RESEARCH ARTICLE



Natural history collections as a basis for sound biodiversity assessments: Plexauridae (Octocorallia, Holaxonia) of the Naturalis CANCAP and Tyro Mauritania II expeditions

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Abstract

Mapping biodiversity is the marathon of the 21st Century as an answer to the present extinction crisis. A century in which science is also characterised by large scientific datasets collected through new technologies aiming to fill gaps in our knowledge of species distributions. However, most species records rely on observations that are not linked to specimens, which does not allow verification of species hypotheses by other scientists. Natural history museums form a verifiable source of biodiversity records which were made by taxonomists. Nonetheless, these museums seem to be forgotten by biologists in scientific fields other than taxonomy or systematics. Naturalis Biodiversity Center (NBC) in Leiden is care keeper of large collections of marine organisms, which were sampled in the Northeast Atlantic during the CANCAP and *Tyro* Mauritania II expeditions (1976–1988). Many octoocrals were sampled and deposited in the NBC collection, where they became available for study and were partially identified by the senior author (M.G.)

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in the 1980s. Nonetheless, no checklist or taxonomic revision was published so far with the complete results. In 2016 the first author visited NBC to examine NE Atlantic Plexauridae octocorals. Plexauridae octocoral-vouchered records were listed and mapped to reveal high standard primary biodiversity records unreported so far for the NE Atlantic Ocean. Twenty-four Plexauridae species with ~ six putative new species to science were discovered and eleven new biogeographical records were made from distinct Macaronesian archipelagos. Finally, new depth range records were found for three species at sea basin level and for eight species at a regional scale.

Keywords

Alcyonacea, CANCAP project, deep water, geographical distribution, *Tyro* Mauritania II, zoological collections

Introduction

The rate of biodiversity loss is accelerating, leading to a tendency for "Big Data" production on species observation-based occurrences instead of specimen-based occurrences as a way to map and protect biodiversity (Troudet et al. 2018). While unvouchered observations may lead to the rapid production of large datasets, specimen-based records are essential for species descriptions and for the scientific repetition principle (Cotterill 1997; Rocha et al. 2014; Troudet et al. 2018). A specimen should be available for further verification or reinterpretation, a fundamental principle of science, because properly labelled specimens are biodiversity raw data based on a researcher interpretation, from which metadata is derived (e.g., their occurrence information) (Hoeksema et al. 2012; Schilthuizen et al. 2015; Troudet et al. 2018). Moreover, vouchered records not only increase precision but are also more complete by providing ancillary data a posteriori, such as geographical positions, images or DNA sequences, which are useful for richer present and future analyses (Hoeksema 2015; Troudet et al. 2015; Troudet et al. 2018).

Natural history museum collections (NHMC) are rich repositories representing a variety of all known life forms (Kemp 2015; Funk 2018). During 300 years of biodiversity exploration, many organisms were collected, catalogued, identified and stored under a systematic order. The name-bearing specimens deposited there are an important source of ancillary data over a long time span (Suarez and Tsutsui 2004).

The Earth's estimated biodiversity is in the order of 10 million species, from which only 10–20% are currently known to science, while the rest still lacks a name, a description and basic knowledge on its biology (Krishtalka and Humphrey 2000; Wilson 2003; Costello et al. 2015). This lack of information on extant species is consequently reflected in an absence of understanding on which species are threatened with extinction or introduced in new environments and what is their distribution (Wilson 2003; Frey 2009; Kemp 2015). Subsequently, there is a lack of fundamental knowledge to understand the biology of species and the human-induced changes in their environment. Regarding the known biodiversity, collections-based science recognizes the value of NHMC as a source of biodiversity data in various disciplines of research (Krishtalka and Humphrey 2000; Graham et al. 2004; Costello et al. 2013; Funk 2018). NHMC species and their distribution datasets from the past, can be used to compare with present-day datasets and understand the species conservation status, prioritize and plan future studies and species management plans (Graham et al. 2004, Lister and Climate Change Research Group 2011, Funk 2018).

NHMC from remote localities or environments that are otherwise difficult to access have additional value. For example, biodiversity data collection faces higher technical challenges at distant habitats such as the deep sea, which is the Earth's largest ecosystem. Therefore, deep sea data gathering is reflected in a few pieces of a puzzled map of discoveries. Tentative exploration of the deep sea is thought to have begun in 1521 with Fernão de Magalhães attempting to sound the Pacific Ocean between two coral islands (Murray and Hjort 1912). Yet, despite recent technological developments, it is still difficult to sample this inaccessible environment due to strong currents, rough bottoms and high costs. Therefore, the deep sea is the least surveyed marine environment although having eminent species richness (Hernández-Ávila et al. 2018).

During modern deep-sea surveys, the systematic collection of benthic marine invertebrates to characterise local fauna is usually secondary, with priority being given to long-distance transects by use of deep-sea imaging technology for species occurrence data and habitat mapping. Despite a paucity in biodiversity data, benthic marine invertebrate samples tend only to be collected as by-catch after which they are only identified at high taxonomical levels or misidentified due to the absence of taxonomists onboard (Renaud et al. 2015). At the same time, new species await an average of 21 years on shelves of NHMC for the unique eye of a trained taxonomist to be described (Fontaine et al. 2012; Costello et al. 2015, Kemp 2015). Historical benthic diversity datasets gathered at NHMC, have proven to be accurate sources of baseline data on species diversity and distribution across the Atlantic Ocean for marine benthos of the Canadian Arctic and for deep-sea reef building scleractinian coral species off the southeastern United States (Ross et al. 2012; Roy and Gagnon 2016). Based on these museum records, distribution of corals and other benthic species was confirmed and new areas for exploration were suggested (Ross et al. 2012, Roy and Gagnon 2016). However, even considering the widespread use of NHMC data, there is still much work to do in order to educate scientists about specimen importance, underutilised collections and the value of NHMC as a way to improve museum collections, support taxonomy and, most of all, the quality and reproducibility of biodiversity knowledge (Costello et al. 2013; Ward et al. 2015).

