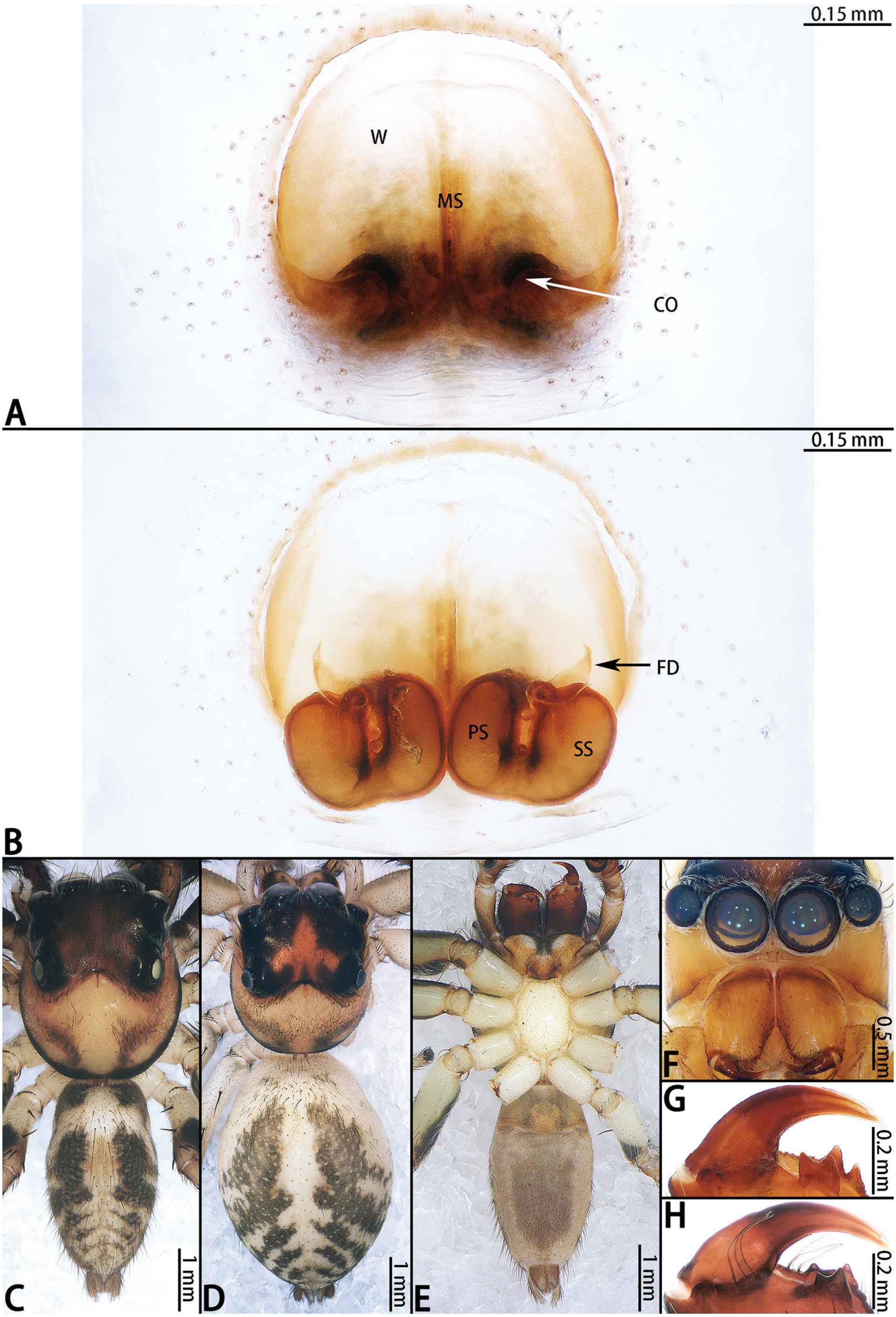

Figure 2. *Colyttus yiwui* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** female paratype habitus, dorsal **E** holotype habitus, ventral **F** frontal view of female paratype. **G** dorsal view of chelicerae, male holotype **H** dorsal view of chelicerae, female paratype.

0.47, ALE 0.28, PLE 0.27, AERW 2.38, PERW 2.28, EFL 1.69. Legs: I 6.16 (1.96 + 2.43 + 1.16 + 0.61), II 5.00 (1.53 + 1.96 + 1.01 + 0.50), III 5.10 (1.59 + 1.66 + 1.31 + 0.54), IV 5.71 (1.66 + 1.98 + 1.53 + 0.54). Habitus similar to that of male except paler.

Epigyne (Fig. 2A, B) as long as wide, windows large, separated by median septum; copulatory openings on each side of septum located posteriorly; copulatory ducts indistinct, primary spermathecae smaller than secondary spermathecae, overall U-shaped; fertilization ducts originating from the anterior entolatetal edge of secondary spermathecae, extending almost transversely.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Dendroicius* gen. nov.

http://zoobank.org/91408531-896D-4729-8C90-AFA460B25E09

Type species. *Dendroicius hotaruae* sp. nov.

Etymology. The generic name is a combination of the word "*Dendro*", referring to the habitat of the genus, and the generic name *Icius* Simon, 1876. The gender is masculine.

Diagnosis. *Dendroicius* gen. nov. can be easily distinguished from *Icius* by the following characters: the male without a stridulatory apparatus; palpal tibia with a dorsal apophysis, dorsal embolic apophysis of bulb near the tegular sclerite; epigyne with a large hood posteriorly, posterior to copulatory opening, copulatory opening circular, depression around copulatory opening, spermathecae posterior to copulatory opening, copulatory ducts curved, fertilization ducts folded 90°, well-developed.

Composition. The new genus currently includes only one species: *Dendroicius hotaruae* sp. nov.

Dendroicius hotaruae sp. nov.

http://zoobank.org/72556AE0-B460-402A-99B9-BA4795328B5E
Figures 3, 4

Type material. ***Holotype*** ♂(IZCAS-Ar40390), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8986N, 101.2683E, elevation ca 550 m, 27.IX.2017, Zilong Bai leg. ***Paratypes*** 1♂4♀(IZCAS-Ar40391–Ar40395), same data as holotype.

Etymology. The species is named after Ms. Hotaru Amamiya, who helped us greatly with this research; noun (name) in genitive case.

Diagnosis. Same as for the genus.

Description. Male (Figs 3, 4C, D, G). Total length 3.24. Carapace 1.58 long, 1.03 wide. Abdomen 1.88 long, 1.03 wide. Clypeus 0.03 high. Eye sizes and interdistances: AME 0.32, ALE 0.16, PLE 0.16, AERW 0.85, PERW 0.94, EFL 0.56. Legs: I 2.54 (0.82 + 1.09 + 0.33 + 0.30), II 1.89 (0.59 + 0.71 + 0.36 + 0.23), III 1.86 (0.57 + 0.61 + 0.41 + 0.27), IV 2.46 (0.77 + 0.90 + 0.48 + 0.31). Carapace dark brown,

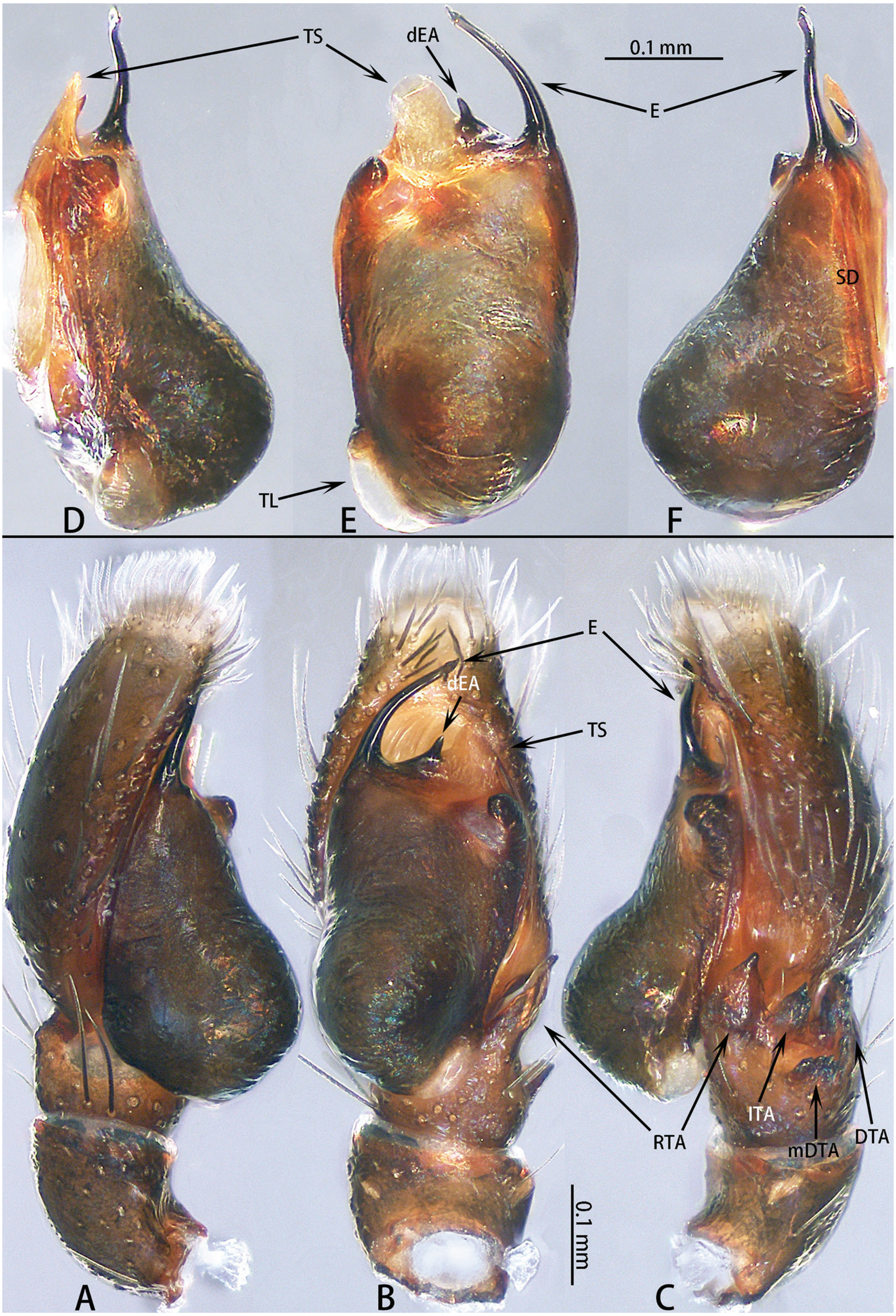

Figure 3. Male palp of *Dendroicius hotaruae* sp. nov. **A–C** holotype, left palp; **D, E** paratype, right palp. **A** prolateral **B** ventral **C** retrolateral **D** bulb, retrolateral **E** same, ventral **F** same prolateral.

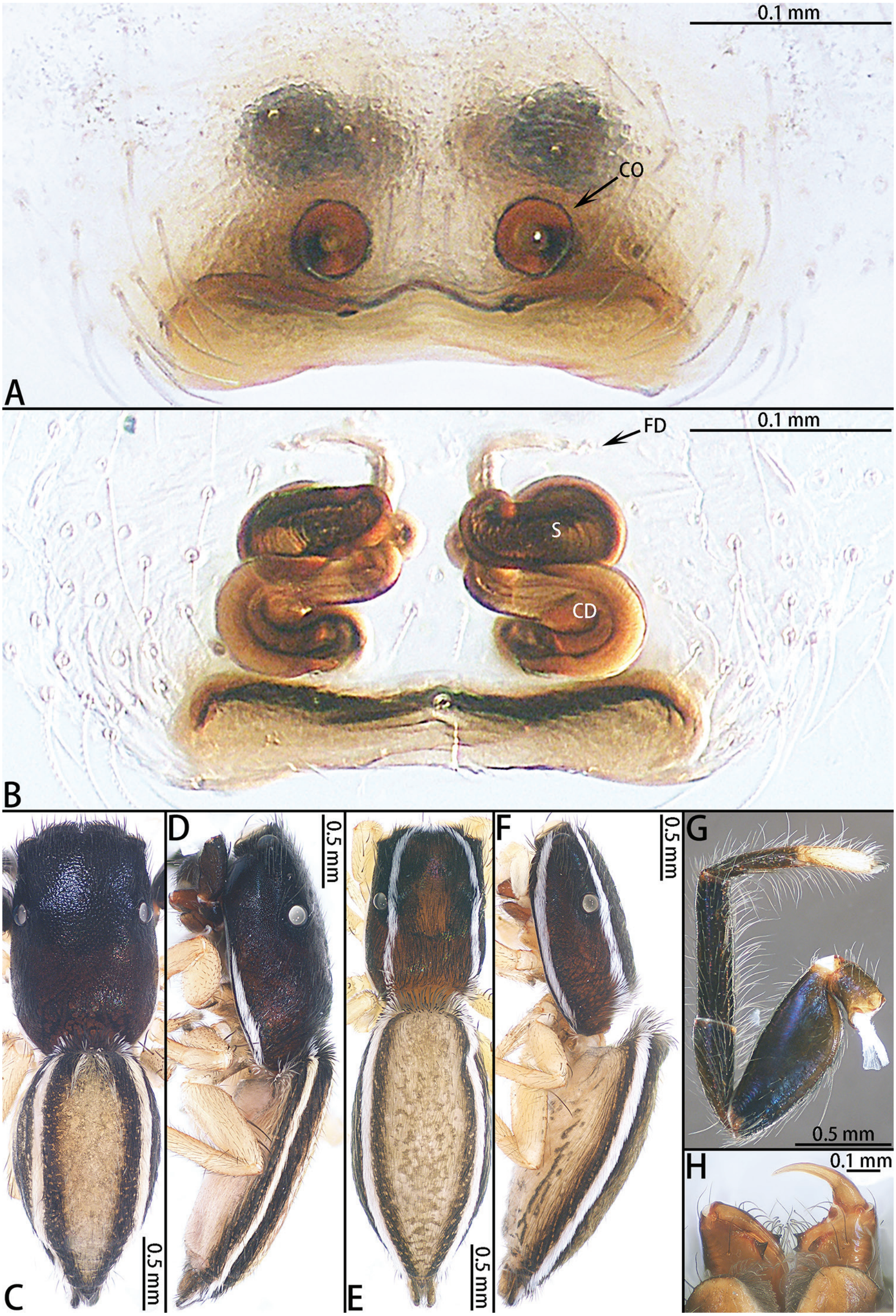

Figure 4. *Dendroicius hotaruae* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** same, lateral **E** female paratype habitus, dorsal **F** same, lateral **G** prolateral view of male left leg I **H** ventral view of female chelicerae.

darker in eye field, almost square, covered with black setae, edge with white setal stripe originating medially, thoracic part sloping acutely. Fovea indistinct. Clypeus black, anterior margin with long setae. Chelicerae black, with one retromarginal fissident tooth with two cusps and one retromarginal tooth. Endites brown. Labium brown. Sternum colored as endites, covered with sparse setae. Leg I black, others yellow. Abdomen elongated oval, dorsum pale brown with one pair of stripes of dense white setae, darker around stripes; venter pale yellow.

Palp (Fig. 3A–F) patella dark brown, slightly wider than long, covered with setae; tibia slightly wider than long, retrolateral tibial apophysis slightly longer than wide, lateral terminal apophysis darker, serrated along edge, dorsal tibial apophysis with small, serrated mesal branch; cymbium longer than wide, slightly longer than the length of the bulb in retrolateral view; bulb longer than wide, with sperm duct extending along margin; embolus short, half as long as bulb, needle shaped; dorsal embolic apophysis small, one fifth the length of embolus; tegular sclerite sheet-like, adjacent to dorsal embolic apophysis.

Female (Fig. 4A, B, E, F, H). Total length 3.52. Carapace 1.38 long, 0.90 wide. Abdomen 2.13 long, 1.09 wide. Clypeus 0.05 high. Eye sizes and inter-distances: AME 0.28, ALE 0.16, PLE 0.09, AERW 0.79, PERW 0.88, EFL 0.62. Legs: I 1.63 (0.55 + 0.62 + 0.26 + 0.20), II 1.40 (0.46 + 0.52 + 0.24 + 0.18), III 1.55 (0.49 + 0.48 + 0.30 + 0.28), IV 2.13 (0.66 + 0.75 + 0.39 + 0.33). Appearance of abdomen and legs as in male but carapace with two pairs of white setal latero-marginal stripes from lateral sides of AME and two longitudinal stripes of white setae from AMEs along PLE to the rear margin of carapace. All legs yellow and abdomen laterally with black pattern.

Epigyne (Fig. 4A, B) wider than long, with a wide hood posteriorly; copulatory openings circular; copulatory ducts long, curved medially; accessory gland indistinct; spermathecae oval; fertilization ducts folded 90°, well-developed.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Euophrys* C. L. Koch, 1834

Type species. *Aranea frontalis* Walckenaer, 1802.

Euophrys xuyei sp. nov.

http://zoobank.org/892D8E78-05A9-443D-A6A4-E85091DF1D33
Figures 5, 6

Type material. ***Holotype*** ♂(IZCAS-Ar40396), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 21.IX.2017, Zhigang Chen leg. ***Paratypes*** 1♂1♀(IZCAS-Ar40397, Ar40398), same data as holotype.

Etymology. The species is named after Mr. Ye Xu, who helped us greatly with this research; noun (name) in genitive case.

Diagnosis. *Euophrys xuyei* sp. nov. can be easily distinguished from other species by the following characters: male palpal tibia slightly longer than RTA in retrolateral view, tapering to a slightly hooded tip; bulb with tegular lobe covering tibia; embolic terminus flat, with small cusps; epigyne with copulatory openings on each side of median septum located posteriorly; copulatory ducts around spermathecae; accessory glands adjacent to copulatory openings.

Description. Male (Figs 5A–C, 6C, D, F, G). Total length 3.03. Carapace 1.70 long, 1.21 wide. Abdomen 1.52 long, 0.98 wide. Clypeus 0.06 high. Eye sizes and inter-distances: AME 0.41, ALE 0.26, PLE 0.23, AERW 0.94, PERW 0.86, EFL 0.64. Legs: I 2.92 (0.89 + 1.11 + 0.51 + 0.41), II 2.35 (0.79 + 0.81 + 0.37 + 0.38), III 2.81 (0.92 + 0.88 + 0.61 + 0.40), IV 3.08 (0.92 + 0.98 + 0.72 + 0.46). Carapace dark brown, cephalic part almost square, thoracic part sloping abruptly, with scattered white setae laterally. Fovea longitudinal, bar shaped. Clypeus dark brown. Chelicerae brown, with two promarginal teeth and one retromarginal enlarged tooth. Endites, labium and sternum colored as chelicerae but paler. Sternum slightly longer than wide, covered

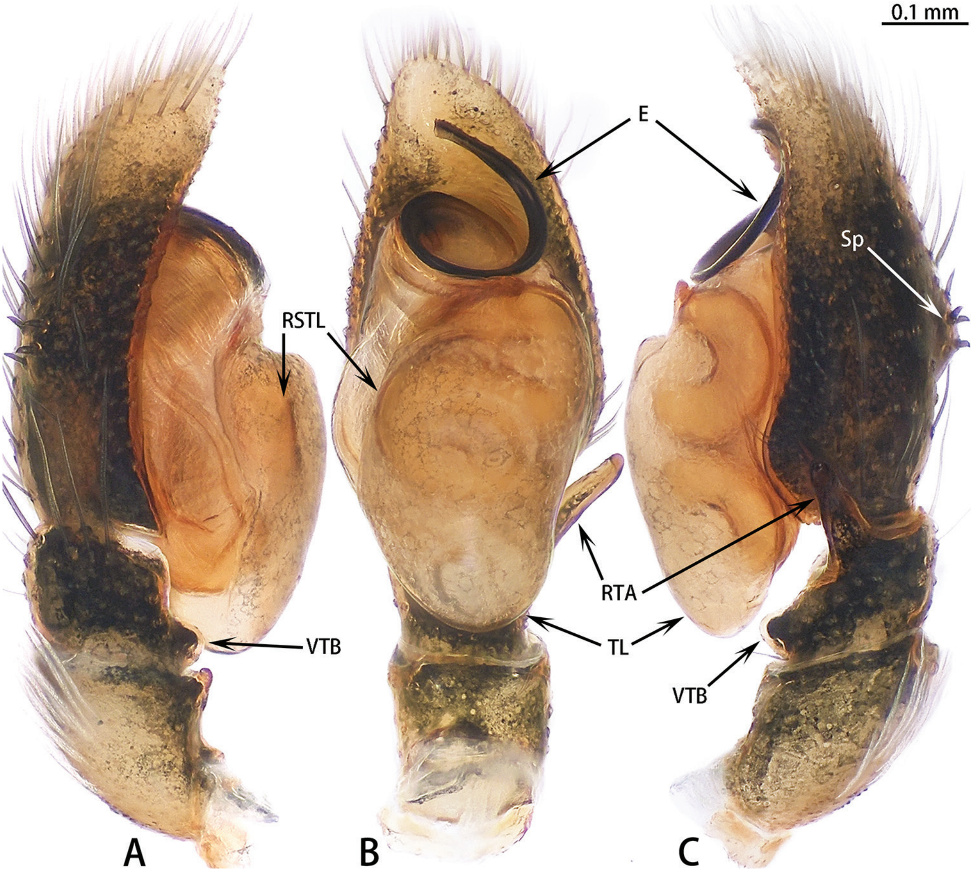

Figure 5. Palp of *Euophrys xuyei* sp. nov., male holotype. **A** prolateral **B** ventral **C** retrolateral.

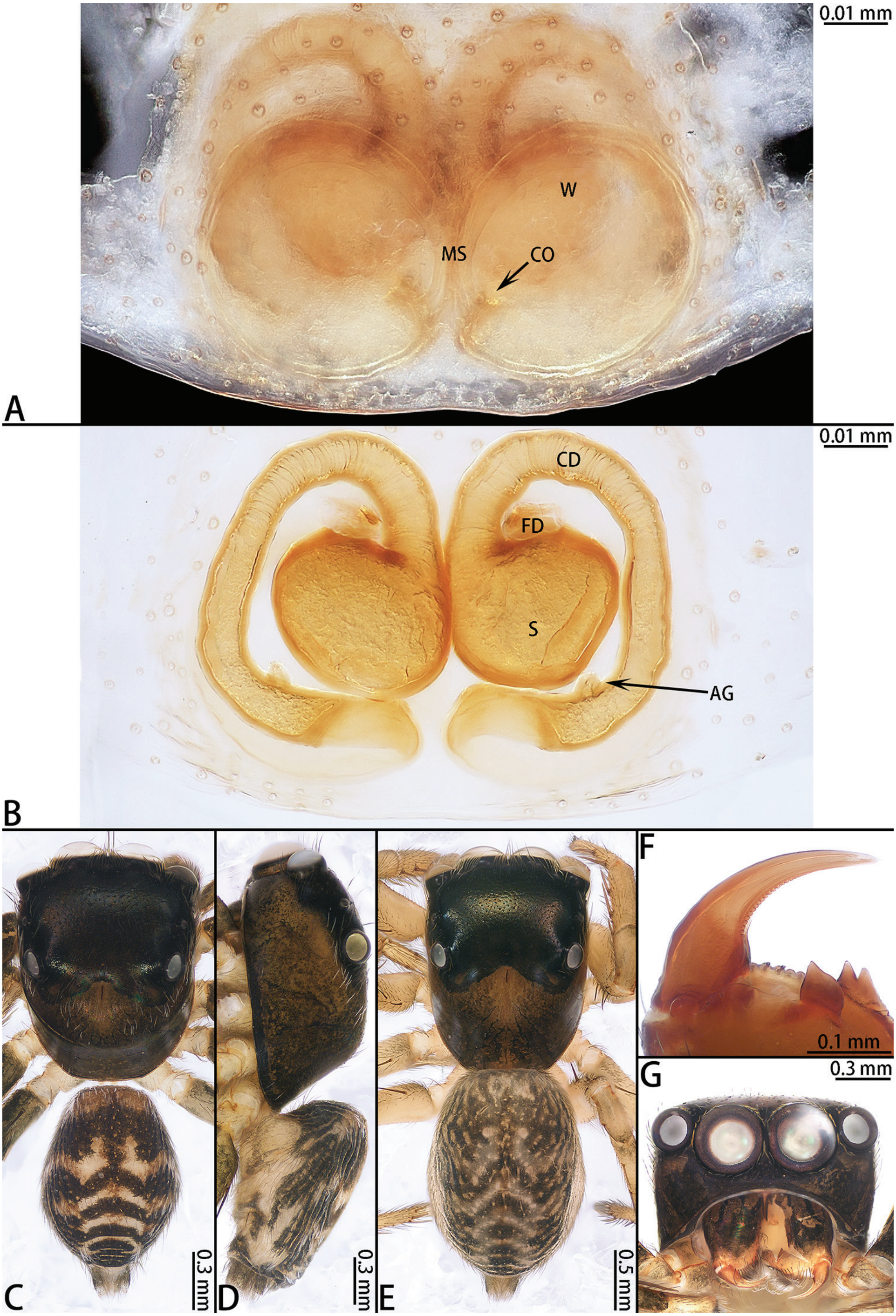

Figure 6. *Euophrys xuyei* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** same, lateral **E** female paratype habitus, dorsal **F** dorsal view of chelicerae, male paratype **G** frontal view of male paratype.

with dark setae. Legs yellow to black. Abdomen elongated oval, speckled laterally, with several chevrons posteriorly, covered with white setae; venter yellow-brown with spots.

Palp (Fig. 5A–C): Patella and tibia dark brown, slightly longer than wide, ventral tibial bump stout; RTA slightly shorter than tibia in retrolateral view, tapering to a slightly hooded tip; cymbium dark brown, longer than wide, widest medially, dorsally with a few short, stout spines in the middle; bulb longer than wide, with sperm duct relatively stout, meandering retrolaterally and tapering prolaterally; tegular lobe distinct, covering tibia; embolus with coiled base; embolic terminus flat with small cusps and thin membrane.

Female (Fig. 6A, B, E). Total length 3.72. Carapace 1.84 long, 1.36 wide. Abdomen 2.02 long, 1.36 wide. Clypeus 0.07 high. Eye sizes and inter-distances: AME 0.47, ALE 0.28, PLE 0.25, AERW 0.82, PERW 0.77, EFL 0.56. Legs: I 3.00 (0.97 + 1.14 + 0.47 + 0.42), II 2.65 (0.90 + 0.92 + 0.44 + 0.39), III 3.20 (1.10 + 1.02 + 0.66 + 0.42), IV 3.69 (1.10 + 1.19 + 0.89 + 0.51). Habitus similar to that of male except paler.

Epigyne (Fig. 6A, B) slightly wider than long, windows large, separated by median septum; copulatory openings on each side of median septum located posteriorly; copulatory ducts wrap around spermathecae; accessory glands adjacent to copulatory openings; spermathecae spherical; fertilization ducts originating from the median anterior edge of spermathecae, extending almost transversely.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Foliabitus* Zhang & Maddison, 2012

Type species. *Foliabitus longzhou* Zhang & Maddison, 2012.

Foliabitus weihangi sp. nov.

http://zoobank.org/CC5F3D88-678D-4BA7-9591-8A83B0D6CEC6
Figures 7, 8

Type material. ***Holotype*** ♂(IZCAS-Ar40399), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 09.V.2018, Weihang Wang leg. ***Paratypes*** 4♂4♀ (IZCAS-Ar40400–Ar40407), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8986N, 101.2683E, elevation ca 523 m, 29.IV.2019, Zilong Bai leg.

Etymology. The species is named after Mr. Weihang Wang, who has helped us greatly with this research; noun (name) in genitive case.

Diagnosis. *Foliabitus weihangi* sp. nov. resembles *F. scutigerus* (Zabka, 1985) and *F. longzhou* Zhang & Maddison, 2012 by the long and coiled embolus, nearly forming a circle, but differs in the following: the RTA is curved towards the bulb medially in ventral view (vs. the RTA straight in ventral view in *F. scutigerus* and *F. longzhou*); the RTA curved without a small cusp distally (vs. with a small cusp distally in *F. longzhou*), the tegular lobe protrudes from the bulb (vs. indistinct in *F. scutigerus* and *F. longzhou*); in the female, the copulatory ducts are S-shaped (vs. C-shaped in *F. longzhou*).

Description. Male (Figs 7A–C, 8C, G). Total length 4.29. Carapace 1.94 long, 1.61 wide. Abdomen 2.35 long, 1.18 wide. Clypeus 0.05 high. Eye sizes and inter-distances: AME 0.43, ALE 0.27, PLE 0.25, AERW 1.34, PERW 1.26, EFL 1.02. Legs: I 7.25 (2.13 + 2.88 + 1.47 + 0.76), II 5.14 (1.66 + 1.78 + 1.10 + 0.60), III 5.50 (1.76 + 1.80 + 1.38 + 0.56), IV 5.61 (1.66 + 1.92 + 1.53 + 0.50). Carapace black, cephalic part with dense, green scale-like setae around eyes. Fovea longitudinal, posterior to PLEs. Clypeus yellow, covered with dense, white setae. Chelicerae black, with two retromarginal teeth and one promarginal tooth. Endites and labium dark brown. Sternum brown, covered with dark setae. Legs pale yellow, except leg I black, covered with long, dark setae. Abdomen elongated oval, dorsum black, with pale pattern; venter black with dark setae.

Palp (Fig. 7A–C): Patella red-brown, almost as long as wide; tibia stocky, slightly wider than long, with sclerotized, hook-shaped RTA, curved towards the bulb; cymbium longer than wide, covered with long setae; bulb longer than wide, tegular lobe distinct, curved retrolaterally; embolus long and coiled, nearly forming a circle.

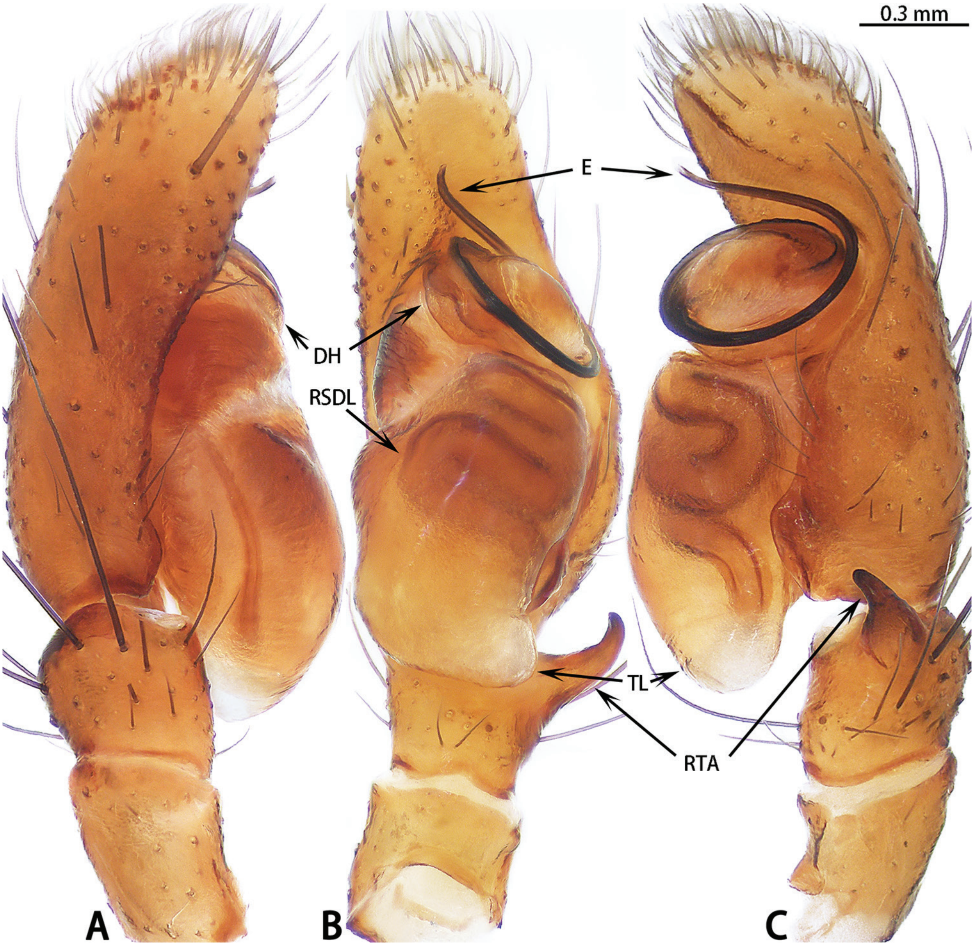

Figure 7. Palp of *Foliabitus weihangi* sp. nov., male holotype. **A** prolateral **B** ventral **C** retrolateral.

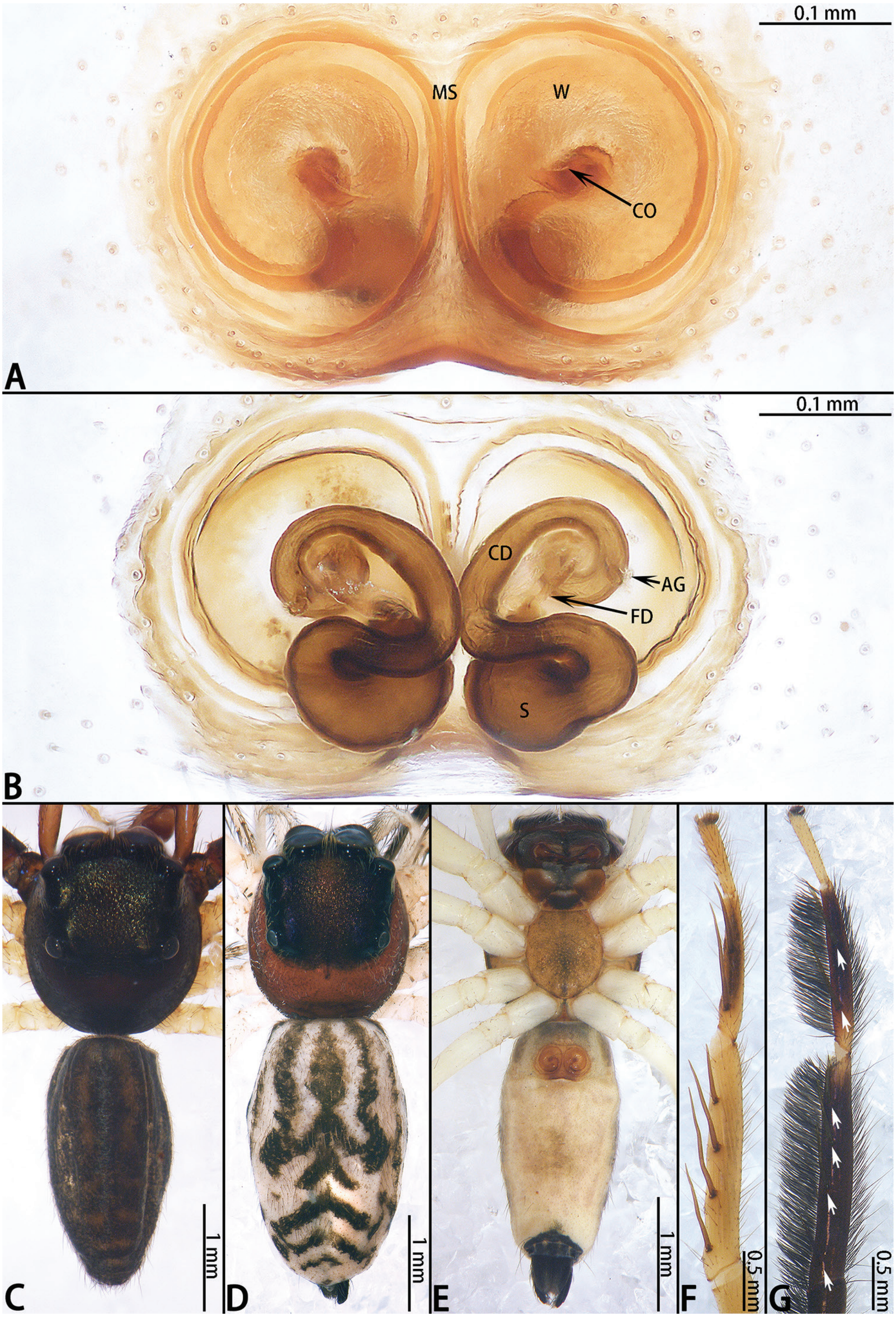

Figure 8. *Foliabitus weihangi* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** female paratype habitus, dorsal **E** same, ventral **F** prolateral view of right leg I, female paratype **G** prolateral view of right leg I, male holotype.

Female (Fig. 8A, B, D–F). Total length 4.82. Carapace 2.04 long, 1.63 wide. Abdomen 2.78 long, 1.60 wide. Clypeus 0.06 high. Eye sizes and inter-distances: AME 0.47, ALE 0.28, PLE 0.27, AERW 1.29, PERW 1.26, EFL 1.12. Legs: I 6.16 (1.96 + 2.43 + 1.16 + 0.61), II 5.00 (1.53 + 1.96 + 1.01 + 0.50), III 5.10 (1.59 + 1.66 + 1.31 + 0.54), IV 5.71 (1.66 + 1.98 + 1.53 + 0.54). Habitus (Fig. 8D) similar to that of male except paler. Abdomen dorsally whitish with black pattern similar to male, ventrally pale yellow, with small black triangular patch near spinnerets.

Epigyne (Fig. 8A, B) wider than long, windows large, separated by median septum; copulatory openings at center of windows; copulatory ducts long, S-shaped; spermathecae oval; fertilization ducts well-developed, membranous, lamellar.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Megaeupoa* gen. nov.

http://zoobank.org/1B7801B2-2A3E-454C-9C4D-9083A5864DF1

Type species. *Megaeupoa yanfengi* sp. nov.

Etymology. The generic name is a combination of the word *Mega* and *Eupoa*, referring to the large size and evolutionary relationship of this new genus. The gender is feminine.

Diagnosis. *Megaeupoa* gen. nov. resembles *Brettus* Thorell, 1895 morphologically by the stout RTA, long, undulating embolus, membranous conductor and the epigyne has one tortuous copulatory duct, but it differs in the following: an absence of ventral fringes of long, dense hairs on legs I (Caleb, Acharya and Kumar 2018), RTA stout, slightly longer than wide in lateral view (vs. the RTA is three times longer than wide in *Brettus*), half of the embolus is obscured by the embolic sheath (vs. uncovered in *Brettus*), terminal apophysis present (vs. terminal apophysis absent in *Brettus*); in the female, the vulva has two pairs of spermathecae (vs. one pair of spermathecae in *Brettus*) and the copulatory ducts are curled (vs. copulatory ducts straight in *Brettus*).

Description. Male. Total length 4.96–5.64. Carapace red-brown, covered with dense, brown setae, posteriorly with white stripes of setae, cephalic part black or brown. Fovea longitudinal. Clypeus black to brown, covered with several white setae. Chelicerae yellow-brown, with five promarginal and 9–13 retromarginal teeth. Endites pale brown. Labium pale brown, covered with brown setae. Sternum colored as endites, covered with brown setae. Legs brown, with long, white, dense setal ring and black ring pattern. Abdomen elongated oval, dorsum with one pair of stripes of dense white setae, transverse dark brown stripes medially; venter pale brown, covered with setae.

Palpal patella covered with dense, white setae dorsally; tibia slightly wider than long, with ventral apophysis, RTA stout, slightly longer than wide in lateral view; cymbium longer than wide; bulb longer than wide; embolus long, undulate, half of the embolus covered by embolic sheath, other half covered by lateral terminal apophysis; conductor membranous, sheet-shaped, adjacent to embolus; median apophysis small; lateral terminal apophysis whip-like, terminal apophysis distinct, stout.

Female. Total length 5.51. Habitus similar to those of male except paler.