Naturalis Biodiversity Center (NBC), the national museum of natural history of the Netherlands, preserves marine benthos collected during eight explorative Dutch expeditions to the subtropical and tropical parts of the Eastern North Atlantic islands and seamounts (Figure 1). The CANCAP and *Tyro* Mauritania II expeditions took place from the Azores to Cape Verde from 1976 to 1988 on board HNLMS *Onversaagd* and HNLMS *Tydeman*, passing through all the Macaronesian archipelagos down to the west coast of Africa in Mauritania and Senegal, while sampling from the surface to 4000 m depth (Den Hartog 1984; Van der Land 1987, 1988). After the expeditions of Prince Albert I of Monaco (Thomson 1927), the CANCAP (CANarian – CAPe Verdean Deep-Sea Basin) project was the most representative set of



Figure 1. The National Museum of Natural History of The Netherlands. Naturalis Biodiversity Center in 2016 (**a**), Marine Invertebrate Collection (**b**), part of the CANCAP and *Tyro* Mauritania II consulted collection (**c**, **d**).

campaigns taking place in the southern NE Atlantic Ocean with the aim of building a representative inventory and collection of organisms from 1260 sampling stations in poorly explored or unexplored regions (Den Hartog 1984). Numerous studies were published on marine benthos collected during these expeditions (see for instance Van Soest 1988; Fransen 1991; Ansín-Agís et al. 2001; Van der Linden 1998; Dijkstra and Goud 2002; Vervoort 2006), including some on octocorals: *Spinimuricea atlantica* (Johnson, 1862) from Madeira (Grasshoff 1992), the genus *Alcyonium* Linnaeus, 1758 (Stokvis and Ofwegen 2006; Sampaio et al. 2016) and some Alcyonacea of the Azores (Braga-Henriques et al. 2013). Yet, several octocorals deposited at NBC have since remained unstudied for 40 years.

Global octocoral taxonomy has been in the hand of fewer than ten scientists during the 20th Century in the time of the taxonomic impediment (see Coleman 2015). This concept is based on decreased investment in taxonomy, NHMC, qualification of scientists in taxonomy and replacement or recruitment of curators and taxonomists that is associated to limited knowledge on biodiversity (Taylor 1976). With most experts currently retired, taxonomic work on octocorals is now a part-time job or hobby for some of them. The number of experts has since decreased and the interest of the new generations for this discipline is reduced or not supported. Currently, there is no curator for Octocorallia in any of the most important natural history museums of Europe. Dr. Leen P. van Ofwegen, curator of Octocorals at NBC (Leiden), was the last when he retired in 2017.

Most recent octocoral taxonomic studies in the Atlantic Ocean have focused on the northwestern Atlantic, with the northeast Atlantic receiving less attention. Within Octocorallia, the family Plexauridae Gray, 1859 is characterised by mostly arborescent colonies, branches appearing laterally, dichotomously or pinnately. Plexauridae polyps are retractile or have calyces where the anthocodiae is withdrawn and their axis has a large, hollow and cross-chambered central core encircled by gorgonin and horny loculated spaces with non-sclerite calcareous matter (Bayer 1956). Plexauridae is one of the most diverse and abundant families of octocorals, with 47 valid genera (Cordeiro et al. 2019) and several of its species known to form coral gardens (Grasshoff 1977). However, it is not the main study object of any of the current leading experts on Octocorallia taxonomy.

At the NE Atlantic Ocean, a Plexauridae species was described by Johnson (1861) for Madeira. Later, the scientific campaigns of Prince Albert I of Monaco resulted in two volumes including new plexaurid species of this area (Studer 1901; Thomson 1927), which were later revised by Carpine and Grasshoff (1985). Thomson (1929) also described some species and the French expedition Biaçores resulted in several records of Plexauridae from the Azores (Tixier-Durivault and D'Hondt 1974). In the 1970s, more species were found at the Mediterranean Sea (Carpine and Grasshoff 1975). Moreover, the last taxonomic revision of this family (still under the name Paramuriceidae Bayer, 1956) was published at the end of the decade (Grasshoff 1977). Twenty-three species in eight genera, occurring from the coast of Ireland to the Gulf of Guinea including the Macaronesian archipelagos, nearby seamounts, and the Mediterranean Sea, were accepted (Grasshoff 1977). Since this revision, little has been added in terms of biodiversity, with only one new species described, Thesea talismani Grasshoff 1986 (see Grasshoff 1986). Another species is also considered for Europe by the European Register of Marine Species (ERMS) (Costello et al. 2001) but this species is Swiftia pallida, which is a synonym of S. dubia (Grasshoff 1986). So far in the southern part of the NE Atlantic Ocean, 17 of the 23 valid NE Atlantic and Mediterranean Sea plexaurid species have been recorded (Grasshoff 1977; Carpine and Grasshoff 1975; Grasshoff 1986).

Plexauridae specimens collected during the CANCAP and *Tyro* Mauritania II expeditions deposited at the NBC were identified by the last author (Table 1; Figure 2). However, his work was never published, with the exception of some records (Grasshoff 1992). With the aim of documenting this valuable source of unpublished information, the Plexauridae specimens collected during these expeditions were examined by the first author: 1) to make available a list of plexaurid octocorals collected during CAN-CAP and *Tyro* Mauritania II expeditions; 2) to use Plexauridae records to produce maps of their geographic and depth ranges in the NE Atlantic Ocean to inform future research, field surveys and management plans; and 3) to demonstrate the value of museum records as a source of high quality biodiversity information.

Table 1. Plexauri, archipelagos and at	dae collect t Mauritan	eed during iia includir	CANCA ng the pre	P and <i>Tyro</i> evious data :	Mauritan available (1	ia II exped references)	itions. Ge and new r	ographical and bathymetri ecords (remarks). Bold scri	Table 1. Plexauridae collected during CANCAP and <i>Tyro</i> Mauritania II expeditions. Geographical and bathymetrical distribution on the southern NE Atlantic archipelagos and at Mauritania including the previous data available (references) and new records (remarks). Bold script indicates new regional records.
Species	Depth Range (m)	Azores (m)	Madeira (m)	Selvagens Islands (m)	Canary Islands (m)	Cape Verde Mauritania (m) (m)	Mauritania (m)	Remarks	References
<i>Bebryce mollis</i> Philippi, 1842	71-1250	105-1250			95–330	875-900		New lower depth limit in Canary Islands (330 m).	Studer 1901; Thomson 1927; Aurivillius 1931; Stiasny 1939, 1940; Thier-Durivault and D'Hondt 1974; Carpine and Grasshoff 1975; Grasshoff 1977, 1985a, 1989, 1992; Carpine and Grasshoff 1985; Brito and Ocaña 2004
Muriceides lepida Carpine & Grasshoff, 1975	79–1350	500-550	300-400		180–330	180-330 1000-1350		New lower depth limit for the species (1350m). Specified regional depth ranges.	Carpine and Grasshoff 1975; Grasshoff 1977, 1981, 1985a
Muriceides paucituberculata (Marion, 1882)	51-2165	454-1350	1968		x	515	51	New at Cape Verde. New lower depth limit at Azores (1350m).	Studer 1901; Thomson 1927; Thomson 1929; Pax and Müller 1954; Tixier-Durivault and D'Hondt 1974; Grasshoff 1977, 1981, 1982b, 1986, 1989; Carpine and Grasshoff 1985; Brito and Ocaña 2004
Paramuricea biscaya Grasshoff, 1977	1094-4152	1650- 2050		2100–2500 1200–1500	1200–1500			Specified regional depth range at the Azores and Selvagens Islands.	Grasshoff 1982a; Brito and Ocaña 2004; Molodtsova et al. 2008
Paramuricea candida Grasshoff, 1977	1069–1350	1069–1350 1069–1350						New lower depth limit for the species and at the Azores (1350m).	Txier-Durivault and D'Hondt 1974; Grasshoff 1977, Mironov and Krylova 2006
Paramuricea grayi (Johnson, 1861)	20–2195		125–2195		40-600	225-1311	40-51		Johnson 1861; Thomson 1929; Carpine and Grasshoff 1985; Grasshoff 1977, 1982a, 1986, 1989, 1992; Altuna, 1991; Brito and Ocaña 2004
<i>Paramuricea</i> aff. <i>macrospina</i> (Koch, 1882)	224–350					224-350			I
cf. Paramuricea sp. I	200					200			I
cf. Paramuricea sp. II	280-330					280-330			1
Placogorgia coronata Carpine & Grasshoff, 1975	50-2200	×	990-1000		550–1800		51	New lower and higher depth limit at the Canary Islands.	Carpine and Grasshoff 1975; Grasshoff 1977, 1981, 1985b, 1986, 1989; Brito and Ocaña 2004
Placogorgia cf. graciosa (Tixier Durivault & d'Hondt, 1974)	1100–1300					1100–1300			I
Placogorgia aff. graciosa (Tixier Durivault & d'Hondt, 1974)	1200					1200			ı

6

Species	Depth Range (m)	Azores (m)	(m) Madeira (m)	Selvagens Canary Islands (m) Islands (m)	Cape Verde Mauritania (m) (m)	fauritania (m)	Remarks	References
Placogorgia intermedia (Thomson, 1927)	800-1350	800-1350					New lower depth limit for the species and at the Azores (1350m).	Pax and Müller 1954; Tixier-Durivault and D'Hondt 1974; Grasshoff 1977, 1982a, 1985b; Carpine and Grasshoff 1985; Mironov and Krylova 2006
Placogorgia terceira Grasshoff, 1977	170–2200	599		200	1311		Specified regional depth at the Canary Islands.	Carpine and Grasshoff 1985; Grasshoff 1977, 1981, 1985a, 1985b, 1992
<i>Placogorgia</i> aff. <i>terceira</i> Grasshoff, 1977	200-1350			200	214-1350			I
Placogorgia sp. I	590-602				590-602			1
cf. <i>Placogorgia</i> sp. II	1200				1200			I
Spinimuricea atlantica (Johnson, 1862)	20875		80-84	145	875			Johnson 1862; Thomson 1927; Tixier-Durivault and D'Hondt 1974; Grasshoff 1977, 1992; Carpine and Grasshoff 1985; Brito and Ocaña 2004; Ocaña et al. 2017
Swiftia sp.	500					500		I
Swiftia cf. dubia (Thomson, 1929)	1320–1350	1320–1350 1320–1350						I
<i>Swiftia</i> aff. <i>dubia</i> (Thomson, 1929)	85					85		I
<i>Thesea talismani</i> Grasshoff, 1986	462–1090				4	462–1090		Grasshoff 1986, 1989; Matos-Pita et al 2016; Ramos et al. 2017
Thesea sp.	200				200			
Villogorgia bebrycoides (Koch, 1887)	56-845	105–845	×	63-400				Thomson 1927; Stiasny 1940; Tixier-Durivault and D 'Hondt 1974; Grasshoff 1977, 1985a, 1992; Carpine and Grasshoff 1985; Brito and Ocaña 2004

Materials and methods

The CANCAP and *Tyro* Mauritania II expeditions from 1976 until 1988 onboard HNLMS *Onversaagd*, HNLMS *Tydeman* and RV *Tyro* operated in the area at 14°31′– 39°41′N and 08°43′–39°41′W. These expeditions used a great variety of gear like trawls, dredges and van Veen grabs for the collection of biological samples, which were subsequently deposited at the NBC (Den Hartog 1984; Figures 1, 2). The electronic database of the NBC, Bioportal, was consulted for records of the Octocorallia collection resulting from these expeditions. A visit of two weeks (17–30 April 2016) allowed the first author to locate, photograph and subsample the Plexauridae gorgonians collected during the above-mentioned campaigns.

The provenance data associated with the specimens was written on original museum specimen labels, which included more information than presented in the previously published station lists (Van der Land 1987, 1988). Information on these specimen labels, which was partially unavailable at NBC's online catalogue (https://bioportal. naturalis.nl/), was consulted to build a reference database containing 15 data fields per museum sample (Table 2).

Museum scientists and technicians were consulted to clarify questions regarding the metadata or to add additional information like catalogue numbers to uncatalogued specimens. Species names and taxonomy were cross-checked using World Register of Marine Species (WoRMS) Cordeiro et al. (2019) in addition to Grasshoff (1977) and Sampaio et al. (2019) to include only valid scientific names. Unidentified specimens were identified based on the revision of the family Plexauridae (Grasshoff 1977), the original descriptions of each species of Plexauridae known to occur in the NE Atlantic Ocean, and reference material from various museums.