Epigyne as long as wide; with posterior hood; windows large, oval; copulatory openings located medially; copulatory ducts curled on either side with two pairs of spermathecae; primary spermathecae small, situated anteriorly, secondary spermathecae large.

Composition. This new genus includes two species: *Megaeupoa yanfengi* sp. nov. and *Megaeupoa gravelyi* (Caleb, 2018), comb. nov.

Distribution. China (Yunnan), India.

Megaeupoa yanfengi **sp. nov.**

http://zoobank.org/32CB491D-7AD6-4CB1-854B-5A0239E4BBCE

Figures 9–11

Type material. ***Holotype*** ♂(IZCAS-Ar40906), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 27.IX.2017, Zhigang Chen, Yunchun Li, Qingyuan Zhao and Jincheng Liu leg. ***Paratypes*** 1♂3♀(IZCAS-Ar40907–Ar40910), same locality as holotype, but 19.IX.2012, Yanfeng Tong leg.

Etymology. The species is named after Mr. Yanfeng Tong, who has helped us greatly with this research; noun (name) in genitive case.

Species compared. *Megaeupoa gravelyi* comb. nov., originally described as *Brettus gravelyi* Caleb in Caleb, Acharya and Kumar (2018).

Diagnosis. The male of *Megaeupoa yanfengi* sp. nov. resembles *M. gravelyi* in having a stout RTA, a long, undulate embolus and a membranous conductor but differs in the following: the RTA terminus is flat in ventral view (vs. subtriangular in *M. gravelyi*), the median apophysis is stout (vs. pointed in *M. gravelyi*), the inferior terminal apophysis is present, the terminal apophysis is semicircular (vs. inferior terminal apophysis absent and terminal apophysis subtriangular in *M. gravelyi*), and the lateral terminal apophysis wraps around the terminal apophysis (vs. next to terminal apophysis in *M. gravelyi*).

Description. Male (Figs 9, 10, 11C–E, G–H). Total length 5.64. Carapace 2.23 long, 1.74 wide. Abdomen 2.94 long, 1.33 wide. Clypeus 0.09 high. Eye sizes and inter-distances: AME 0.59, ALE 0.36, PLE 0.33, AERW 1.64, PERW 1.57, EFL 1.10. Legs: I 4.48 (1.36 + 1.64 + 0.89 + 0.59), II 4.28 (1.30 + 1.53 + 0.87 + 0.58), III 4.48 (1.33 + 1.50 + 1.02 + 0.63), IV 6.12 (1.84 + 1.98 + 1.63 + 0.67). Carapace red-brown, covered with dense, brown setae, posteriorly with white stripes of setae, cephalic part black. Fovea longitudinal. Clypeus black to brown, covered with several white setae. Chelicerae yellow-brown, with five promarginal and nine retromarginal teeth. Endites pale brown. Labium pale brown, covered with brown setae. Sternum colored as endites, covered with brown setae. Legs brown, with long, white, dense setal annulations. Abdomen elongated oval, dorsum with one pair of stripes with dense, white setae, transverse dark brown stripes medially; venter pale brown, covered with setae.

Palp (Figs 9A–D, 10A, B): Patella covered with dense, white setae dorsally; tibia slightly wider than long, with subtriangular ventral apophysis, RTA stout, slightly longer than wide in lateral view, terminus flat; cymbium longer than wide; bulb longer

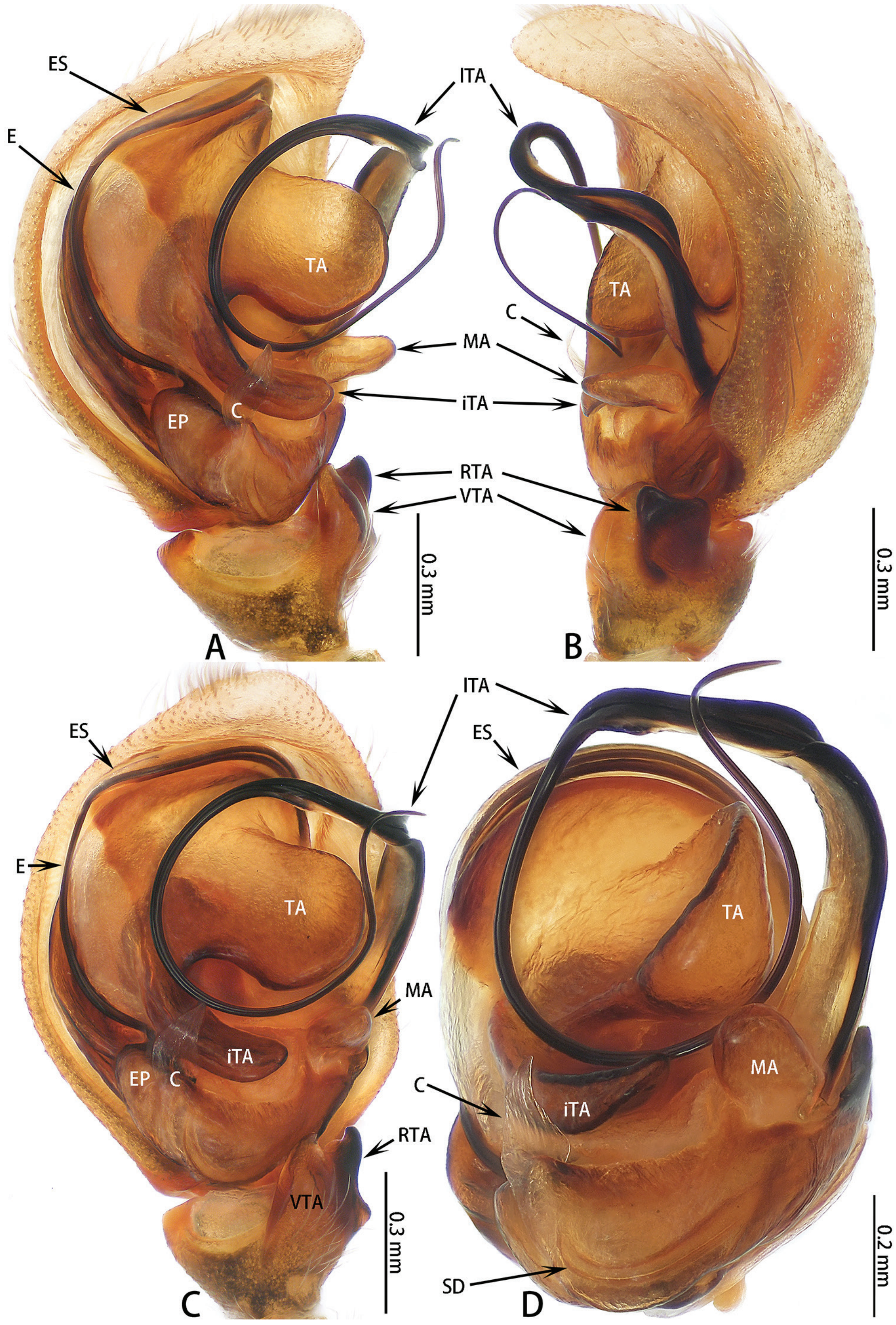

Figure 9. Palp of *Megaeupoa yanfengi* sp. nov. **A–C** male holotype; **D** male paratype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, posterior.

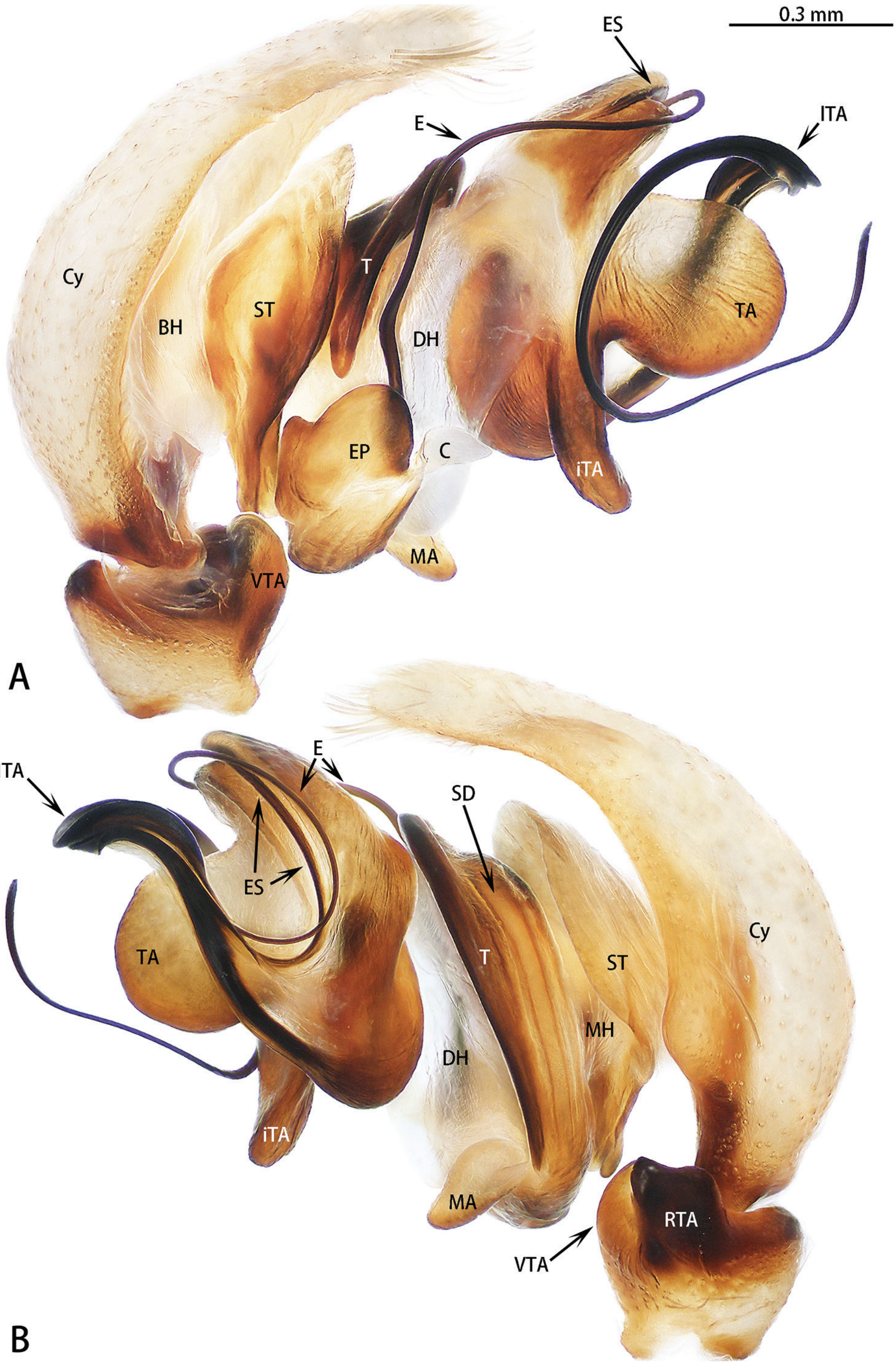

Figure 10. Right palp of *Megaeupoa yanfengi* sp. nov., male paratype (images flipped horizontally). **A** prolateral **B** retrolateral.

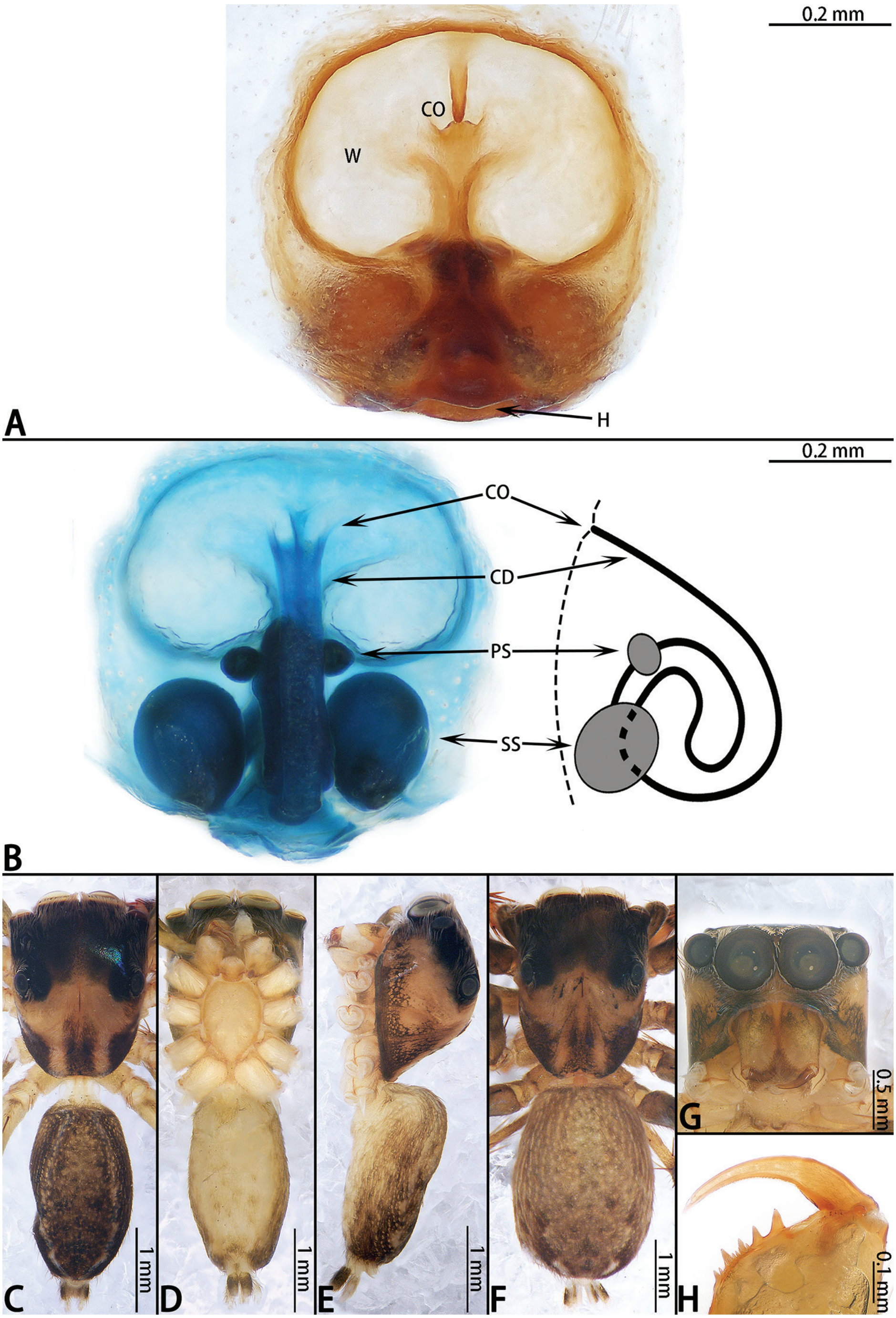

Figure 11. *Megaeupoa yanfengi* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal and schematic duct course shown in lateral view **C** male holotype habitus, lateral **D** male paratype habitus, ventral **E** male paratype habitus, lateral **F** female habitus, dorsal **G** frontal view of male paratype **H** dorsal view of chelicerae, paratype male.

than wide; embolus filiform, undulate, half of embolus obscured by embolic sheath, other half enclosed by lateral terminal apophysis; conductor membranous, sheet-shaped, adjacent to embolus; median apophysis three times longer than wide, stout; inferior terminal apophysis thin, four times longer than wide, lateral terminal apophysis filiform, embolus curled circularly, terminal apophysis semicircular.

Female (Fig. 11A, B, F). Total length 5.51. Carapace 2.35 long, 1.76 wide. Abdomen 3.09 long, 1.90 wide. Clypeus 0.09 high. Eye sizes and inter-distances: AME 0.62, ALE 0.37, PLE 0.26, AERW 1.87, PERW 1.71, EFL 1.22. Legs: I 4.29 (1.34 + 1.53 + 0.84 + 0.58), II 4.08 (1.27 + 1.38 + 0.88 + 0.55), III 4.33 (1.23 + 1.48 + 1.01 + 0.61), IV 5.81 (1.59 + 2.01 + 1.50 + 0.71). Habitus similar to that of male.

Epigyne (Fig. 11A, B) as long as wide; hood located posteriorly; windows large, oval; copulatory openings located medially; copulatory ducts curled on either side with two pairs of spermathecae; primary spermathecae small, situated anteriorly, secondary spermathecae larger than primary spermathecae.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Nigorella* Wesolowska & Tomasiewicz, 2008

Type species. *Nigorella aethiopic*a Wesolowska & Tomasiewicz, 2008.

Nigorella mengla sp. nov.

http://zoobank.org/40E914DD-A047-4855-958A-7DCC3EC0C446
Figures 12, 13

Type material. ***Holotype*** ♂(IZCAS-Ar40911), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 20.IX.2017, Yanfeng Tong leg. ***Paratypes*** 4♂1♀(IZCAS-Ar40912–Ar40916), same data as holotype.

Etymology. The specific name is a noun in apposition and refers to the type locality.

Diagnosis. *Nigorella mengla* sp. nov. resembles *N. sichuanensis* Peng, Xie & Kim, 1993 and *Evarcha orientalis* (Song & Chai, 1992) by the bifurcated RTA and dorsal embolic apophysis behind the embolus but differs in the following: the palpal tibia is wider than long (vs. longer than wide in *N. sichuanensis*); the tegular lobe is folded (vs. straight in *N. sichuanensis* and *E. orientalis*). In the female, the spermathecae are S-shaped (vs. spermathecae coiled in *N. sichuanensis*), and the hoods are deeper (vs. unobvious in *E. orientalis*).

Description. Male (Figs 12, 13C, E). Total length 8.23. Carapace 4.5 long, 3.19 wide. Abdomen 4.04 long, 2.69 wide. Clypeus 0.22 high. Eye sizes and inter-distances: AME 0.79, ALE 0.38, PLE 1.04, AERW 2.35, PERW 2.34, EFL 1.02. Legs: I 7.97 (2.50 + 3.28 + 1.28 + 0.91), II 5.19 (1.64 + 1.88 + 0.96 + 0.71), III 8.01 (2.81 + 2.56 + 1.61 + 1.03), IV 7.85 (2.45 + 2.56 + 1.84 + 1.00). Carapace black, red-brown

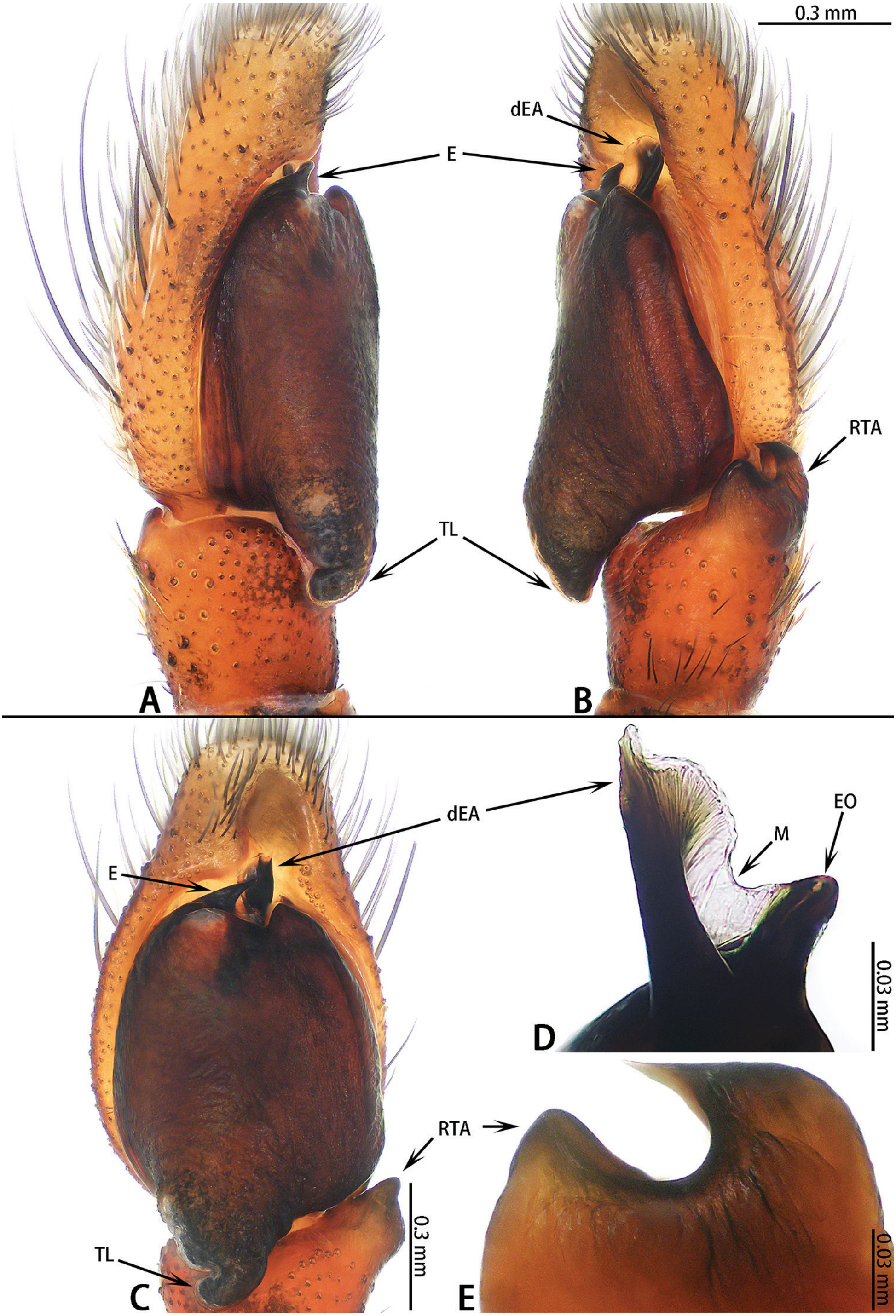

Figure 12. Palp of *Nigorella mengla* sp. nov. **A–C** male holotype; **D, E** male paratype **A** prolateral **B** retrolateral **C** ventral **D** embolic division, dorsal view **E** RTA, retrolateral view.