Specimens records were organised and plotted in ArcGIS 10.6 to visualise the geographical distribution and a depth plot was prepared to visualise the vertical distribution of the gorgonians. This data was compared with previous zoogeographical and bathymetrical distribution knowledge on Plexauridae species of the NE Atlantic (e.g., Studer 1901; Thomson 1927; Tixier-Durivault and D'Hondt 1974; Carpine and Grasshoff 1975, 1985; Grasshoff 1977, 1986, 1989; Brito and Ocaña 2004). New species records were analysed by region as well as new geographical and vertical distribution records.

Results

Biodiversity of Plexauridae from CANCAP and Tyro Mauritania II

Approximately 24 species of Plexauridae were found after studying 86 colonies, 27 fragments of gorgonians and ~24 colonies or colony fragments of gorgonians, which were sampled during the cruises of CANCAP and *Tyro* Mauritania II at the southern NE Atlantic Ocean (Tables 1, 3). The specimens were identified by the last author (M.G.) (13 species), by Dr. L.P. van Ofwegen (one species) and the first author (15 species) after the discovery of uncatalogued and unidentified specimens that were part-

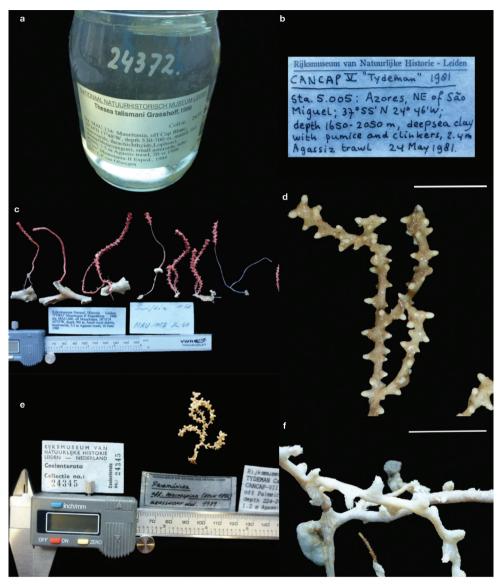


Figure 2. CANCAP and *Tyro* Mauritania II Plexauridae collection: **a** label of a catalogued record of *Thesea talismani* in Mauritania **b** label of previously unidentified and uncatalogued record from the Azores archipelago **c** different colonies of a new species from a coral garden filmed in situ in 2016 but stored in NBC since 1988 **d** cf. *Placogorgia* sp. I (RMNH. COEL. 42336) found mixed with specimens of the primnoid *Callogorgia verticillata* (Pallas, 1766) **e** the putative new record of *Paramuricea macrospina* in the NE Atlantic Ocean **f** detail of a new record for the Azores archipelago, *Paramuricea biscaya* (RMNH. COEL. 423339). Scale bars: 1 cm.

ly separated from or mixed with the catalogued species (Figures 2, 3; Table 3). Moreover, seven species were identified by two specialists (I.S. and M.G. or I.S. and L.P. van O.) (Tables 1, 3). Of the 24 plexaurid species, six lack certainty in their identification (listed as cf. or aff.) and six seem to represent species new to science (listed as sp., sp. I,

Metadata	Description
Museum Number	Museum catalogue number
Taxa	Species name
Identifier	Name of expert who identified the specimen
Expedition name	Scientific campaign in which the gorgonian was sampled
Expedition code	Scientific campaign code in which the gorgonian was sampled
Station	Station from where the gorgonian was sampled
Location	Location from where the gorgonian was sampled
Latitude	Latitude of sampling station where the gorgonian was sampled
Longitude	Longitude of sampling station where the gorgonian was sampled
Depth	Depth where the gorgonian was sampled
Substrate type	Bottom type at the location from where the gorgonian was sampled
Sampling method	Gear with which the gorgonian was sampled
Sampling date	Date in which the gorgonian was sampled
N specimens	Number of specimens covered by the catalogue number
Other notes	Other details about the specimen or sampling

Table 2. Database structure with metadata fields from museum labels of Plexauridae collected during CANCAP and *Tyro* Mauritania II expeditions in the NE Atlantic Ocean.

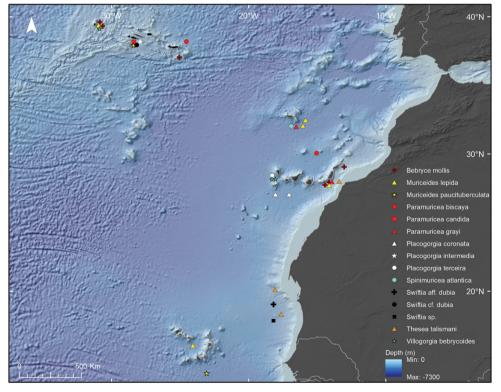


Figure 3. Map of Plexauridae collected during CANCAP and *Tyro* II Mauritania cruises except uncertain Cape Verdean records (see Figure 4).

and sp. II) (Tables 1, 3). The taxonomic description of these species will be presented in future works. The study produced 49 additional records of Plexauridae species that are mostly not encountered elsewhere in the NE Atlantic Ocean (Figures 2–5; Table 3).

Biogeography of Plexauridae from CANCAP and Tyro Mauritania II

Geographical coordinates associated with the specimens were plotted in a map of the NE Atlantic Ocean. Specimens were from all Macaronesian archipelagos, as well as from off the Mauritanian coast (Table 1; Figure 3). The Cape Verde archipelago has appeared as the region with the highest species richness (11 species in four genera) followed by the Azores archipelago where eight species of six genera were recorded, the Canary Islands (seven species in five genera), the Madeira islands (three species in three genera) and Mauritania (three species in two genera), and lastly the Selvagens Islands and Morocco (one species each) (Figures 3, 4; Table 3). The generic diversity of Plexauridae is higher in the Azores than in other NE Atlantic regions. Moreover, species identified in the Azores have a more accurate identification, especially if compared with the Cape Verde plexaurid fauna, where 11 species represent four genera but, near half of them are putative new species to science (Figures 3, 4; Table 3). The uncertainty associated with the identification of another four species from the Cape Verde islands, namely *Paramuricea* aff. *macrospina, Placogorgia* cf. *graciosa, Placogorgia* aff. *graciosa, Placogorgia* aff. *graciosa, Placogorgia* aff. *terceira*, may also represent new fauna (Figure 4; Tables 1, 3).