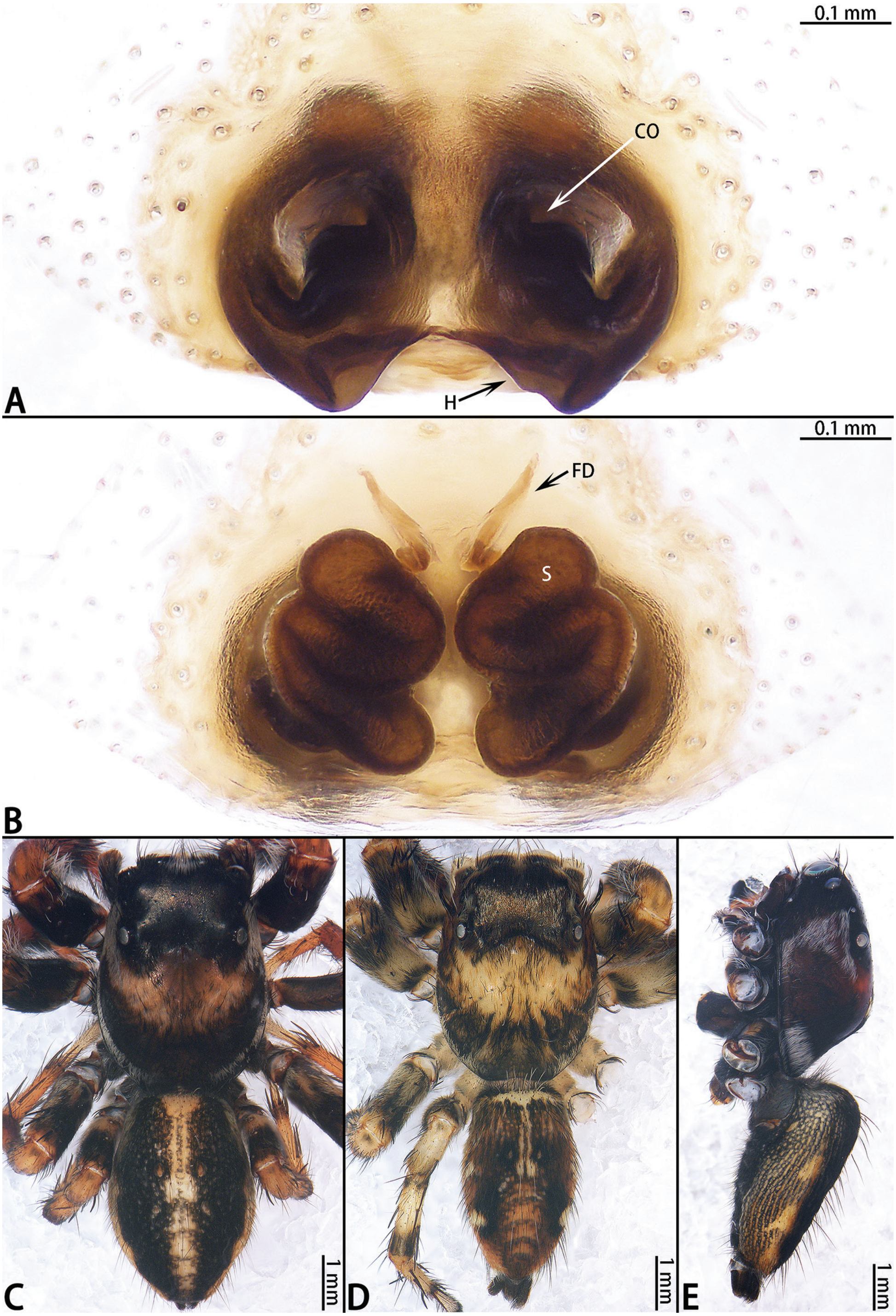

Figure 13. *Nigorella mengla* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** female paratype habitus, dorsal **E** male paratype habitus, lateral.

medially, carapace edge and sides of cephalic part with white setal stripes, thoracic part sloping abruptly, clothed with white and dark setae. Fovea indistinct. Clypeus orange-brown to dark brown, covered with thin setae. Chelicerae black, with two retromarginal teeth and one promarginal tooth. Endites and labium black. Sternum black, covered with dark setae. Legs red-brown except femora with black pattern. Abdomen elongated oval, dorsum with two pairs of muscle depressions, with white line centrally, white line widens medially; venter black with dark setae; sides black with white spots.

Palp (Fig. 12A–E): Tibia slightly wider than long, RTA bifurcated, ventral branch blunt, dorsal ramus well-developed, pointed; cymbium flattened, covered with long setae; bulb almost round, with sperm duct extending along margin, tegular lobe folded; embolus stout, dorsal embolic apophysis behind embolus, connected to embolus with membrane.

Female (Fig. 13A, B, D). Total length 7.85. Carapace 4.30 long, 2.94 wide. Abdomen 4.12 long, 2.04 wide. Clypeus 0.19 high. Eye sizes and inter-distances: AME 0.65, ALE 0.41, PLE 0.33, AERW 2.36, PERW 2.35, EFL 1.02. Legs: I 6.43 (2.20 + 2.58 + 0.92 + 0.73), II 6.10 (2.00 + 2.45 + 0.88 + 0.77), III 7.42 (2.56 + 2.50 + 1.48 + 0.88), IV 7.08 (2.18 + 2.48 + 1.56 + 0.86). Habitus similar to that of male except paler.

Epigyne (Fig. 13A, B) wider than long, with pair of hoods near epigastral furrow; copulatory openings situated medially, C-shaped; copulatory ducts indistinct; spermathecae S-shaped; fertilization ducts well-developed.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Onomastus* Simon, 1900

Type species. *Onomastus nigricaudus* Simon, 1900.

Onomastus chenae sp. nov.

http://zoobank.org/5D31CB6D-4D53-48E2-80EB-613A6B860611
Figures 14, 15

Type material. ***Holotype*** ♂(IZCAS-Ar40917), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 27.IX.2017, Zhigang Chen, Yunchun Li, Qingyuan Zhao and Jincheng Liu leg. ***Paratypes*** 5♂8♀(IZCAS-Ar40918–Ar40930), same data as holotype.

Etymology. The species is named after Ms. Chen Zeng, who helped us greatly with this research; noun (name) in genitive case.

Diagnosis. Males of *Onomastus chenae* sp. nov. are similar to *O. kanoi* Ono, 1995 by having the same shaped spur, a mesal branch of conductor, and a wide conductor. However, *O. chenae* sp. nov. can be distinguished by having three apophyses on the median apophysis (vs. two in *O. kanoi*); the epigyne is wider than long (vs. longer than wide in *O. kanoi*), and the copulatory opening is located posteriorly (vs. medially in *O. kanoi*).

Description. Male (Figs 14A–C, 15C, E–G). Total length 3.66. Carapace 1.60 long, 0.92 wide. Abdomen 2.30 long, 0.75 wide. Clypeus 0.02 high. Eye sizes and inter-distances: AME 0.34, ALE 0.10, PLE 0.12, AERW 0.88, PERW 0.67, EFL 0.47. Legs: I 4.67 (1.28 + 1.85 + 1.00 + 0.44), II 4.55 (1.36 + 1.65 + 1.01 + 0.53), III 4.81 (1.28 + 1.62 + 1.40 + 0.51), IV 5.90 (1.67 + 1.95 + 1.79 + 0.49). Carapace white, black ring around PLEs and PMEs, cephalic part covered with golden setae. Fovea longitudinal, PLEs situated posteriorly. Clypeus white, covered with white setae. Chelicerae white with five promarginal and five retromarginal teeth. Endites, labium and sternum white. Legs white, base of tibia with black spot. Abdomen elongated oval, white.

Palp (Fig. 14A–C): Patella with subtriangular patellar apophysis, longer than wide; tibia as long as wide, without retrolateral apophysis; cymbium longer than wide, covered with setae; bulb approximately as long as wide, structure of bulb is complex; sperm duct clearly visible; spur on mesal branch of conductor hook shaped; conductor wide; embolic division occupying large area on bulb with developed conductor; embolus filiform, very long; median apophysis with three apophyses.

Female (Fig. 15A, B, D, E). Total length 3.76. Carapace 1.61 long, 1.05 wide. Abdomen 2.2 long, 0.73 wide. Clypeus 0.02 high. Eye sizes and inter-distances: AME 0.36, ALE 0.10, PLE 0.60, AERW 0.99, PERW 0.70, EFL 1.69. Legs: I 4.59 (1.29 +

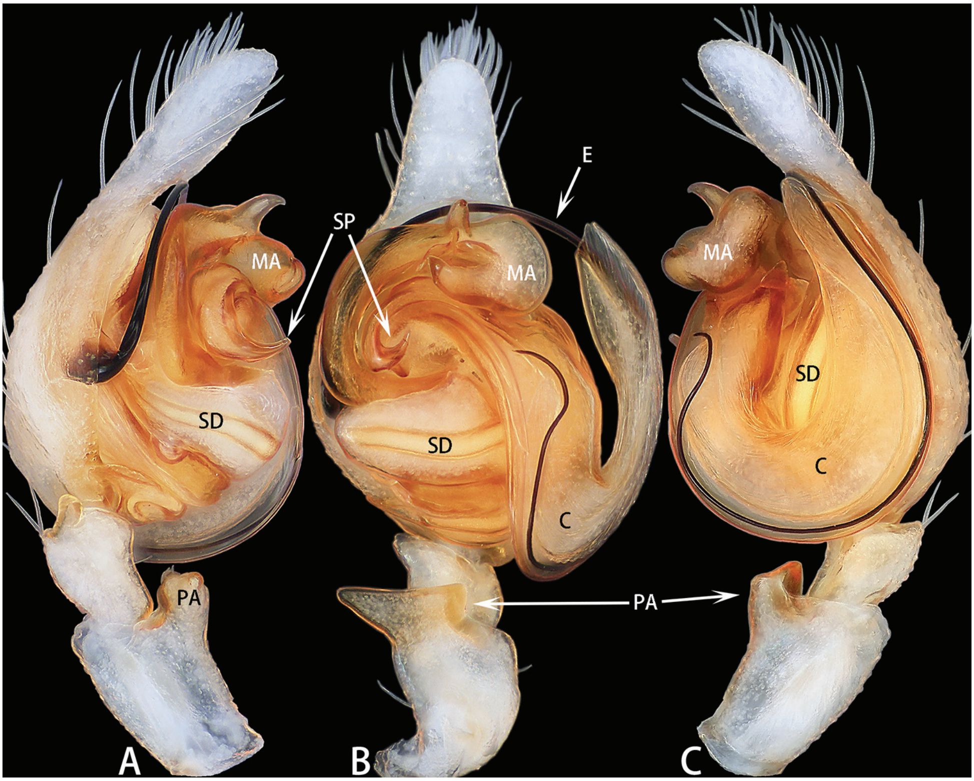

Figure 14. Palp of *Onomastus chenae* sp. nov., male holotype. **A** prolateral **B** ventral **C** retrolateral.

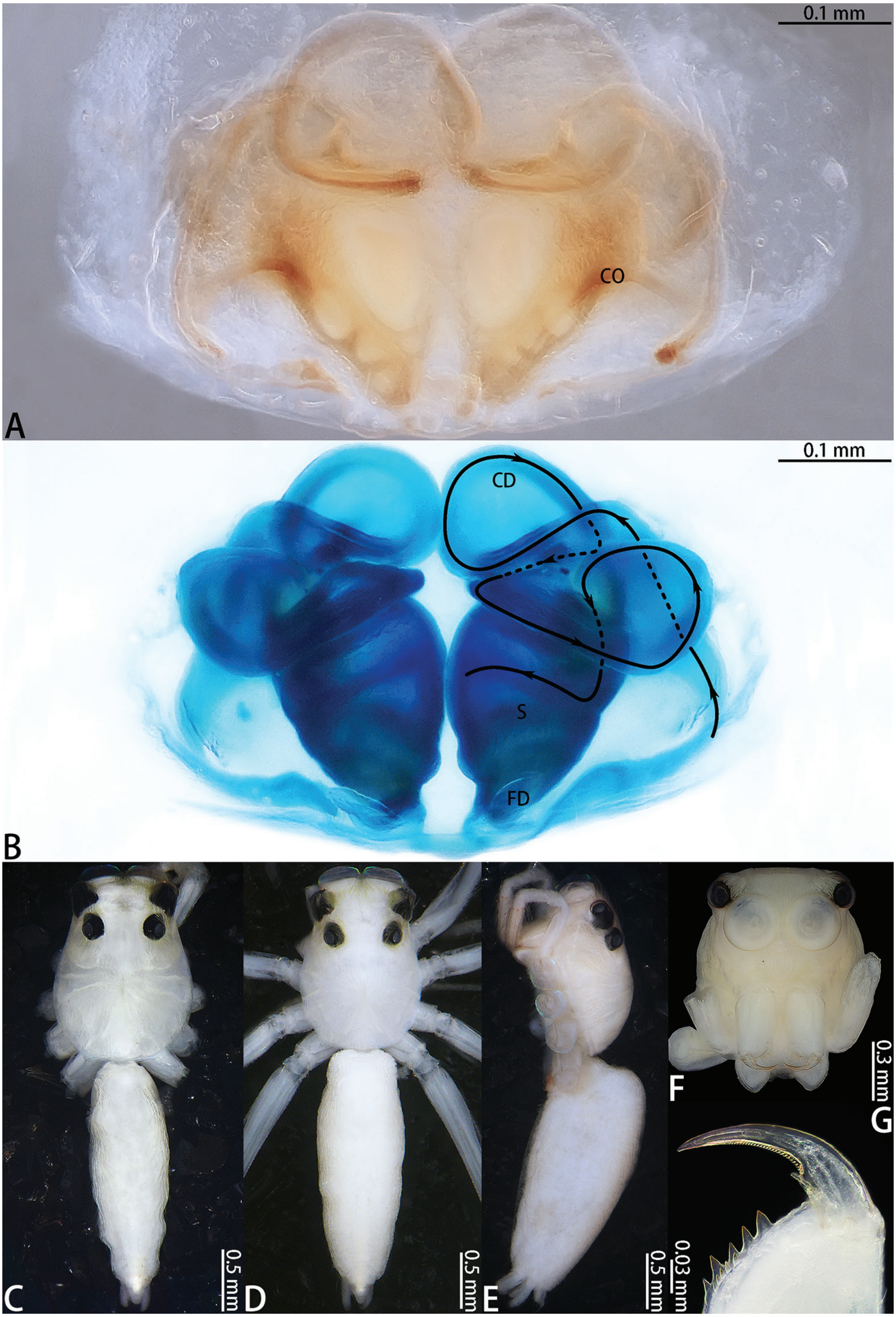

Figure 15. *Onomastus chenae* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** female paratype habitus, dorsal **E** same, lateral **F** frontal view of male paratype **G** dorsal view of chelicerae, paratype.

1.86 + 1.01 + 0.43), II 4.45 (1.31 + 1.70 + 1.02 + 0.42), III 4.89 (1.31 + 1.59 + 1.45 + 0.54), IV 5.96 (1.68 + 1.98 + 1.76 + 0.54). Habitus similar to that of male.

Epigyne (Fig. 15A, B) wider than long; transverse copulatory openings sclerotized posteriorly; copulatory ducts and spermathecae visible on epigynal surface, copulatory ducts meandering; spermathecae oval posteriorly.

Distribution. Known only from the type locality in Yunnan, China.

Genus *Synagelides* Strand, 1906

Type species. *Synagelides agoriformis* Strand, 1906.

Synagelides platnicki sp. nov.

http://zoobank.org/D99DB9E7-6486-4471-9BDD-C5D20635D47B

Figures 16, 17

Type material. ***Holotype*** ♂(IZCAS-Ar40931), China: Yunnan: Xishuangbanna, Mengla County, Menglun Township, XTBG, Leprosy Village, 21.8932N, 101.2883E, elevation ca 550 m, 27.IX.2017, Zhigang Chen, Yunchun Li, Qingyuan Zhao and Jincheng Liu leg. ***Paratypes*** 6♂7♀(IZCAS-Ar40932–Ar40944), same data as holotype.

Etymology. The species is named after the late Norman I. Platnick (1951–2020, see Li 2020b) to commemorate his immense contribution to arachnology; noun (name) in genitive case.

Diagnosis. *Synagelides platnicki* sp. nov. resembles *S. lushanensis* Xie & Yin, 1990 by having the same shaped median apophysis and a coiled embolus but differs by the following: the length of the RTA is four times as long as the length of the cymbium (vs. two times the length in *S. lushanensis*), the dorsal tibial apophysis is absent (vs. present in *S. lushanensis*) and the retrolateral median apophysis is L-shaped in retrolateral view (vs. straight in *S. lushanensis*); in the female, the hood of the epigyne is as long as wide (vs. two times longer than wide in *S. lushanensis*), and the copulatory duct is coiled 360° (vs. S-shaped in *S. lushanensis*).

Description. Male (Figs 16, 17C, D, F, G). Total length 3.22. Carapace 1.50 long, 0.99 wide. Abdomen 1.85 long, 0.75 wide. Clypeus 0.03 high. Eye sizes and interdistances: AME 0.35, ALE 0.20, PLE 0.19, AERW 0.98, PERW 1.03, EFL 0.90. Legs: I 3.93 (1.18 + 1.02 + 1.00 + 0.44 + 0.29), II 2.14 (0.63 + 0.24 + 0.52 + 0.49 + 0.26), III 2.44 (0.71 + 0.26 + 0.58 + 0.60 + 0.29), IV 3.24 (0.89 + 0.36 + 0.84 + 0.79 + 0.36). Carapace red-brown, widest between coxae II and III, covered with white setae. Clypeus dark brown. Fovea subtriangular. Chelicerae yellow-brown, with two promarginal teeth and one retromarginal tooth. Endites yellow-brown. Sternum brown, covered with thin setae. Femur of leg I red, other femora with black pattern ventrally. Abdomen elongated oval, dorsum with two pairs of white dorso-lateral spots, covered with white setae on the spots and laterally; venter black.

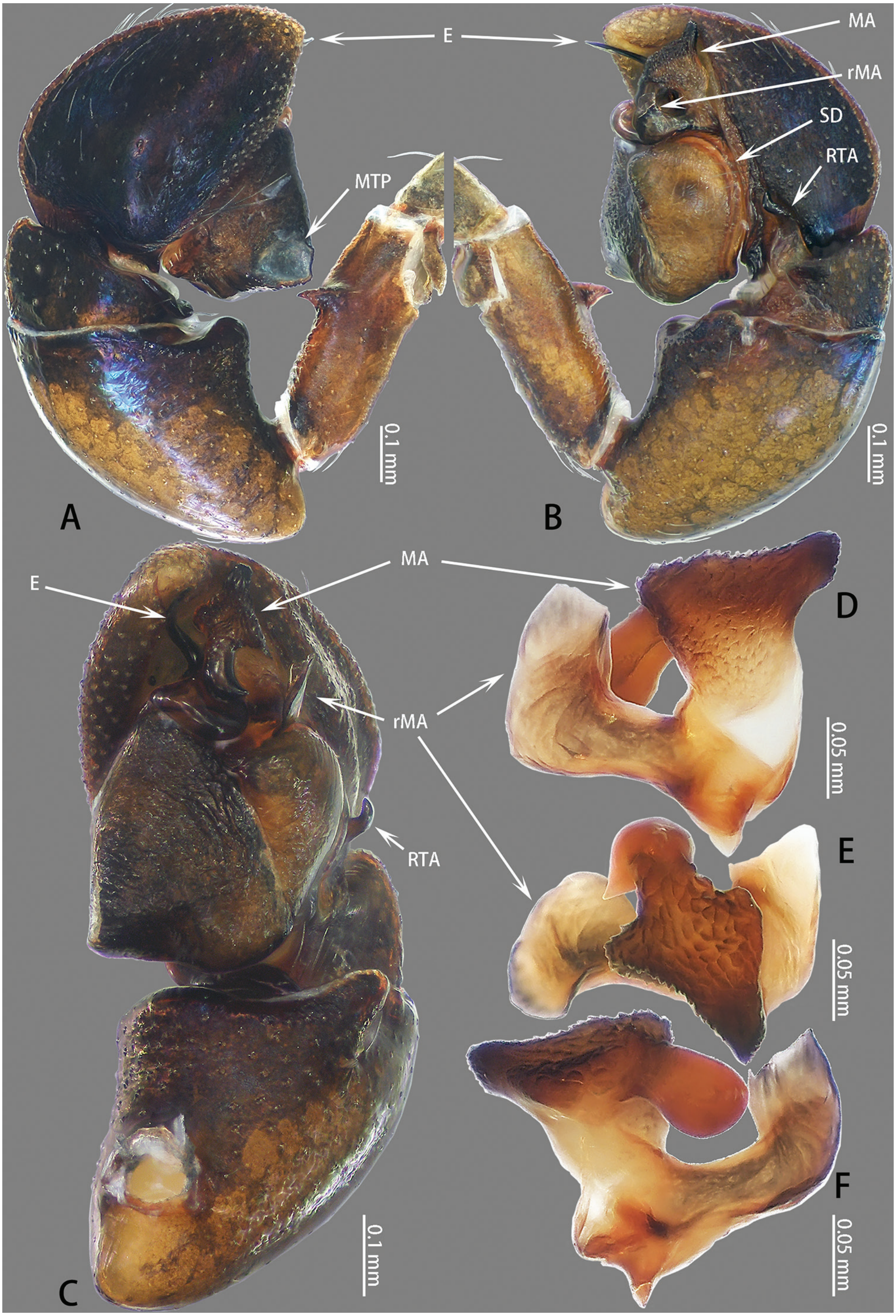

Figure 16. Palp of *Synagelides platnicki* sp. nov. **A–C** male holotype; **D–F** retrolateral median apophysis on right palp, male paratype. **A** prolateral **B** retrolateral **C** ventral **D** retrolateral **E** ventral **F** prolateral.

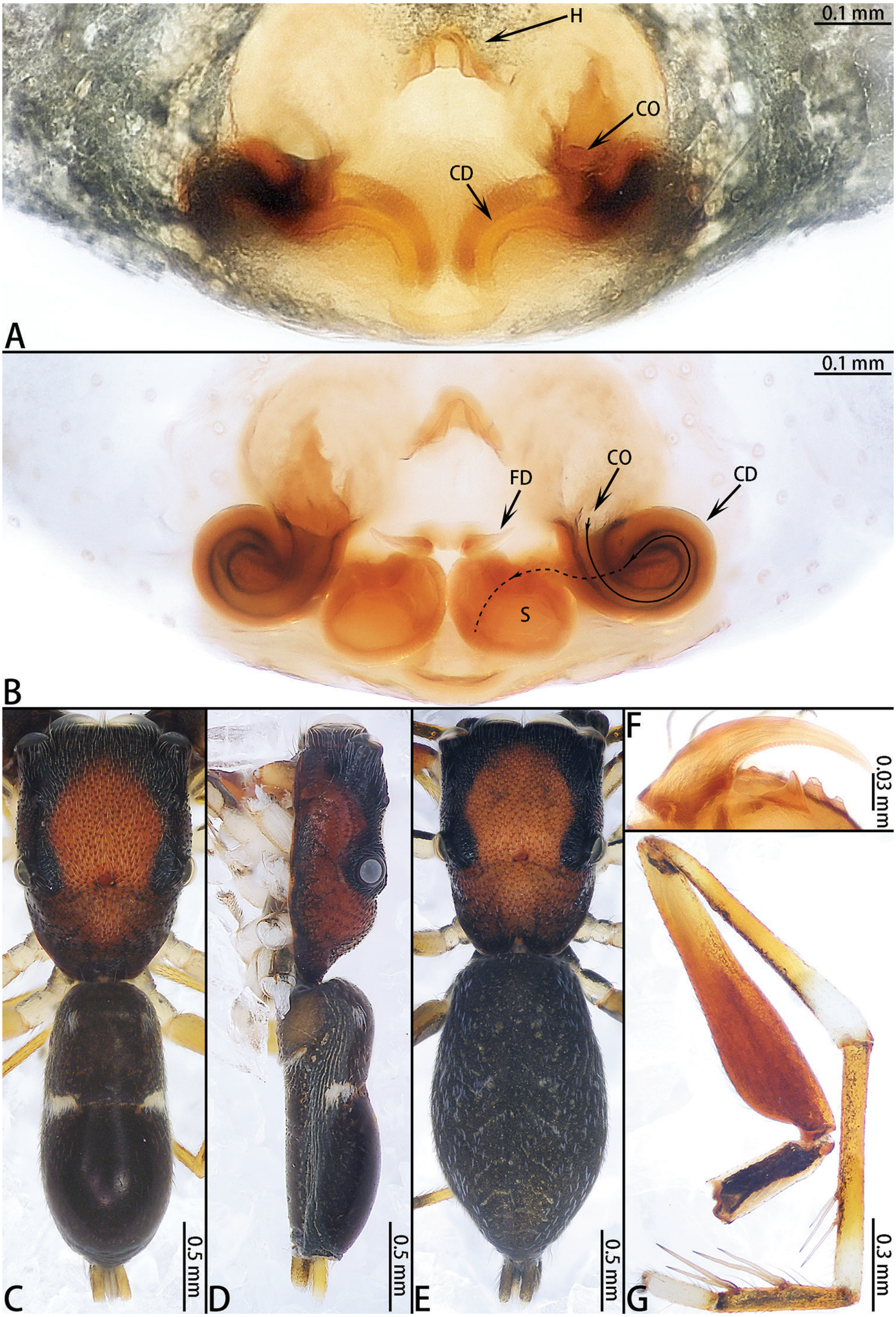

Figure 17. *Synagelides platnicki* sp. nov., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male holotype habitus, dorsal **D** male paratype habitus, lateral **E** female paratype habitus, dorsal **F** dorsal view of chelicerae, paratype male **G** prolateral view of left leg I, male paratype. female.

Palp (Fig. 16A–F) femur brown, approximately three times longer than wide, with ventral median apophysis; patella brown, almost as long as wide, with ventral bulge; tibia wider than long, with RTA tapering towards tip, slightly longer than tibia, tip slightly bent ventrally then dorsally; cymbium flattened, widest medially; bulb widest at base; embolus coiled 360°, median apophysis with serrated apophysis, terminus blunt; retrolateral median apophysis L-shaped.

Female (Fig. 17A, B, E). Total length 3.68. Carapace 1.48 long, 0.98 wide. Abdomen 2.14 long, 1.03 wide. Clypeus 0.02 high. Eye sizes and inter-distances: AME 0.33, ALE 0.20, PLE 0.20, AERW 1.03, PERW 1.03, EFL 0.85. Legs: I 2.91 (0.88 + 0.69 + 0.70 + 0.37 + 0.27), II 1.99 (0.61 + 0.23 + 0.47 + 0.41 + 0.27), III 2.14 (0.61 + 0.25 + 0.49 + 0.51 + 0.28), IV 2.73 (0.75 + 0.30 + 0.70 + 0.69 + 0.29). Habitus similar to that of male.

Epigyne (Fig. 17A, B) wider than long, with anterior hood, copulatory openings located medially; copulatory ducts visible on epigynal surface, coiled 360°, connecting with anterior edge of spermathecae; spermathecae spherical, touching medially; fertilization ducts originating from the median anterior edge of spermathecae, extending almost transversely.

Distribution. Known only from the type locality in Yunnan, China.

Discussion

The following two jumping spiders were also collected from Xishuangbanna Tropical Botanical Garden (XTBG).

Irura mandarina Simon, 1903

Irura mandarina Simon 1903: 735 (♀); Prószyński 2017: 18, fig. 6D (♀)
Kinhia prima Żabka 1985: 233, figs 246–250 (♂) syn. nov.
Irura prima: Prószyński 2017: 18, fig. 6E (♂).

Comments. Conspecificity of the *Irura mandarina* female and *I. prima* (Żabka, 1985) male is based on a large number of spider specimens collected at the same locality in XTBG with similarities in size and color pattern.

Ptocasius montiformis Song, 1991

Ptocasius montiformis Song 1991: 163, figs 1A–D (♀); Song, Zhu and Chen 1999: 543, figs 313T–U (♀)
Evarcha digitata Peng & Li 2002: 469, figs 1A–D (♂); Prószyński 2018: 155, fig. 15I (♂) syn. nov.

Comments. Conspecificity of the *Ptocasius montiformis* female and *Evarcha digitata* male is based on a large number of spider specimens collected at the same locality in XTBG with similarities in size and color pattern.

Adding the new species reported here, a total of 121 jumping spider species are reported from Xishuangbanna, of which, 77 species (marked with an asterisk) were collected in XTBG by us. A checklist of Xishuangbanna jumping spiders follows, and for a complete list of taxonomic references see WSC (2020).

1. *Afraflacilla ballarini* Cao & Li, 2016*
2. *Agorius tortilis* Cao & Li, 2016*
3. *Attulus penicillatus* (Simon, 1875)*
4. *Bavia capistrata* (C. L. Koch, 1846)
5. *Bavirecta exilis* (Cao & Li, 2016)*
6. *Bianor angulosus* (Karsch, 1879)
7. *Bristowia heterospinosa* Reimoser, 1934*
8. *Burmattus pococki* (Thorell, 1895)
9. *Burmattus sinicus* Prószyński, 1992*
10. *Carrhotus sannio* (Thorell, 1877)
11. *Carrhotus sarahcrewsae* Cao & Li, 2016*
12. *Carrhotus yunnanensis* (Song, 1991)
13. *Chalcoscirtus lii* Lei & Peng, 2010*
14. *Chalcoscirtus nenilini* Marusik, 1990*
15. *Cheliceroides longipalpis* Zabka, 1985*
16. *Chinattus dactyloides* (Xie, Peng & Kim, 1993)
17. *Chinattus wengnanensis* Cao & Li, 2016*
18. *Chinophrys mengyangensis* Cao & Li, 2016*
19. *Chrysilla acerosa* Wang & Zhang, 2012
20. *Cocalus menglaensis* Cao & Li, 2016*
21. *Colyttus proszynskii* Caleb, Chatterjee, Tyagi, Kundu & Kumar, 2018*
22. *Colyttus yiwui* sp. nov.*
23. *Cosmophasis xiaolonghaensis* Cao & Li, 2016*
24. *Cytaea tongi* Wang & Li, 2020*
25. *Cytaea yunnanensis* Cao & Li, 2016*
26. *Dendroicius hotaruae* sp. nov.*
27. *Dexippus pengi* Wang & Li, 2020*
28. *Emathis sumatranus* Prószyński & Deeleman-Reinhold, 2012*
29. *Epeus bicuspidatus* (Song, Gu & Chen, 1988)
30. *Epeus flavobilineatus* (Doleschall, 1859)
31. *Epeus indicus* Prószyński, 1992
32. *Epocilla calcarata* (Karsch, 1880)*
33. *Euophrys subwanyan* Wang & Li, 2020*
34. *Euophrys xuyei* sp. nov.*

35. *Eupoa yunnanensis* Peng & Kim, 1997
36. *Evarcha orientalis* (Song & Chai, 1992)*
37. *Evarcha pococki* Zabka, 1985
38. *Foliabitus weihangi* sp. nov.*
39. *Gedea fungiformis* (Xiao & Yin, 1991)*
40. *Gedea pinguis* Cao & Li, 2016*
41. *Gelotia liuae* Wang & Li, 2020*
42. *Gelotia syringopalpis* Wanless, 1984
43. *Gelotia zhengi* Cao & Li, 2016*
44. *Harmochirus brachiatus* (Thorell, 1877)
45. *Harmochirus insulanus* (Kishida, 1914)*
46. *Hasarius adansoni* (Audouin, 1826)
47. *Hyllus diardi* (Walckenaer, 1837)*
48. *Icius bamboo* Cao & Li, 2016*
49. *Icius minimus* Wesolowska & Tomasiewicz, 2008*
50. *Irura longiochelicera* (Peng & Yin, 1991)
51. *Irura lvshilinensis* Wang & Li, 2020*
52. *Irura mandarina* Simon, 1903*
53. *Irura yunnanensis* (Peng & Yin, 1991)*
54. *Lechia squamata* Zabka, 1985*
55. *Megaeupoa yanfengi* sp. nov.*
56. *Menemerus bivittatus* (Dufour, 1831)
57. *Myrmapeni borneensis* (Peckham & Peckham, 1907)*
58. *Myrmaplata plataleoides* (O. Pickard-Cambridge, 1869)*
59. *Myrmaplata turriformis* (Badcock, 1918)*
60. *Myrmarachne angusta* (Thorell, 1877)
61. *Myrmarachne brevis* Xiao, 2002
62. *Myrmarachne circulus* Xiao & Wang, 2004
63. *Myrmarachne cornuta* Badcock, 1918
64. *Myrmarachne elongata* Szombathy, 1915*
65. *Myrmarachne gisti* Fox, 1936
66. *Myrmarachne jacksoni* Prószyński & Deeleman-Reinhold, 2010*
67. *Myrmarachne lugubris* (Kulczyński, 1895)
68. *Myrmarachne melanocephala* MacLeay, 1839
69. *Myrmarachne melanotarsa* Wesolowska & Salm, 2002*
70. *Nannenus menghaiensis* Cao & Li, 2016*
71. *Nigorella mengla* sp. nov.*
72. *Onomastus nigrimaculatus* Zhang & Li, 2005
73. *Onomastus chenae* sp. nov.*
74. *Pancorius latus* Cao & Li, 2016*
75. *Pancorius magnus* Zabka, 1985*
76. *Phaeacius malayensis* Wanless, 1981
77. *Phintella accentifera* (Simon, 1901)*

78. *Phintella arcuata* Huang, Wang & Peng, 2015
79. *Phintella bifurcata* Prószyński, 1992*
80. *Phintella debilis* (Thorell, 1891)*
81. *Phintella dives* (Simon, 1899)*
82. *Phintella lepidus* Cao & Li, 2016*
83. *Phintella pygmaea* (Wesolowska, 1981)*
84. *Phintella sancha* Cao & Li, 2016*
85. *Phintella suavisoides* Lei & Peng, 2013
86. *Phintella vittata* (C. L. Koch, 1846)
87. *Phintelloides jesudasi* (Caleb & Mathai, 2014)*
88. *Phintelloides versicolor* (C. L. Koch, 1846)
89. *Plexippus petersi* (Karsch, 1878)
90. *Portia fimbriata* (Doleschall, 1859)*
91. *Portia labiata* (Thorell, 1887)
92. *Portia quei* Zabka, 1985
93. *Ptocasius kinhi* Zabka, 1985*
94. *Ptocasius montiformis* Song, 1991*
95. *Ptocasius paraweyersi* Cao & Li, 2016*
96. *Ptocasius strupifer* Simon, 1901*
97. *Rhene albigera* (C. L. Koch, 1846)
98. *Rhene atrata* (Karsch, 1881)
99. *Rhene flavigera* (C. L. Koch, 1846)*
100. *Rhene mengla* Wang & Li, 2020*
101. *Rhene rubrigera* (Thorell, 1887)
102. *Rhene setipes* Zabka, 1985*
103. *Rhene triapophyses* Peng, 1995*
104. *Siler semiglaucus* (Simon, 1901)
105. *Siler zhangae* Wang & Li, 2020*
106. *Spartaeus jaegeri* Logunov & Azarkina, 2008
107. *Spartaeus spinimanus* (Thorell, 1878)*
108. *Spartaeus thailandica* Wanless, 1984
109. *Stenaelurillus fuscus* Cao & Li, 2016*
110. *Stertinius borneensis* Logunov, 2018*
111. *Synagelides cavaleriei* (Schenkel, 1963)
112. *Synagelides platnicki* sp. nov.*
113. *Synagelides yunnan* Song & Zhu, 1998*
114. *Telamonia vlijmi* Prószyński, 1984
115. *Thiania bhamoensis* Thorell, 1887
116. *Thiania suboppressa* Strand, 1907*
117. *Thyene bivittata* Xie & Peng, 1995
118. *Thyene orientalis* Zabka, 1985*
119. *Thyene triangula* Xie & Peng, 1995*
120. *Toxeus maxillosus* C. L. Koch, 1846*
121. *Zeuxippus yunnanensis* Peng & Xie, 1995

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Multilocus, phenotypic, behavioral, and ecological niche analyses provide evidence for two species within *Euphonia affinis* (Aves, Fringillidae)

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Abstract

The integration of genetic, morphological, behavioral, and ecological information in the analysis of species boundaries has increased, allowing integrative systematics that better reflect the evolutionary history of biological groups. In this context, the goal of this study was to recognize independent evolutionary lineages within *Euphonia affinis* at the genetic, morphological, and ecological levels. Three subspecies have been described: *E. affinis godmani*, distributed in the Pacific slope from southern Sonora to Guerrero; *E. affinis affinis*, from Oaxaca, Chiapas and the Yucatan Peninsula to Costa Rica; and *E. affinis olmecorum* from Tamaulipas and San Luis Potosi east to northern Chiapas (not recognized by some authors). A multilocus analysis was performed using mitochondrial and nuclear genes. These analyses suggest two genetic lineages*:* *E. godmani* and *E. affinis*, which diverged between 1.34 and 4.3 My, a period in which the ice ages and global cooling fragmented the tropical forests throughout the Neotropics. To analyze morphometric variations, six morphometric measurements were taken, and the Wilcoxon Test was applied to look for sexual dimorphism and differences between the lineages. Behavioral information was included, by performing vocalization analysis which showed significant differences in the temporal characteristics of calls. Finally, Ecological Niche Models were estimated with MaxEnt, and then compared using the method of Broennimann. These analyses showed that the lineage distributed in western Mexico (*E. godmani*) has a more restricted niche than the eastern lineage (*E. affinis*) and thus we rejected the hypotheses of niche equivalence and similarity. Based on the combined evidence from genetic, morphological, behavioral, and ecological data, it is concluded that *E. affinis* (with *E. olmecorum* as its synonym) and *E. godmani* represent two independent evolutionary lineages.