Specimens ancillary data has also revealed new species records. Some plexaurids are known to occur in most of the NE Atlantic basin; however, within it, the CANCAP records have widened their distribution ranges on a regional scale. Here we report *Muriceides lepida* Carpine & Grasshoff, 1975 in Madeira, Canary and Cape Verde archipelagos (Figures 3, 4; Table 1, 3) for the first time. In the Cape Verde archipelago, *Muriceides paucituberculata* (Marion, 1882), *Paramuricea* aff. *macrospina* (Koch, 1882), *Placogorgia* aff. *graciosa* (Tixier-Durivault and d' Hondt, 1974), *Placogorgia* aff. *graciosa* (Tixier-Durivault and d' Hondt, 1974), *Placogorgia* aff. *terceira* Grasshoff, 1977 are newly reported (Figures 3, 4; Tables 1, 3). *Placogorgia* aff. *terceira* was also found at the Canary Islands along with *P. terceira* (Figure 3; Tables 1, 3). Finally, *Paramuricea biscaya* Grasshoff, 1977 has its geographic distribution extended to the Selvagens Islands and the Azores (Figure 3; Tables 1, 3).

Bathymetric distribution update of Plexauridae

In terms of bathymetric distribution, the depth range of various plexaurids is now also upgraded. Overall, most species were collected from their known bathymetrical range during CANCAP (Table 1). However, three species have increased their depth range in the NE Atlantic Ocean: *Muriceides lepida* Carpine & Grasshoff, 1975, *Paramuricea candida* Grasshoff, 1977 and *Placogorgia intermedia* (Thomson, 1927) (Tables 1, 3;

Species	Collection number	N	Identifier	Scientific campaign	Station	Location	Gear	Subtrate type
Bebryce mollis Philippi, 1842	RMNH.COEL. 24337	11 fragments	Manfred Grasshoff 1989	<i>Tjdeman</i> Canary Islands – CANCAP II	2.004, 28°03'N, 14°29'W, 180–330 m	Canary Islands, S of Fuerteventura, Punta de Jandia	rectangular dredge	epifauna of mixed bottom
	RMNH.COEL. 24338	6 specimens/ fragments	Manfred Grasshoff 1989	<i>Tjdeman</i> Canary Islands – CANCAP II	2.014, 28°03'N, 14°29'W, 200 m	Canary Islands, S of Fuerteventura, Punta de Jandia	rectangular dredge	many sponges, other epizoa
	RMNH.COEL. 24339	3 fragments	Manfred Grasshoff 1989	Tydeman Azores – CANCAP V	5.010, 37°41'N, 25°31'W, 150 m	Azores, S of São Miguel	van Veen grab	coarse sand, gravel, calcareous stones
	RMNH.COEL. 24340	4 specimens/ fragments	Manfred Grasshoff 1989	Tydeman Azores – CANCAP V	5.153, 39°26'N, 31°06'W, 150–168 m	Azores, E of Flores	rectangular dredge	chama bed with fossil shells
	RMNH.COEL. 24341	7 specimens/ fragments	Manfred Grasshoff 1989	Tydeman Azores – CANCAP V	5.166, 39°30'N, 31°06'W, 150 m	Azores, NE of Flores	rectangular dredge	shells
	RMNH.COEL. 42337	1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Selvagens-Canary Islands – CANCAP IV	4.096, 29°08'N, 13°25'W, 125 m	Canary Islands, E of Lanzarote	rectangular dredge	I
<i>Muriceides</i> <i>lep ida</i> Carpine & Grasshoff, 1975	RMNH.COEL. 24357	3 specimens	Manfred Grasshoff 1989	<i>Onversaagd</i> Madeira- Marokko – CANCAP I	1.104, 32°37'N, 16°49'W, 400 m	S of Madeira	triangular and rectangular dredge	I
	RMNH.COEL. 24358	1 specimen	Manfred Grasshoff 1989	<i>Tydeman</i> Canary Islands – CANCAP II	2.004, 28°03'N, 14°29'W, 180–330 m	Canary Islands, S of Fuerteventura, Punta de Jandia	rectangular dredge	epifauna of mixed bottom
	RMNH.COEL. 24359	1 specimen	Manfred Grasshoff 1989	<i>Tydeman</i> Madeira- Mauritania – CANCAP III	3.054, 32°43'N, 16°44'W, 300–320m	SE Madeira	rectangular dredge	I
	RMNH.COEL. 24360	2 specimens	Manfred Grasshoff 1989	Tydeman Azores – CANCAP V	5.187, 39°27'N, 31°05'W, 500–550 m	Azores, E of Flores	rectangular dredge	fossil corals
	RMNH.COEL. 24361	2 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VI	6.096, 16°36'N, 24°39'W, 1000–1350 m	Cape Verde Islands, SW of Razo	rectangular dredge	rocky bottom with epifauna
Muriceides paucituberculata (Marion, 1882)	RMNH.COEL. 24356	3 specimens, 1 fragment	Manfred Grasshoff 1989	Tydeman Azores – CANCAP V	5.090, 38°09'N, 28°31'W, 1320–1350 m	Azores, S of Pico	1.2 m Agassiz trawl	hard bottom with fossil corals
	RMNH.COEL. 24376	7 fragments	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.026, 14°52'N, 23°33'W, 515 m	Cape Verde Islands, S of Santiago	1.2 m Agassiz trawl	I