Keywords
Euphonia affinis, *Euphonia godmani*, independent evolutionary lineages

Introduction

The integration of genetic, morphological, ecological, and behavioral data in systematic studies provides information on the evolutionary history of species and their populations, allowing a better assessment of species limits (Cadena and Cuervo 2010, Köhler et al. 2010, Padial et al. 2010, Pavlova et al. 2014), as well as understanding the role of geographical and ecological factors on population divergence within species (Padial et al. 2010, Hernández et al., 2018). De Queiroz (2007) proposed that different types of data (e.g., morphological, ethological, ecological, molecular, etc.) are needed to determine operationally whether the lineages under study are evolving separately, and thus can be considered to represent different species. Species differentiation is affected by the time elapsed since the speciation event, a problem that should be considered in species delimitation studies. Padial et al. (2010) explained two ways to approach this problem: one is integration by congruence, and the other is integration by accumulation. In the first case (integration by congruence), taxonomists will consider two lineages as different species when there are concordant patterns of divergence among several taxonomic characters which result a full lineage separation. Meanwhile the integration by accumulation framework implies that divergences in any number of attributes (taxonomic characters) can provide evidence for the existence of a species, and in this case it is important to distinguish the group of characters (or even a single character) that promotes divergence and is reflected in the separation of lineages.

Species limits on birds have been studied using different approaches, including the use of morphological characters (Navarro-Sigüenza et al. 2001), coloration (Frith and Frith 1983, Rathbun et al. 2015), genetic variation (Olsson et al. 2013), songs (Sosa-López et al. 2013), and ecological niche modeling (Ruiz-Sánchez et al. 2015). In general, the objectives of these studies have been to resolve boundaries within species complexes and to evaluate subspecies recognized by taxonomic authorities such as the AOU (American Ornithology Union) and the IOC World Bird List (International Ornithology Committee).

DNA sequences have been useful to complement morphological and geographical information. Phylogenetics, molecular clocks, diversification rates, genetic populations and coalescence analyses have documented that geological complexity, heterogeneity of the environment, and climatic oscillations may have influenced patterns of genetic diversity, demography and divergence within species (de-Nova et al. 2012, Gu et al. 2013, Smith et al. 2014, Rodríguez-Gómez and Ornelas 2015). On the other hand, ecological niche modeling has provided information that supports the results of genetic studies on species delimitation (Raxworthy et al. 2007, Ruiz-Sánchez et al. 2015) and has helped discern whether speciation has been mediated by niche conservatism or ecological niche divergence (Brook et al. 2006, Wiens 2004, Wiens and Graham

2005). While vocal displays can be important prezygotic barriers to interspecific mating (Catchpole and Slater 2008), and many avian lineages have been discovered and, in part, diagnosed as distinct on the basis of differences in vocalization (Alström and Ranft 2003, Halley et al. 2017). However, with the application of the integrative taxonomy it has become possible to incorporate diverse information such as multilocus, morphological and ecological data to hypothesize species limits (Mckay et al. 2014, Minoli et al. 2014, Perez and Borges-Martins 2019, Venkatraman et al. 2018). This approach has been very useful even for cryptic species (Ramos et al. 2019).

Euphonia affinis is a member of the family Fringillidae, subfamily Euphoniinae (Zuccon et al. 2012). *Euphonia affinis* appears to be phylogenetically related to *E. chlorotica, E. luteicapilla*, *E. finschi*, *E. plumbea*, *E. concinna*, and *E. trinitiis* (Isler and Isler 1987, Imfeld et al. 2020). Like all Euphoniinae, its distribution is restricted to the Neotropics. Specifically, *E. affinis* is a resident of the tropical lowlands from Mexico to Costa Rica (AOU 2003). In Mexico, the species is distributed along both slopes, from Sonora in the west and San Luis Potosi in the east, south to Central America (Howell and Webb 1995: fig. 1). Two subspecies are currently recognized based on geographical and morphological descriptions (AOU 1998). *Euphonia affinis godmani* Brewster, 1889 is endemic to western Mexico and is distributed from Sonora to central Guerrero. *Euphonia affinis affinis* Lesson, 1842 is distributed from eastern San Luis Potosi, southeastern Tamaulipas, Veracruz, Puebla and north-southwestern Oaxaca and the Yucatan Peninsula to Honduras, and on the Pacific Coast of Central America from Nicaragua to northwestern Costa Rica. The morphological characteristics that distinguish both subspecies are the subcaudal covert feathers, which are white in *E. affinis godmani* and yellow in *E. affinis affinis* in both males and females (Fig. 1). Dickerman (1981) described a third subspecies, *Euphonia affinis olmecorum*, based on differences in female coloration, which is paler than females of *E. affinis affinis*. *Euphonia affinis olmecorum* is distributed along the Gulf Coast of Mexico, from southeastern Tamaulipas and eastern San Luis Potosi to northern Chiapas (Hilty 2018); however, some taxonomic authorities do not recognize this subspecies, treating it as part of *E. affinis affinis* (Clement 2011). Currently, there are no studies of intraspecific limits for the species described in Euphoniinae. However, there is morphological and biogeographic evidence that the number of species is underestimated, with several species having wide ranges of distribution and more than one morphotype. Also, Imfeld et al. (2020) found genetic divergence between two subspecies of *E. xanthogaster* of similar magnitude to that between recognized species. Taken together, these observations indicate that species limits studies in Euphoniinae are needed.

In the present work, we applied integrative taxonomy to identify the independent evolutionary lineages within *Euphonia affinis* using four types of characters, multilocus genetic data, morphometric data, behavioral, and environmental niches. Based on the allopatric distribution of subspecies *E. a. affinis* (Eastern Mexico and Central America) and *E. a. godmani* (West of Mexico), as well as in the distinctive character of subcaudal feathers, we expect to recognize at least two independent evolutionary lineages that can be proposed to elevate at the species level.

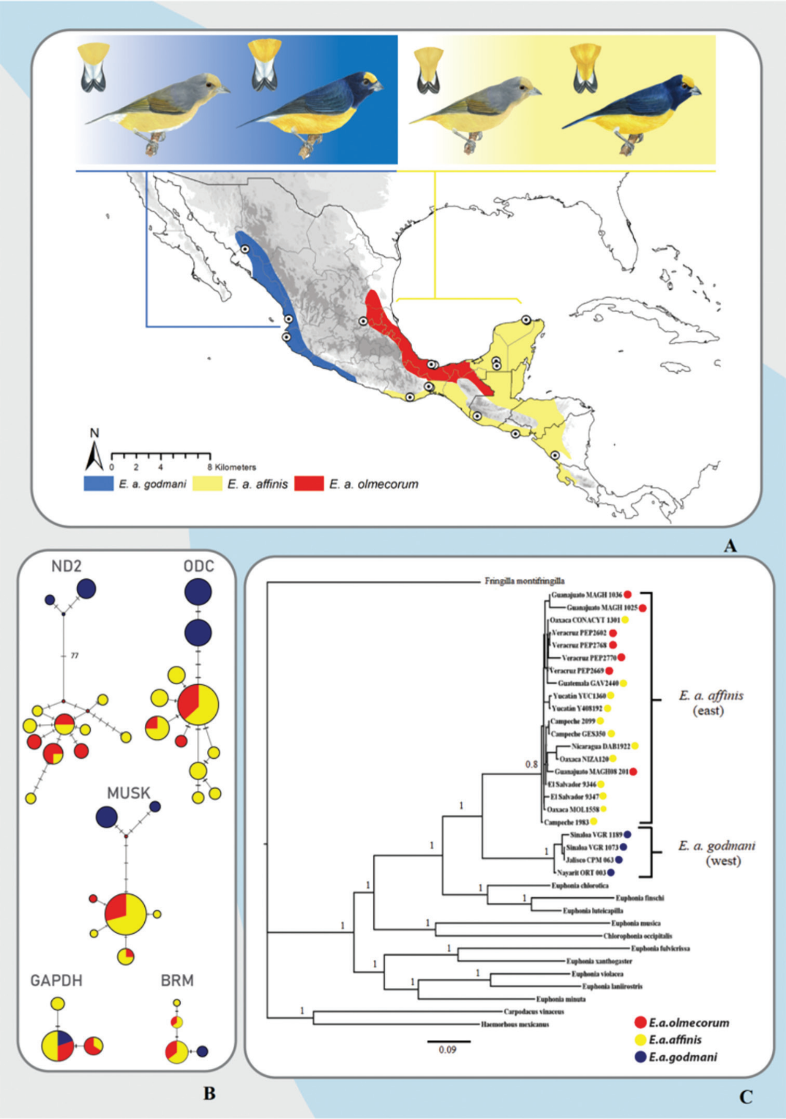

Figure 1. Geographic distribution and morphotypes of *Euphonia affinis*, sampling, phylogeny, and haplotype networks. **A** geographic distribution of *E. affinis*: in blue *E. a. godmani*, in yellow *E. a. affinis*, and in red *E. a. olmecorum* (Geographic distribution modified from NatureServe shapefile in ArcGIS, ArcMAP 10.2.2; Esri, Redlands, CA, USA). Tissue sampling locations are indicated by circles in the map. Plumage morphotypes of *E. a. godmani* (female and male) with white undertail coverts, and *E. a. affinis* (female and male) with yellow undertail coverts. The previously proposed subspecies *E. a. olmecorum* (not shown) is similar to *E. a. affinis*, but paler plumage in females and a purple-blue back in males have been reported. **B** haplotype networks obtained for the mitochondrial gene ND2 and the nuclear genes ODC, MUSK, GAPDH intron 11, and BRM intron 15. Samples from the western distribution, assigned as *E. a. godmani*, are shown in blue and from the eastern distribution, assigned as *E. a. affinis* are indicated in yellow, *E. a. olmecorum* in red. **C** bayesian Inference concatenated phylogeny of *E. a. godmani* (west) and *E. a. affinis*-*E. a. olmecorum* (eastern Mexico, Central America).

Our goals were to: 1) obtain a phylogenetic hypothesis for *Euphonia affinis* subspecies using multilocus genetic data. 2) Associate the genetic variation and divergence times with historical geographic processes and barriers. 3) Describe the pattern of morphometric, behavioral, and environmental variation in *Euphonia affinis*, and associate it with genetic variation and phylogenetic relationships. Hence, our hypothesis is that multiple independent evolutionary lineages exist within the *Euphonia affinis* complex, and our objective is to define them with the integration of multilocus genetic data, morphometric, behavioral, and environmental data. Furthermore, we discuss a potential promotion of those lineages to species status.

Materials and methods

Taxon sampling and sequencing procedures

For the ingroup we used 19 tissues from *Euphonia affinis affinis* and four from *E. affinis godmani*; for the outgroup we obtained one tissue sample from *Chlorophonia occipitalis,* two from *Euphonia chlorotica,* one from *E. luteicapilla* and one from *Haemorhous mexicanus* (Suppl. material 1, Table S1). We completed our outgroup dataset with sequences from Genbank of *Euphonia chlorotica*, *E. finschi*, *E. lanirostris*, *E. minuta*, *E. musica*, *E. violacea*, *E. xanthogaster*, *Fringilla montifringilla*, *F. teydea*, *Carpodacus vinaceus* and *Haemorhous mexicanus* (Suppl. material 1, Table S2).

Genomic DNA was isolated using the Qiagen DNeasy™ kit (Qiagen Inc., Valencia, CA, USA) following the manufacturer's protocol. We amplified five molecular markers: one mitochondrial ND2 (NADH Dehydrogenase Subunit 2, Sorenson et al. 1999) and four nuclear genes ODC (Ornithine Decarboxylase, Allen and Omland 2003), GAPDH intron 11 (Glyceraldehyde-3-phosphate dehydrogenase, Friesen et al. 1997), BRM intron 15 (BRM transcription regulatory protein, Marthinsen et al. 2009), and MUSK (Muscle, skeletal receptor tyrosine-protein kinase, Kimball et al. 2009). Technique specifications are given in Suppl. material 1, Table S3. Amplifications were done via PCR in 12.5 µl reactions. PCR and products were visualized on a 1% agarose gel. DNA sequencing was performed by the High-Throughput Genomics Unit service (University of Washington). We edited and aligned chromatograms in Sequencher v4.8 (GeneCodes Corporation, Ann Arbor, MI). All sequences were deposited in GenBank; with the accession numbers ND2: MT452146–MT452170, ODC: MT452191–MT452215, GAPDH: MT452124–MT452145, BRM: MT452098–MT452123 and MUSK MT452171–MT452190. (Also included in https://github.com/almamelisa/Euphonia-affinis-complex).

Phylogenetic analysis

We constructed the alignment of each gene using the CLUSTAL IW (Thompson et al. 1994) function in BIOEDIT (Hall 1999). Then, we used JModelTest 0.1.1 (Posada

2008) to estimate evolutionary models for each molecular marker. We conducted phylogenetic analyses in MrBayes v3.2.3 (Huelsenbeck and Ronquist 2003) for Bayesian Inference (BI), using a partitioned dataset including the four nucleotide genes ODC, MUSK, GAPDH, and BRM; ND2 was partitioned by codon position (see Table 2). For the BI, we ran the process for 10 million generations, sampling every 1,000 generations. We examined the convergence of the chains with Tracer v1.6 (Rambaut and Drummond 2013) and discarded the first 25% of generations as burn-in.

Genetic diversity and structure

To resolve heterozygotes in nuclear sequences, we used a Bayesian approach in PHASE v 2.1 (Stephens et al. 2001), selecting the pairs of haplotypes with a posterior probability higher than 0.90. Then, we used DnaSP v5.0 (Librado and Rozas 2009) to estimate the number of haplotypes (H), haplotype (Hd) nucleotide diversities (π), and Fst. Genetic distances were obtained with MEGA 5 (Tamura et al. 2013). Finally, we obtained the haplotype network for each gene with the median-joining algorithm using Network v4.6 (Bandelt et al. 1999) through DnaSP.

Tests of divergence times

Divergence times were estimated from the multilocus dataset with three genes, the mitochondrial gene ND2, and the two nuclear genes with sequences for all samples and outgroups (ODC and GAPDH) using Beast v1.8 (Drummond et al. 2013). As point calibration, we used a secondary dating based on the divergence between Fringillidae and the New World nine-primaried Oscines 17.1104 My with a 95% HPD of 14.7743–19.6278 calculated by Oliveros et al. (2019). We assigned a Normal distribution to the secondary dated point. Additionally, we defined partitions with different evolutionary rates corresponding to each gene fragment (ND2 = 0.029 s/s/My, ODC = 0.0014 s/s/My and GAPDH = 0.0012 s/s/My), based on Lerner et al. (2011). We used a Yule model as a tree prior (Gernhard 2008). For the molecular clock model, we selected the normal relaxed molecular clock following Drummond et al. (2006) and Li and Drummond (2012). We performed 20 million generations, sampling every 1,000 and corroborating the appropriate effective sample size (ESS > 200) with TRACER v1.6 (Rambaut and Drummond 2013). Finally, in TREE ANNOTATOR v 1.8.0 (Rambaut and Drummond 2013), we did a burn-in of 5,000 trees and produced the maximum clade credibility tree with 95% highest probability densities. The tree was visualized with FigTree v1.4.2 (Rambaut 2014).

Morphometrics

Six morphometric measurements of 355 specimens (233 males and 122 females) were taken from the following collections (see Suppl. material 2, also included in https://github.com/almamelisa/Euphonia-affinis-complex): Museo de Zoología Alfonso L. Herrera

(UNAM), Colección Nacional de Aves-Instituto de Biología (UNAM), Moore Laboratory of Vertebrate Zoology, American Museum of Natural History, Louisiana Museum of Natural History, Academy of Natural Sciences, Museum of Comparative Zoology, and Delaware Museum of Natural History. The morphometric measurements (following the recommendations of Baldwin et al. 1931) were: bill length (**BL**, from the upper base of the bill to the tip of the upper mandible), bill width (**BW**), bill depth (**BD**, from the upper mandible to the base of the bill at the distal edge of the nostrils), wing chord (**WC**, distance from the carpal joint the tip of the longest primary), tarsus length (**TL**), and tail length (**TLE**, distance from the uropygial gland to the tip of the longest rectrix). All measurements were taken only by the first author to avoid bias in the process using a dial caliper with a precision of 0.1 mm, except for tail length, which was taken with a millimeter ruler and in three independent events. To obtain our final data set we averaged the three independent events for every measure. Since both our molecular phylogenetic results and our analysis of the previously proposed plumage color differences do not provide evidence of *E. affinis olmecorum* as an independent evolutionary lineage, we decided to analyze morphometric variation, vocalization, and ecological niche only between *E. affinis affinis* and *E. affinis godmani*.

The normality was tested with the Shapiro-Wilk test of normality in R (R Core Team 2017). Since, the normality was rejected in all except one of the groups, we evaluated the sexual dimorphism with the Unpaired Two-Samples Wilcoxon Test, also with basic R functions. We obtained significance differences between male and females in three variables WC, TLE, and BD (see results), so we evaluated these variables differences between the lineages in a separated way for males and females with the Unpaired Two-Samples Wilcoxon Test. The rest of the variables were evaluated jointly for both sexes and also with the Wilcoxon test. With the previous arrangement, we also did a Principal Component Analysis based on the correlation matrix with the R package Factominer (Lê and Husson 2008). Graphs were generated in R package Factorextra (Kassambara and Mundt 2016). All the scripts and input data are in https://github.com/almamelisa/Euphonia-affinis-complex.

Vocalization

We obtained 19 recordings of *Euphonia affinis* calls from the Xeno-Canto (XC; http://www.xeno-canto.org) open access database. We used only call recordings in which the subspecies was identified and in which *Euphonia* was identified as the foreground species. We visualized and measured spectrograms of these recordings using the Raven Pro 1.6 software (Cornell University, Ithaca, NY). We visually inspected the spectrograms, and from each recording we selected one call section that did not overlap with any background vocalizations or other sounds. In recordings where more than one call variant occurred (for example, variants with differing number of notes), we selected one of the most frequent type. The most common call type for this species consists of a short series (2 to 4 notes) of whistled notes with decreasing pitch. Since recording conditions were not standardized, we only took frequency and duration measurements, which are not heavily affected by distance. We measured low and high frequencies (LowFreq and HiFreq), change in frequency (DeltaF), duration of call (DeltaT), number of notes (Notes) and emission rate (Speed; number of notes divided by duration). All measured variables were rescaled by *log* transforming them.

Unpaired Two-Samples Wilcoxon Test were carried out on individual variables to test for differences between the two groups. We also performed a principal component analysis (PCA) to explore the relation between the two groups in multivariate space. All the scripts and input data are in https://github.com/almamelisa/Euphonia-affinis-complex.

Ecological niche modeling and paleodistribution

The georeferenced records were obtained from the specimens used in the morphometric and genetic analyses, 102 for *E. affinis affinis* and 29 for *E. affinis godmani*. To define the M area (accessibility area; *sensu* Soberón & Peterson, 2005) for each evolutionary lineage herein identified, we plotted the record points onto the biogeographic provinces of the Neotropical region (Morrone 2014) and chose the provinces that matched the record points for both lineages, using the shapefiles provided by Löwenberg-Neto (2014). Such considerations assumed that these regions may define the accessible historical area and specific restriction region for each lineage (Svenning and Skov 2004).

For the first explorative analysis, we used the 19 bioclimate layers from WorldClim and assessed which variables were the most important for the model, according to the Jackknife test calculated in MaxEnt (Royle et al. 2012). In a second modeling exercise, we generated the species models using those non-correlated ($r < 0.8$) environmental variables in combination with the most relevant environmental variables identified in the first approach. According to previous published works (Ortega-Andrade et al. 2015, Hernández et al. 2018), these additional steps allowed us to reduce overfitting of the generated distribution models, minimizing the collinearity problems among variables (Dormann et al. 2013). Pearson correlation test among bioclimatic variables was performed in R with the basic commands. Final models were performed considering only those 12 climatic variables: BIO3 = Isothermality (BIO2/BIO7) (* 100), BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range (BIO5-BIO6), BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO14 = Precipitation of Driest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, BIO 18 = Precipitation of Warmest Quarter, and BIO 19 = Precipitation of Coldest Quarter. The climatic layers were used in ascii format and ~ 1 km resolution, and they were cut to the shape of the M area using the R package Raster (Hijmans 2019). We generated the final Ecological Niche Model (ENM) for each lineage using 75% of the record points as training data and 25% as testing data. We performed 25 replicates, 500 iterations, with 0.00001 as the convergence limit and 0.5 prevalence.

To evaluate the models we calculated the partial ROC (Receiver Operating Characteristic) in the web tool Niche Tool Box (https://shiny.conabio.gob.mx:3838/nichetoolb2/), the parameters were 0.05 proportions of omission, 50 random points percentage and 500 iterations. Also, in MaxEnt, we made four models projections one in the M area of each lineage and the remaining three were made to obtain the paleodistribution; we projected the ENM in the last maximum glacial period (~ 22,000 years ago) considering two general circular models: MIROC-ESM (Hasumim and Emori 2004) and CCSM (Collins et al. 2004). We also projected the ENM onto the last interglacial period (~120,000–140,000) (Otto-Bliesner et al. 2007). Finally, using the R packaged Ecospat (Di Cola et al. 2017) we evaluated the ecological overlap between the lineages, to quantify equivalence and similarity among groups using the Broennimann´s method (Broennimann et al. 2012). It consists of three steps: the first one is to calculate the density of occurrences and environmental factors across the axes of the environmental principal component analysis; the second is to evaluate the superposition niche along the gradient of multivariate analysis. Finally, the Schoener's D observed (Schoener 1968) and the statistical similarity *I* observed (Warren et al. 2008) are compared with the 100 repetitions of randomly generated simulated values for *D* and *I* (Warren et al. 2008, Broennimann et al. 2012). This final step consists in testing two hypotheses, the equivalence and similarity among groups. The hypotheses of niche equivalence and similarity are rejected if the empirically observed *D* and *I* values are significantly different from the values expected from the pseudoreplicates. All the scripts and input information are in https://github.com/almamelisa/Euphonia-affinis-complex.

Results

Genetic diversity and phylogenetic analyses

The multilocus dataset analyses revealed a well-supported monophyly for the *Euphonia affinis* complex and recovered two main phylogroups: one included the samples from western Mexico (*E. affinis godmani*) and the other comprised samples from eastern Mexico and Central America (*E. affinis affinis* and *E. affinis olmecorum*) (Fig. 1). The sister group of *E. affinis* complex was the clade including *E. chlorotica*, *E. luteicapilla*, and *E. finschi*. As shown in Table 2, the genetic distances between *E. a. affinis* and *E. a. godmani* have values similar to genetic distances between the other species.

The haplotype network obtained with ND2 sequences showed two geographically structured haplogroups: a western group and an eastern-CA group (Fig. 1), respectively, with two haplotypes of *E. affinis godmani* and 10 that included samples of *E. affinis affinis* and *E. affinis olmecorum* separated by 77 permutations. ND2 had the highest total haplotypic diversity (see Table 1). These same two groups were obtained for ODC, MUSK, and BRM genes. The only exception was the GAPDH network, which did not recover these geographically structured groups. Also, in Table 1 we show the results of nucleotide diversity, Tajima's *D*, nucleotide composition, molecular evolutionary models, parsimony informative sites, monomorphic sites, and the alignment base pairs.

Table 1. Diversity indices, nucleotide content, evolution model, variation sites, and alignment base pairs of mtDNA and nDNA.

Gene	H-A	Hd			Pi			D	NC				MEM	PIS	MS	Alignment BP
		Hd	Σ	SD	Pi	σ	SD		%T	%C	%A	%G				1049
ND2	12	0.95	7E-04	3E-02	0.019	7E-05	8E-03	-0.01*	26	32.5	31.6	10.4	TVM+G	358	598	(997–1041)
ODC	7	0.56	6E-03	8E-02	0.004	9E-07	9E-04	-0.67*	36.6	16.9	27.3	19.1	HKY	10	535	556
MUSK	11	0.86	1E-03	4E-02	0.004	3E-07	5E-04	-0.70*	32.6	16.8	30.5	20.3	TPM1uf	8	476	500
GAPDH	3	0.17	5E-03	7E-02	0.0006	1E-07	7E-02	-1.13*	25.4	19.9	21	33.7	HKY	1	262	280
BRM	4	0.5	5E-03	8E-02	0.002	2E-06	3E-04	-0.30*	34.6	12.9	34.6	17.9	HKY	2	288	304

H-A number of haplotypes and alleles. Hd haplotype diversity. Pi nucleotide diversity. D'Tajima. NC nucleotide composition. MEM Molecular evolution model. PIS Parsimony informative Sites. MS monomorfic sites. Alignment BP. For ND2 in () range of sequence large. P< 0.01*

Divergence times

Euphonia affinis godmani and *E. affinis affinis* split 2.6 Mya (1.5–4.0 Mya, 95% HPD), during the Late Pliocene-Early Pleistocene (Fig. 2). According to our analyses, the family Fringillidae is divided in three subfamilies: the oldest, Fringillinae, originated 14.21 Mya (10.2–17.9 Mya, 95% HPD, Highest Posterior Density), the split between Carduelinae and Euphoniinae was 12.9 Mya (9.2–16.8, 95% HPD), the Euphoniinae origen was 8.5 Mya (5.9–11.2 Mya, 95% HPD), and Carduelinae diverged 8.1 Mya (4.9–11.4 Mya, 95% HPD. Our estimate for the split between Fringillidae and *Plectrophenas nivalis* was 16.38 Mya (13.3–19.5 Mya, 95% HPD) while our point of calibration was 17.1104 Mya with a 95% HPD (14.7743–19.6278; Oliveros et al. 2019). Also, our results for the Fringillinae node age and the split between Carduelinae and Euphoniinae are consistent with the ages calculated for *Euphonia* and *Chlorophonia* phylogeny in Imfeld et al. (2020). However, there are also some differences between the ages calculated by us and by Imfeld et al. (2020), since they calculated that the split between *E. affinis* and *E. luteicapilla* was less than 1 Mya, whereas we calculated that the split between *E. affinis* and the rest of Euphonias was 4.3 Mya ago, and *E. affins* seems to be a sister group of *E. chlorotica*, *E. luteicapilla* and *E. finschi*.

Morphometrics

A total of 355 specimens was analyzed, of which 180 were males and 97 females of *E. affinis affinis*, and 53 males and 25 females of *E. affinis godmani*. Morphometric sexual dimorphism was found in three variables: TLE (Tail Length), WC (Wing Chord), and BD (Bill Depth) (Fig. 3, Table 3). Males showed statistically significant differences between *E. affinis godmani* and *E. affinis affinis* for these three characters, whereas females differed significantly in only two characters (WC and BD, Fig. 3). For the variables TL (Tail Length), BL (Bill Length), and BW (Bill width) we found significant differences between both groups (Fig. 3, Table 3). PCA analyses for males showed an 83.5% proportion of variance explained for two principal components, while females showed

Table 2. Genetic distances.

	ND2				ODC				MUSK				GAPDH				BRM			
	1	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
1																				
2	0.11**				0.01**				0.01**				0.00**				0.01**			
3	0.14*	0.17*			0.01**	0.01**			0.02**	0.02**			0.05**	0.05**			0.16*	0.06*		
4	0.15*	0.16*	0.09*		0.01**	0.01**	0.01*		–	–	–		0.05**	0.05*	0.00**		0.07*	0.07*	0.07*	
5	0.14*	0.15*	0.09*	0.03*	0.01**	0.01**	0.01*	0.01**	–	–	–	–	0.121*	0.121*	0.115*	0.115*	–	–	–	–

1. *E. a. affinis* 2. *E. a. godmani* 3. *E. chlorotica* 4. *E. luteicapilla* 5. *E. finschi*. P <0.005** P < 0.05*

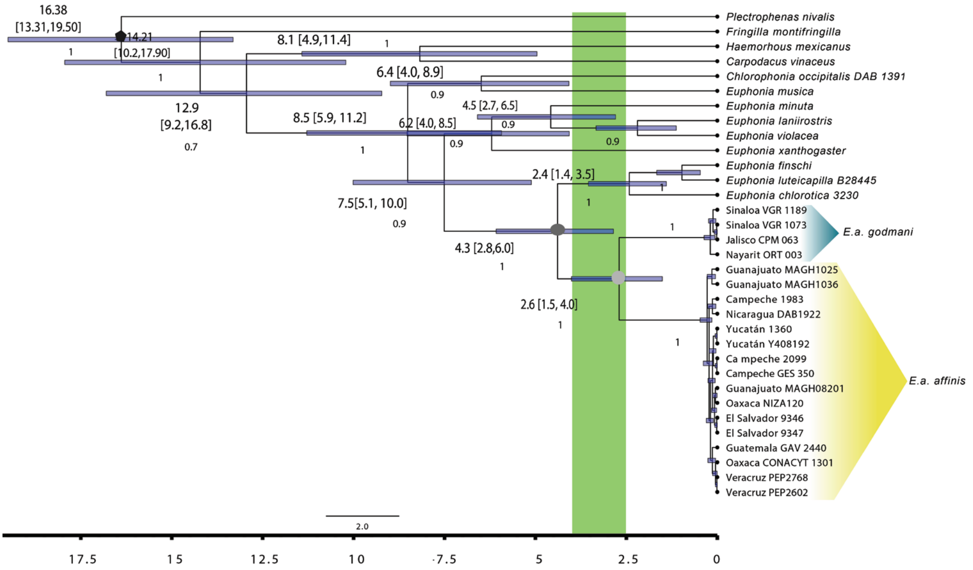

Figure 2. Ultrametric phylogenetic tree obtained by BEAST using ND2, ODC, and GAPDH concatenated matrix**.** The rhombus node represents the calibration point 17.1104 My with a 95% HPD of (14.7743, 19.6278) (see methods), dark gray circle node represents the *E. affinis* origin and light gray circle node represents the break between *E. a. godmani* and *E. a. affinis*. Above the branch the diversification dates (My) and in brackets the 95% HPD. Below branch the number indicated the posterior probability. The green area corresponds to the period when lowland dry forests had a greater expansion in Western Mexico.

an 80.2% proportion of explained variance explained. Both Component plots showed that *E. affinis godmani* was distributed in quadrant 2, while *E. affinis affinis* had a wide distribution. The dispersion plot showed a partial overlap between *E. affinis affinis* and *E. affinis godmani*, but wing chord and bill depth were clearly differentiated in boxplots. These were also the two most important variables included in the first principal component in both sexes, according to the eigenvectors (Fig. 3).

PCA analyses for both sexes showed that the first two principal components explained a large proportion of the variance (70.37%, Table 3). Contrary to the previous graphs, both sex component plots show a total overlap between the two lineages.

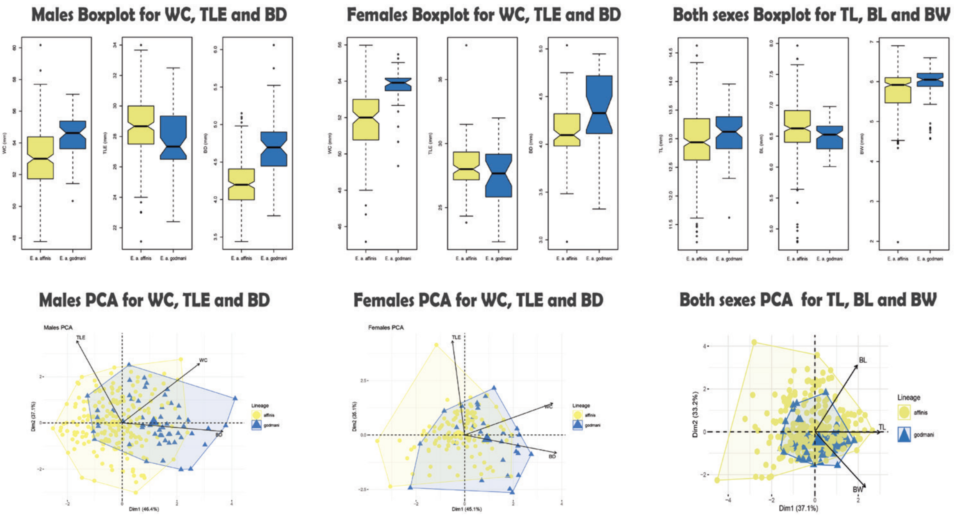

Figure 3. Morphometric analyses results. **A)** Females boxplots and PCA for WC, TLE, and BD morphometric characters. **B)** Males boxplot and PCA for WC, TLE, and BD morphometric characters. **C)** Boxplot and PCA for TL, BL, and BW. WC, TLE, and BD characters were analyzed by separated sex, because the analyses indicated sexual dimorphism (see results and Table 3). Bill length (BL, from the upper base of the bill to the tip of the upper mandible), bill width (BW), bill depth (BD, from the upper mandible to the base of the bill at the distal edge of the nostrils), wing chord (WC, distance from the carpal joint the tip of the longest primary), tarsus length (TL), and tail length (TLE, distance from the uropygial gland to the tip of the longest rectrix).

Table 3. Median, Unpaired Two-Samples Wilcoxon Test to evaluate differences between lineages and sexes, p-value < 0.05 (in bold).

			Between lineages			
		Both sexes		PC1	PC2	PC3
	affinis	*godmani*	*p-value*	37.1%	33.2%	29.6%
TL	12.93(11.1–14.6)	13.12 (11.6–13.9)	**3.10E-02**	0.74	-0.0047	-0.67
BL	6.62(4.7–7.9)	6.52(6.0–6.9)	**1.36E-04**	0.48	0.76	0.42
BW	5.92(1.9–6.9)	6.05(4.5–6.6)	**1.42E-03**	0.57	-0.63	0.51
		Females		PC1	PC2	PC3
	affinis	*godmani*	*p-value*	45.96%	34.74%	19.28%
WC	52.16 (46.6–55.97)	53.83 (49.3–55.2)	**1.15E-04**	0.77	0.4	-0.48
TLE	28 (23.8–37.6)	27.66 (22.3–32.0)	0.227	-0.24	0.93	0.26
BD	4.11 (3.4–5.0)	4.32 (3.3–4.9)	**5.68E-03**	0.84	-0.09	0.52
		Males		PC1	PC2	PC3
	afifnis	*godmani*	*p-value*	47.7%	35.5%	16.8%
WC	53(47.7–60.1)	54.61(51.4–57.0)	**7.64E-08**	0.7	0.56	-0.41
TLE	28.66(21.0–34.0)	27.33 (22.4–32.5)	**3.27E-03**	-0.4	0.85	0.31
BD	4.19(3.5–5.1)	4.68(3.7–6.6)	**1.43E-13**	0.87	-0.06	0.48
			Sexual dimorphism			
	E. a. affinis				***E. a. godmani***	
	females	males	*p-value*	Females	males	*p-value*
TL	13.017(11.1–14.6)	12.908(11.3–14.1)	0.11	13.213(12.3–13.9)	11.6–13.9)	0.43
BL	6.607(4.7–7.6)	6.633(5.0–7.9)	0.09	6.537(6.0–6.9)	6.523(6.0–6.9)	0.60
BW	5.947(4.5–6.9)	5.914(1.9–6.6)	0.99	6.043(4.5–6.4)	6.06(4.5–6.6)	0.81
WC	52.167(46.6–55.9)	53(47.7–60.1)	**3.19E-04**	53.833(49.3–55.2)	54.613(51.4–57.0)	**6.22E-03**
TLE	28(23.8–37.6)	28.667(21.0–34.0)	**1.48E-02**	27.667(22.3–32–0)	27.333(22.4–32.5)	0.78
BD	4.117(3.4–5.0)	4.1985(3.5–5.1)	0.08	4.327(3.3–4.9)	4.683(3.7–6.0)	**4.40E-03**

Vocalization

None of the frequency variables measured differed significantly between *godmani* and *affinis* groups (N =19). On the other hand, we found that the emission rate of *E. a. affinis* is much lower than that of *E. a. godmani*, on average 2.9 notes/s versus 5.09 notes/s. These differences are statistically significant ($W = 0$, $p < 0.001$). The first two Principal Components together explain 78.75% of variance. The first PC separates both groups unambiguously (Fig. 4), and has a highly positive correlation with call duration, as well as a highly negative correlation with emission rate (notes per second).

Distribution modeling, paleodistribution, and ecological niche overlap

Our models obtained a high mean value for AUC (Area Under the Curve) ratio values and statistically significant, 1.68 for *E. affinis affinis* and 1.81 for *E. affinis godmani* (***P < 0.05), this indicates a good fit of ENM's. According to the Jackknife test and contribution variables obtained by MaxEnt, the most important variable for *E. affinis affinis* model was BIO 15 (precipitation seasonality), and the variable BIO8 (mean temperature of wettest quarter) for *E. affinis godmani*. We present the ENM predictions in four levels in Fig. 4; the first ones are the present predictions for the two lineages and the overlap between them, in general, both models predicted the previously known area of distribution for both species (Fig. 4), with an overlap in the West Pacific coast. In the second level, we observed that *E. affinis godmani* has a limited ability to predict its ecological niche in the geographic areas where *E. affinis affinis* is distributed, while *E. affinis affinis* projected its ecological niche on a large geographic area of distribution for *E. affinis godmani*.

The third part is the projection of the models in Last Glacial Maximum conditions (LGM 21–18,000 years ago), for *E. affinis affinis* showing a reduction in their environmental suitability along the present distribution, with predictions in areas like the Yucatan Peninsula and the western coast of Mexico with a gap at the western coast of the Tehuantepec Isthmus, unlike Present predictions where Central America has only small patches with predictions for *E. affinis affinis* (Fig. 4). For *E. affinis godmani* we found predictions in the western coast of Mexico, with a large gap between the central Mexican Coast west and the western coast of the Tehuantepec Isthmus, it also has a small patch prediction in the Yucatan Peninsula. The fourth part is the Last Interglacial (~ 120,000–140,000 years ago), for both lineages, the areas with high environmental suitability increased with respect to LGM, for *E. affinis affinis* it including the western Yucatan Peninsula, the Central western Mexican coast, and the Tehuantepec Isthmus to the western coast of Central America. For *E. affinis godmani*, the prediction areas are the West Mexican coast and the western Yucatan Peninsula.