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Species	Collection number	z	Identifier	Scientific campaign	Station	Location	Gear	Subtrate type
Paramuricea biscaya Grasshoff, 1977	RMNH.COEL. 24342	3 specimens	Manfred Grasshoff 1989	<i>Tjdeman</i> Selvagens-Canary Islands – CANCAP IV	4.107, 30°03'N, 15°52'W, 2100–2500 m	Selvagens archipelago	2.4 m Agassiz trawl	I
	RMNH.COEL.42339	1 specimen	Íris Sampaio 2018	Tydeman Azores – CANCAP V	5.005, 37°55'N, 24°46'W, 1650–2050 m	Azores, NE of São Miguel	2.4 m Agassiz trawl	deep sea clay with pumice and clinkers
Paramuricea candida Grasshoff, 1977	RMNH.COEL. 24343	3 specimens, a few fragments	Manfred Grasshoff 1989	Tydeman Azores – CANCAP V	5.090, 38°09'N, 28°31'W, 1320–1350 m	Azores, S of Pico	1.2 m Agassiz trawl	hard bottom with fossil corals
Paramuricea grayi (Johnson, 1861)	RMNH.COEL. 17911	2 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Canary Islands – CANCAP II	2.047, 28°11'N, 14°02'W, 100–125 m	Canary Islands, SE of Fuerteventura, Punta de Gran Tarajal	1.2 m Agassiz trawl	mixed bottom
	RMNH.COEL.17912	1 specimen	Manfred Grasshoff 1989	<i>Onversaagd</i> Madeira- Marokko – CANCAP I	1.094, 32°39'N, 16°49'W, 125–150 m	S of Madeira	triangular dredge	mainly shells and shell agglomerates
Paramuricea aff. macrospina (Koch, 1882) *	RMNH.COEL. 24344	1 specimen	Manfred Grasshoff 1989	<i>Tjdeman</i> Cape Verde Islands – CANCAP VII	7.172, 16°53'N, 25°07'W, 300–350 m	Cape Verde Islands, W of São Vicente, canal of São Vicente	rectangular dredge	small catch
	RMNH.COEL. 24345	2 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.113, 16°42'N, 23°01'W, 224–248 m	Cape Verde Islands, W of Sal, off Palmeira	1.2 m Agassiz trawl	calcareous nodules
cf. Paramuricea sp. I #	RMNH.COEL. 42372	1 specimen	Íris Sampaio 2018	<i>Tjydeman</i> Cape Verde Islands – CANCAP VII	7.171, 16°54'N, 25°06'W, 200 m	Cape Verde Islands, W of São Vicente, canal of São Vicente	rectangular dredge	no sediment, only epizoa
cf. Paramuricea sp. II #	RMNH.COEL. 42344	2 specimens, 3 fragments	Íris Sampaio 2018	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.179, 16°58'N, 25°03'W, 280–330 m	Cape Verde Islands, W of São Vicente, canal of São Vicente	3.5m Agassiz trawl	sponges and soft corals
Placogorgia coronata Carpine & Grasshoff, 1975	RMNH.COEL. 24347	1 specimen	Manfred Grasshoff 1989	<i>Tjdeman</i> Canary Islands – CANCAP II	2.131, 27°40'N, 18°10'W, 1200–1800 m	Canary Islands, SW of Hierro, off Punta de Orchilla	1.2 m Agassiz trawl	I
	RMNH.COEL. 24348	1 specimen	Manfred Grasshoff 1989	<i>Tjdeman</i> Canary Islands – CANCAP II	2.162, 27°35'N, 17°59'W, 550–800 m	Canary Islands, S of Hierro, off Punta de la Restinga	rectangular dredge	volcanic rocks
<i>Placogorgia</i> cf. <i>graciosa</i> (Tixier Durivault & d'Hondt, 1974) *	RMNH.COEL. 42341	1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Cape Verde Islands – CANCAP VI	6.049, 14°52'N, 24°32"W, 1100–1300 m	Cape Verde Islands, SW of Fogo	Agassiz trawl	basaltic rocks and sandy clay
<i>Placogorgia</i> aff. <i>graciosa</i> (Tixier Durivault & d'Hondt, 1974) *	RMNH.COEL. 42342	3 specimens/ fragments	fris Sampaio 2018 (unknown identifier of the genus level)	Tydeman Cape Verde Islands – CANCAP VII	7.140, 16°35'N, 24°36'W, 1200 m	7.140, 16°35'N, 24°36'W, Cape Verde Islands, S of Razo 1200 m	rectangular dredge	old lobster spot with about 500m nylon rope, with numerous epizoa

Natural history collections as a basis for sound biodiversity assessments...

Species	Collection number	Z	Identifier	Scientific campaign	Station	Location	Gear	Subtrate type
Placogorgia intermedia (Thomson, 1927)	RMNH.COEL. 24349	1 specimen, 2 fragments	Manfred Grasshoff 1989	Tjdeman Azores – CANCAP V	5.090, 38°09'N, 28°31'W, 1320–1350 m	Azores, S of Pico	1.2 m Agassiz trawl	hard bottom with fossil corals
Placogorgia terceira Grasshoff, 1977	RMNH.COEL. 42369	1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Selvagens-Canary Islands – CANCAP IV		4.153, 28°38'N, 17°59'W, Canary Islands, SW of Palma 200 m	1.2m Agassiz trawl	I
Placogorgia aff. terceira Grasshoff, 1977 *	RMNH.COEL. 42370	1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Selvagens-Canary Islands – CANCAP IV		4.153, 28°38'N, 17°59'W, Canary Islands, SW of Palma 200 m	1.2 m Agassiz trawl	I
	RMNH.COEL. 24350	2 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VI	6.096, 16°36'N, 24°39'W, 1000–1350 m	Cape Verde Islands, SW of Razo	rectangular dredge	rocky bottom with epifauna
	RMNH.COEL. 24351	5 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VI	6.021, 15°01'N, 23°44'W, 600–400 m	Cape Verde Islands, W of São Tiago	rectangular dredge	mud and basalt rocks
	RMNH.COEL. 24352	2 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.041, 14°57'N, 24°38'W, 580 m	Cape Verde Islands, E of Cima	1.2 m Agassiz trawl	gorgonians and sponges
	RMNH.COEL. 24353	1 specimen	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.052, 15°06'N, 23°15'W, 594 m	Cape Verde Islands, SW of Maio	van Veen grab	practically no sediment
	RMNH.COEL. 24354	1 specimen	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.136, 16°33'N, 24°17'W, 214 m	Cape Verde Islands, SE of São Nicolau, off Preguiça	rectangular dredge	calcareous nodules/algae
	RMNH.COEL. 24355	2 specimens	Manfred Grasshoff 1989	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.174, 16°45'N, 25°07'W, 1070- 1130 m	Cape Verde Islands, SW of São Vicente	1.2 m Agassiz trawl	basaltic gravel with echinoderms
	RMNH.COEL. 42345 RMNH.COEL. 42371	1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.179, 16°58'N, 25°03'W, 280–330 m	Cape Verde Islands, W of São Vicente, canal of São Vicente	3.5 m Agassiz trawl	sponges and soft corals
Placogorgia sp. 1 #	RMNH.COEL. 42336	1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.131, 16°32'N, 24°16'W, 590-602 m	Cape Verde Islands, SE of São Nicolau	1.2 m Agassiz trawl	muddy bottom with gorgonids and sponges
cf. Placogorgia sp. 11 #	RMNH.COEL. 42371	1 specimen	fris Sampaio 2018 (unknown identifier of the genus level)	<i>Tjdtman</i> Cape Verde Islands – CANCAP VII	7.140, 16°35'N, 24°36'W, 1200 m	7.140, 16°35'N, 24°36'W, Cape Verde Islands, S of Razo 1200 m	rectangular dredge	old lobster spot with about 500m nylon rope, with numerous epizoa
Spinimuricea atlantica (Johnson, 1862)	RMNH.COEL. 17910	Specimen not located	I	<i>Onversaagd</i> Madeira- Marokko – CANCAP I	1.092, 32°39'N, 16°50'W, 80–84 m	S of Madeira	rectangular dredge	corals (mainly dead) and shells
Swiftia sp. #	RMNH.COEL. 42327 RMNH.COEL. 42328 RMNH.COEL. 42329 RMNH.COEL. 42329	11 specimens	Genus level: Manfred Grasshoff. Íris Sampaio is describing the new species.	<i>Tjro</i> Mauritania II	MAU 040, 18°51'N, 16°53'W, 500 m	off Mauritania	3.5 m Agassiz trawl	fossil coral debris, macrourids