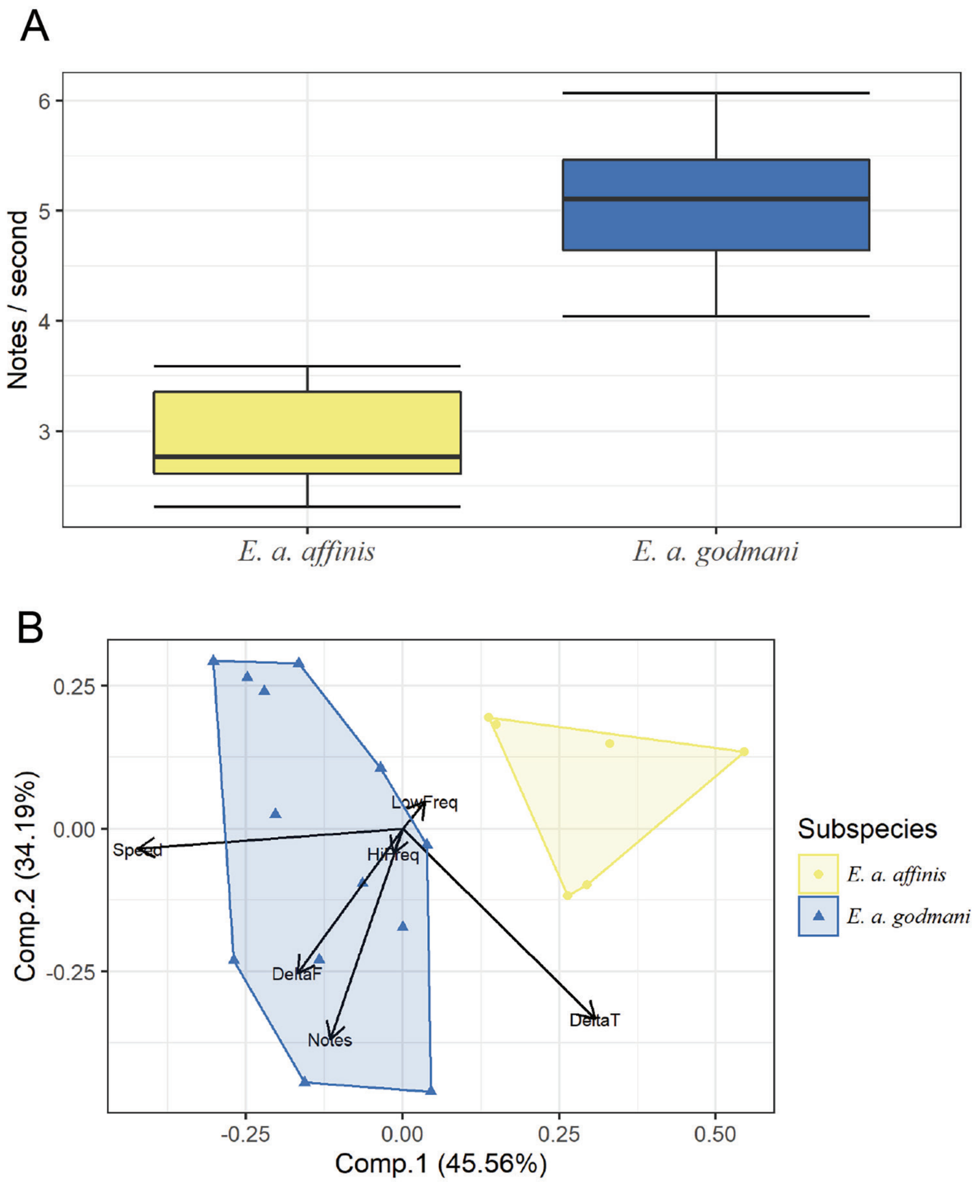

Figure 4. Vocalization analysis. Boxplot of note emission rate **A** and PCA of measured vocal characters **B** Calls differ between the two groups in temporal structure, but not in frequency or number of notes.

The results of ecological overlap for the environmental PCA exhibit a large niche of *E. a. affinis*, while *E. a. godmani* exhibits an ecological niche compaction. A total variance of 83.67% is explained for the three principal components, with 41.04% for PC1,

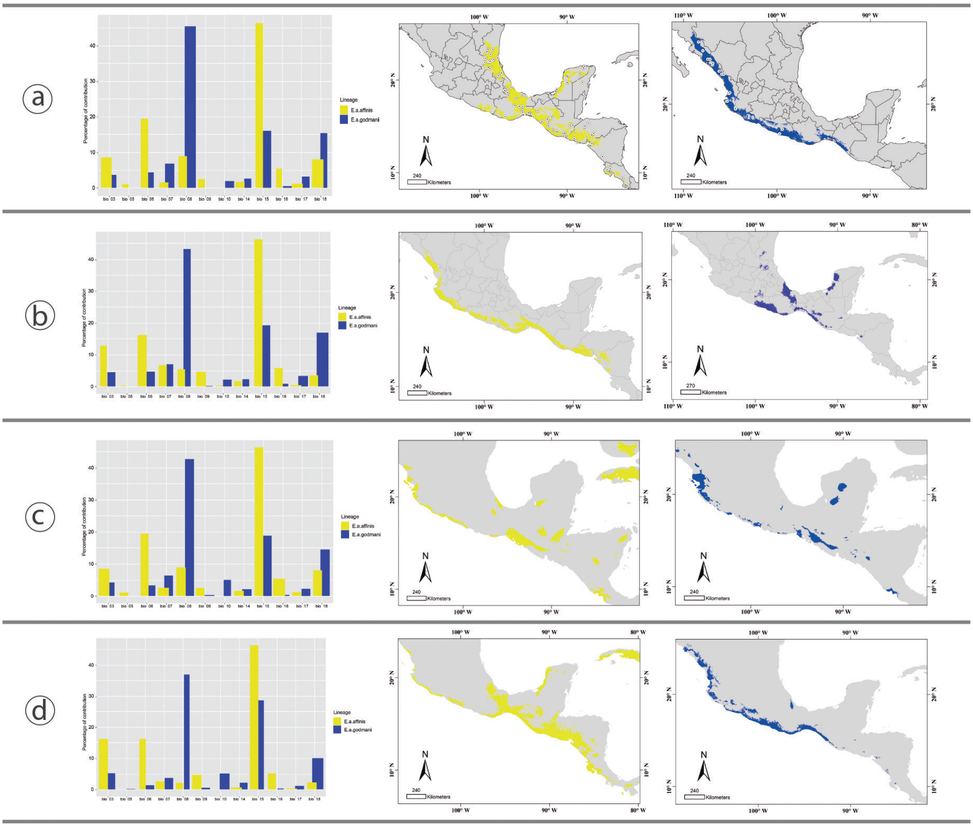

Figure 5. Ecological niche modelling and its projection in the geographic areas for *E. a. affinis* (yellow) and *E. a. godmani* (blue). In all four panels (a-d), the contribution values of each environmental variable of ENM's is illustrated in the left and the projection of the Ecological niche conditions in the geographic distribution area is shown in the maps. **a** Ecological Niche projected in the current geographic distribution area of *E. affinis* and *E. a. godmani*. **b** ENM's projected into the geography for each lineage. **c** ENM of *E. a. affinis* and *E. a. godmani* projected in the Last Maximum Glacial ecological conditions. **d** ENM of *E. a. affinis* and *E. a. godmani* projected in the Last Inter Glacial ecological conditions.

29.886% for PC2 and 12.733% for PC3 (Fig. 5). The *D* and *I* statistic observed values were close to zero 0.01174013 and 0.05643784 respectively. We can reject the niche equivalency because the *D* observed value does not fall within the density of 95% of the random simulated values, however we obtained a no significant *p* value (0.9901). In contrast, the niche similarity test between *E. affinis affinis* and *E. affinis godmani* shows that they are less similar than expected by chance (Fig. 5), since there is not significant climatic niche conservatism (p = 0.31683, p = 27723) between them. With this evidence we reject the niche conservatism hypothesis between *E. a. affinis* and *E. a. godmani*, so we can say that the niches are divergent (Warren et al. 2008, 2010; Broennimann et al. 2012).

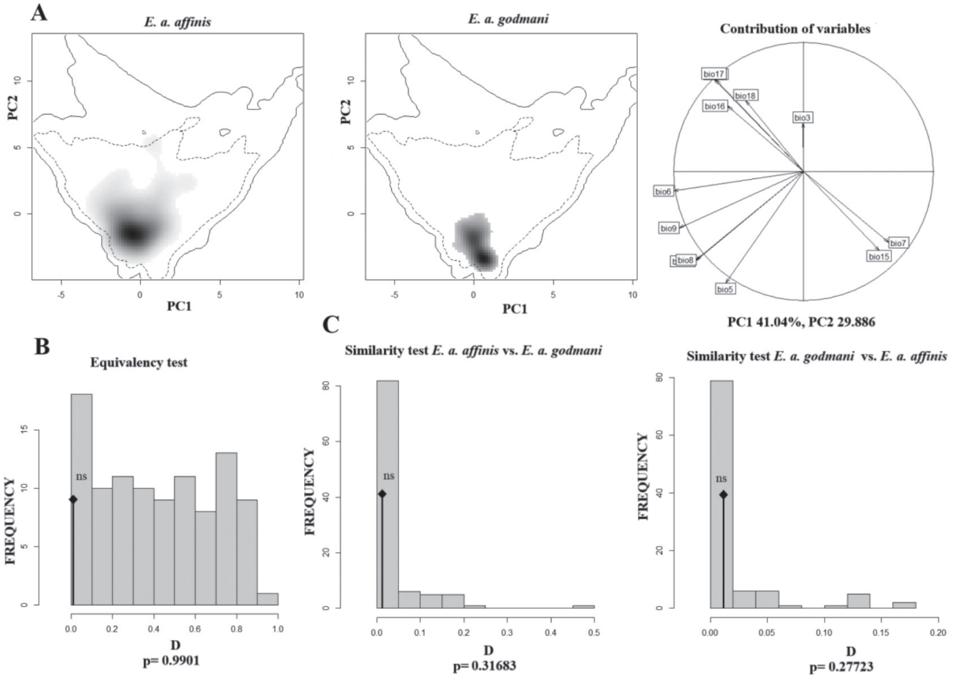

Figure 6. Equivalence and similarity tests in environmental space for *E. a. affinis* and *E. a. godmani*. **A** PCA of Ecological niche for of *E. affinis* lineages and the variables contribution to the analyses. The gray gradient indicates the density of the occurrences of the lineages, and the dashed and solid line indicates the 50% and 100% of the environmental background **B** graphical results of the equivalency tests comparing the two lineages. For both tests (equivalence and similarity) we only presented values for the D metrics. For all graphs the D observed values of the overlap niche analyses are present with the black diamond. The *p* value is showing in each graphic, all of them not significant for these analyses **C** graphical results of the similarity test comparing the two lineages in both directions (*E. a. affinis* vs. *E. a. godmani* and vice versa), ns = Not significant, p > 0.05.

Descriptions

Euphonia affinis **(Lesson, 1842), stat. nov.**

Tanagra affinis Lesson 1842, *Rev. Zool.* 5: 175.
Tanagra affinis affinis; Miller et al. 1957, *Cooper Ornithol. Soc. Pac. Coast Avifauna* 33: 298.
Euphonia affinis affinis; Dickerman, 1981, *Occ. Pap. Mus. Zool. Louisiana State. Univ.* 59: 3.
Euphonia affinis olmecorum Dickerman, 1981, *Occ. Pap. Mus. Zool. Louisiana State. Univ.* 59: 4, syn. nov.

Morphological characterization. Males. Yellow forehead, back black with bluish to violet glow, black throat, yellow from chest to belly, yellow subcaudal coverts feathers (Hilty 2018). Morphometric characters, wing chord 52.167 mm, tail length 28.667 mm and bill depth 4.1985 mm.

Females. Forehead olive-yellow and gray, olive-green back. The throat is olive-yellow, with a yellow belly, subcaudal coverts feathers also in yellow (Hilty 2018). Morphometric characters, wing chord 52.167 mm, tail length 28 mm and bill depth 4.117 mm.

Geographical distribution. Through Gulf slope of Mexico from Nuevo Leon, S Tamaulipas and E San Luis Potosí to N Chiapas, Yucatan Peninsula, E of Guatemala, Belize to N Honduras; in the Pacific slope from W Oaxaca, Mexico to NW Costa Rica (Hilty 2018).

Euphonia godmani **Brewster 1889, stat. nov.**

Euphonia godmani Brewster, 1889, *Auk* 6: 90.
Tanagra affinis godmani; Miller et al. 1957, *Cooper Ornithol. Soc. Pac. Coast Avifauna* 33: 298.
Euphonia affinis godmani; Dickerman, 1981, *Occ. Pap. Mus. Zool. Louisiana State. Univ*. 59: 1.

Morphological characterization. Male. Very similar to *E. affinis* with white undertail coverts feathers (Hilty 2018). Morphometric characters, wing chord 54.613 mm, tail length 27.333 mm and bill depth 4.683 mm. Female. Paler respect to *E. affinis* and with white belly and with undertail coverts feathers (Hilty 2018). Morphometric characters, wing chord 53.833 mm, tail length 27.667 mm and bill depth 4.327 mm. Geographical distribution: Along to Pacific slope of Mexico from SE Sonora S to C Guerrero (Hilty 2018).

Discussion

We provide molecular, morphological, behavioral, and environmental niche evidence supporting the existence of two evolutionary lineages within the *Euphonia affinis* complex (*E. godmani* and *E. affinis*). De Queiroz (2007) proposed that different types of data (morphological, ethological, ecological, molecular, etc.) can support species delimitation, if the lineages under study are evolving separately and can then be considered different species. Therefore, in our study we show these lineages have disjunct distributions, they have different plumages (white undertail coverts in *E. godmani*, and yellow undertail coverts in *E. affinis*, Hilty 2018), and we found significant differences in morphometric measurements. We did not find evidence of a third lineage corresponding to the subspecies *E. affinis olmecorum* proposed by Dickerman (1981); rather, it represents intraspecific variation within *E. affinis*.

Phylogenetics and genetic variation

We found three lines of evidence in the molecular data to support the taxonomic split of the *E. affinis* complex at species level. The first is the reciprocal monophyly between *E. affinis* and *E. godmani* found in the multilocus analysis using mitochondrial and nuclear genes, where the samples of *E. affinis olmecorum* are included into *E. affinis*. These results agree with the proposals by Ridgway and Friedman (1901) and the taxonomic proposal of Navarro-Sigüenza and Peterson (2004). The second line of evidence is the genetic distance between the western and eastern groups, which is similar to other *Euphonia* species close to the *E. affinis* complex (Table 2). These genetic distance values are also similar to distances found in other bird complexes distributed in Mexico and Central America that have been recognized as distinct species (Puebla-Olivares et al. 2008, Arbeláez-Cortés and Navarro-Sigüenza 2013, Zamudio-Beltrán and Hernández-Baños 2015). The third line of evidence is the high index of genetic fixation FST (Table 2) and the haplogroups in the haplotype networks (Fig. 1). It is important to mention that the haplotype networks showed geographical correspondence, with *E. godmani* in western Mexico, and *E. affinis* in eastern Mexico and Central America. These results are consistent with studies of other bird species distributed in Mesoamerica (Smith et al. 2011, Ramírez-Barrera et al. 2018).

Morphometrics

Our analysis revealed significant differences between *E. a. godmani* and *E. a. affinis* in six characters among lineages. Bill Depth and Wing Chord are bigger for *E. a. godmani*, while *E. a. affinis* has bigger dimensions on Tail Length. Even though the rest of characters have significant differences, in the PCA plots the Tail Length, Bill Length and Bill Width characters do not show dispersion between both lineages, so we can assign Wing Chord, Tail Lenth and Bill Depth as diagnostic characters for males, and Wing Chord and Bill Depth as diagnostic characters for females. These results are similar to *Phaethornis mexicanus* morphometric patterns, a species also distributed along the Atlantic and Pacific Slope, where the Pacific lineage also shows bigger dimensions vs. the Atlantic lineage (Arbeláez-Cortés and Navarro-Sigüenza, 2013).

Vocalization

Our results show that there are significant differences in the temporal characteristics of calls between *E. godmani* and *E. affinis* while we found that there is little divergence in spectral structure or frequency measurements. *E. godmani* emits call notes at a significantly faster rate than *E. affinis*. Many bird species are highly sensitive to temporal cues in recognizing conspecific vocalizations (Dooling and Prior, 2016), which suggests that while call structure and frequency in this complex has been conserved, variation in tempo could be an important cue in conspecific recognition.

Ecological niche similarity

Euphonia affinis and *E. godmani* represent two different lineages with no significant conservatism in their ecological niches (west vs. east). The env-PCA, also, showed a larger ENM for *E affinis*, respect to *E. godmani*, also the western lineage has a limited ability to predict its ENM in the geographic area of *E. affinis*. The western coast of Mexico is characterized by a highly contrasting dry season vs. a wet season over the year, this characteristic is unique with respect to the eastern tropical area, so *E. godmani* has become restricted to these conditions. These results are similar to other taxa with sister lineages distributed along the Pacific and Atlantic slopes in Mesoamerican (Hernández-Canchola and León-Paniagua, 2017). It is interesting that *E. godmani* shows a reduction in ecological niche, while *E. affinis* presents a broader ecological niche. That may suggest a scenario where *E. godmani* was able to invade the western area of Mexico, and, in the absence of ecological competition from other Euphonias, it adapted and specialized to the floristic resources, as well as to the temperature and precipitation conditions of the area. While *E. affinis* conserved a broader ecological niche, as reflected in its geographical distribution, allowed it to explore more regions and resources, even in the presence of different species of Euphoniinae.

Biogeographical history

Lineage divergence between *E. godmani* (western Mexico) and *E. affinis* (eastern Mexico and Central America) occurred ~ 2.6 Mya (1.5–4.0 Mya HPD 95%), a range between the Pliocene and Pleistocene epochs. During the Pliocene, the Sierra Madre Occidental and the Transmexican Volcanic Belt finished emerging, which made the Pacific Slope drier than the Atlantic slope, due to the hillside effect (Graham and Dilcher, 1995). Additionally, the drier conditions were favored by meteorological phenomena that made the Pacific coast warmer than the Atlantic coast in the northern hemisphere (Molnar and Cane 2007). These events were decisive for the conformation of the tropical deciduous forest that extended throughout the Pacific from western Mexico to western Panama. According to studies of paleontological and molecular evolution, botanical elements present in the dry forests today were already present in said area since the Miocene (Graham and Dilcher 1995, Becerra 2005 de-Nova et al. 2012) however, from the Middle Pliocene to the late Pliocene these elements were unified as a plant community, promoting the diversification of some botanical groups (Becerra et al. 2005, de-Nova et al. 2012). Also, significant isolated periods of dry forest have been attributed to diversification in the Pacific Slope area (Becerra 2005, de-Nova et al. 2012, Willis et al. 2015). As a consequence, this province is characterized by a pattern of a high number of endemic lineages and species (Zaldívar et al. 2004, García-Deras et al. 2007, Zarza et al. 2008, Ramírez-Barrera et al. 2018). We found two threads of evidence that support the relationship between divergence of lineages for *E. affinis* and the origin of dry forests. The first evidence is the age of 2.6 Mya when the West and East lineages diverged during the late Pliocene, which coincides with the establishment of dry forests in Western Mexico. The other evidence is the adaptation and restriction of the environmental niche of *E. a. godmani* to the environmental conditions of Western Mexico. Other biogeographic events of Mesoamerica that shaped the biota were the closure of the Isthmus of Panama during the late Pliocene and the orographic changes in the Atlantic slope by the last raise of Transmexican Volcanic Belt and the Sierra Madre Oriental. However, the Atlantic Slope shows a wide mosaic of environments and ecosystems (Graham and Dilcher 1995), in contrast to the dry forest-dominated West slope, which could explain the more extensive environmental niche of *E. a. affinis*.

In addition to the consequences of the orographic changes of the Pliocene, during the Late Pliocene, global and continuous cooling periods were frequent, and during the Pleistocene the climatic oscillations were defined by glacial and interglacial periods (Zachos et al. 2001). During the glaciations, the species inhabiting temperate zones expanded their distribution to lower altitudes (Moreno-Letelier et al. 2014), while the geographic distribution of tropical vegetation was reduced. Tropical forests were affected by periods of low humidity which favored the reduction of the distributional range of several species, thus probably promoting speciation in plant species (Gentry 1982) as well as in the fauna of these forests, including birds (Smith and Klicka 2010). The divergence between Mesoamerican lowlands species has been attributed to these climatic changes, for example, amphibians (Greenbaum et al. 2011), reptiles (Ruane et al. 2014), mammals (Castañeda-Rico et al. 2014), and birds (Arbeláez-Cortés and Navarro-Sigüenza 2013). This work shows that orographic and environmental changes promoted the divergence of two lineages within *E. affinis*, probably due to isolation events and environmental adaptations, which in turn could accentuate the present differences in morphological, genetic, behavioral, and ecological characteristics previously described.

Conclusions

We incorporated different kinds of information to help us identify lineages within the *Euphonia affinis* species complex and understand the speciation process (De Queiroz 2005, 2007, 2011, Padial et al. 2010). We have demonstrated a sharp genetic split between *E. a. affinis* and *E. a. godmani* and we found a similar pattern in morphometrics, vocalizations, as well as in ecological niche data. So, we can conclude that our data support the consideration of *E. affinis* and *E. godmani* as two species.

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Supplementary material 1

Tables S1, S2, S3. Sampling, genbank sequences and sequences of primers

Authors: Melisa Vázquez-López, Blanca E. Hernández-Baños

Data type: species data

Link: https://doi.org/10.3897/zookeys.952.51785.suppl1

Supplementary material 2

Raw morphometric data and collection information

Authors: Melisa Vázquez-López and Blanca E. Hernández-Baños

Data type: morphological data

Link: https://doi.org/10.3897/zookeys.952.51785.suppl2