Collection number	Z	Identifier	Scientific campaign	Station	Location	Gear	Subtrate type
RMNH.COEL. 42340) 3 specimens	Genus level: Manfred Grasshoff 1989; Species level: Íris Sampaio 2018	Tjdeman Azores – CANCAP V	5.090, 38°09'N, 28°31'W, 1320–1350 m	Azores, S of Pico	1.2 m Agassiz trawl	hard bottom with fossil corals
RMNH.COEL. 42374	4 1 specimen	Íris Sampaio 2018	<i>Tydeman</i> Madeira- Mauritania – CANCAP III	3.158, 19°22'N, 16°51'W, 85 m	off Mauritania	2.4 m Agassiz trawl	hard bottom, sponges, brown algae
RMNH.COEL. 24371	l l specimen	L.P. van Ofwegen	<i>Tyro</i> Mauritania II	MAU 041, 18°51'N, 16°56'W, 800–840 m	off Mauritania	3.5 m Agassiz trawl	muddy bottom, tubeworms, asteroids, red shrimp
RMNH.COEL. 24372	2 3 specimens	L.P. van Ofwegen	<i>Tyro</i> Mauritania II	MAU 134, 20°44'N, 17°48'W; depth 530–700 m	Mauritania, off Cap Blanc	3.5 m Agassiz trawl	mainly fish (macrourids, thrachichthyids, <i>Lophius</i>), shrimp, asteroids, tube worms
RMNH.COEL. 42373	3 2 specimens	Íris Sampaio 2018	<i>Tydeman</i> Canary Islands – CANCAP II	2.058, 27°58'N, 13°24'W, 500 m	Morocco, W of Cape Yubi	5 m beam trawl	muddy bottom
RMNH.COEL. 42343	3 4 specimens/ fragments	Íris Sampaio 2018	<i>Tydeman</i> Cape Verde Islands – CANCAP VII	7.171, 16°54'N, 25°06'W, C 200 m	Cape Verde Islands, W of São Vicente, canal of São Vicente	rectangular dredge	no sediment, only epizoa
RMNH.COEL. 24370	3 specimens	Manfred Grasshoff	Tjdeman Azores – CANCAP V	5.153, 39°26'N, 31°06'W, 150–168 m	Azores, E of Flores	rectangular dredge	chama bed with fossil shells
RMNH.COEL. 42338	3 3 specimens	Íris Sampaio 2018	<i>Tydeman</i> Selvagens-Canary Islands – CANCAP IV	4.153, 28°38'N, 17°59'W, Canary Islands, SW of Palma 200 m	Canary Islands, SW of Palma	1.2 m Agassiz trawl	
RMNH.COEL. 42346	5 7 specimens	Íris Sampaio 2018	<i>Tydeman</i> Selvagens-Canary Islands – CANCAP IV	4.143, 28°38'N, 17°58'W, Canary Islands, SW of Palma 110–86 m	Canary Islands, SW of Palma	rectangular dredge	muddy bottom with oysters

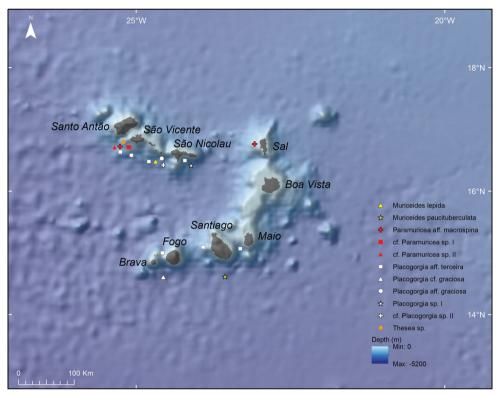


Figure 4. Map of Plexauridae collected during Tydeman Cape Verde Islands - CANCAP VI and VII cruises.

Figure 5). *Muriceides lepida*, previously reported to live at 79–718 m depth (Carpine and Grasshoff 1975) is now reported at its deeper record from 1000–1350 m depth at the Cape Verde archipelago (Tables 1, 3; Figures 4, 5). *Paramuricea candida* Grasshoff, 1977 known to inhabit the range of 1069–1235 m depth (Tixier-Durivault and D'Hondt 1974; Grasshoff 1977) is now known to live down to 1350 m depth (Tables 1, 3; Figure 5). The same new high depth record of 1350 m depth is herein reported for *P. intermedia*, previously known to occur between 800–1235 m depth (Tixier-Durivault and D'Hondt 1974; Grasshoff 1977) (Tables 1, 3; Figure 5). Also, if *Paramuricea* aff. *macrospina* is in fact *P. macrospina*, this species widens its geographical distribution as it expands its greater depth limit to 350 m in the NE Atlantic Ocean (Cape Verde islands) (Tables 1, 3; Figures 4, 5). So far it is only known to occur at the Mediterranean, where it lives at 38–200 m depth (Carpine and Grasshoff 1975; Grasshoff 1977).

While the overall depth range has increased for three species, the vertical distribution range has increased or has been specified at a regional level in eight of the species identified with certainty. The exceptions are *Villogorgia bebrycoides* (Koch, 1887), *Paramuricea grayi* (Johnson, 1861), *Spinimuricea atlantica* (Johnson, 1862) and *Thesea talismani* Grasshoff, 1986 (Table 1). Considering the available data and the new records (Carpine and Grasshoff 1975; Grasshoff 1977, 1981, 1985a), we now know *M. lepida*'s specific depth ranges at the Azores, Madeira, Canary and Cape Verde archipelagos (Tables 1, 3; Figures 3, 5). In the Azorean archipelago, three species have

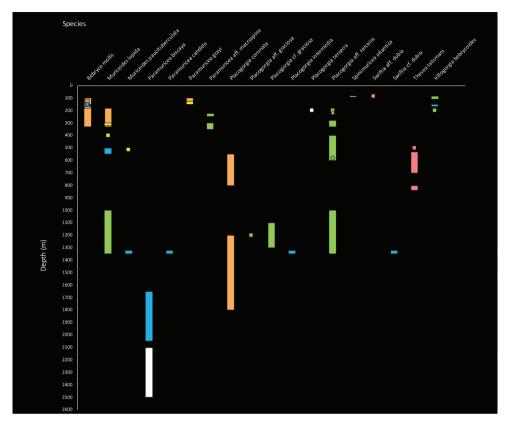


Figure 5. Bathymetric distribution of Plexauridae identified to species at different sampling stations of CANCAP and *Tyro* Mauritania II cruises on the NE Atlantic Ocean. Symbols represent precise records while bars represent distribution ranges. Colours represent distinct regions: Azores (blue), Madeira (yellow), Selvagens (white), Canary Islands (orange), Cape Verde (green) and Mauritania (rose).

increased their greater depth limit to 1350 m: *M. paucituberculata, P. candida* and *P. intermedia* (Pax and Müller 1954; Tixier-Durivault and D'Hondt 1974; Grasshoff 1977) (Tables 1, 3; Figure 5). There is a new depth record of *P. biscaya* from 1650–2050 m (Table 1, Figure 5). In Madeira is presently known that *M. lepida* occurs at 300–400 m depth and that *P. biscaya* occurs at Selvagens between 2100 and 2500 m depth (Table 1, Figure 5). At Canary Islands, *Bebryce mollis* Philippi, 1842 has a greater depth limit at 330 m (Brito and Ocaña 2004) (Tables 1, 3; Figure 5). Moreover, *P. coronata* has increased its regional depth range from 1200 m to 550–1800 m depth (Brito and Ocaña 2004) (Tables 1, 3; Figure 5). Also, *M. lepida* is now known to occur between 180 and 320 m depth and *P. terceira* at 200 m depth (Table 1, Figure 5).

In the Cape Verde archipelago, *M. lepida* has a record between 1000 and 1350 m depth and *M. paucituberculata* at 515 m depth (Tables 1, 3; Figures 4, 5). Moreover, there are many depth records at the archipelago with taxonomic uncertainty (Table 1). Lastly, at Mauritania *M. paucituberculata* is present at 51 m depth, *Swiftia* aff. *dubia* (Thomson, 1929) at 85 m depth and a new species of *Swiftia* sp. at 500 m depth (Tables 1, 3; Figure 5).

Discussion

CANCAP and *Tyro* Mauritania II are the 20th Century's most comprehensive scientific expeditions after the earlier campaigns of Prince Albert I of Monaco in the Northeast Atlantic Ocean (Sampaio et al. 2019). By visiting NBC and examining the octocoral specimens collected during the CANCAP and *Tyro* Mauritania II expeditions, reliable and new taxonomic records were discovered, and a complete dataset was built based on the specimens and their labels in the museum collection. The value of handwritten specimen labels cannot be overstated considering the history they harbour on the collection and collector. Fortunately, most labels are still preserved with specimens or stored in special files of NHMC. While 131 specimens/fragments were photographed and subsampled for future taxonomic studies, the auxiliary data consulted from labels was compiled in a database used to map the geographic distributions and depth ranges of various Plexauridae (Table 2; Figures 2, 3, 4). Some records were already published or are available on the Bioportal database (Grasshoff 1992; Braga-Henriques et al. 2013). However, this is the first complete inventory of Plexauridae collected during the NBC campaigns.

The Plexauridae collected during these expeditions led to reference specimens of 12 species and new records of 24 species (Table 3). It also led to the discovery of – six putative new species in Mauritania and Cape Verde archipelago, representing an increased sampling effort applied to previously unexplored subtropical NE Atlantic areas (Van der Land 1987, 1988, Figures 3, 4). Future taxonomic investigations will clarify the taxonomic assignment of some of the specimens, e.g., *Placogorgia* aff. *terceira*, which can either represent new fauna or new records of known fauna. Provenance data stored with specimens in this NHMC have produced an extended geographical distribution range for six plexaurid species in the Cape Verde islands, three in the Canary islands, and one each in the Azores and Selvagens Islands (Figures 3, 4). Moreover, they increased the knowledge on the bathymetric distribution of three species at the NE Atlantic scale but also of eight species within each Macaronesian archipelago (Figure 5).

Reference material for comparisons with recently collected specimens in taxonomic studies, new species and new records of Plexauridae within the NE Atlantic Ocean would have not been possible without examination of the material at Leiden and assistance from museum scientists and technicians. Moreover, clarification on data incongruences and the discovery of uncatalogued records at the NHMC has provided the museum with new data to be updated and made available to scientists (e.g., *Villogorgia bebrycoides* RMNH. COEL. 42338; Table 3). Without examination of museum material, uncatalogued specimens would not have been identified, mapped and made available for future studies.

Henceforth, the present study has provided a more complete inventory of Plexauridae diversity in six regions of the NE Atlantic based on material at NBC that was collected 40 years earlier. This new knowledge will provide an important biodiversity baseline of the species occurring in the NE Atlantic, which will enable the detection of changes in species diversity and composition due to recent anthropogenic and climate change impacts.

Biodiversity of NE Atlantic Plexauridae

The CANCAP and *Tyro* Mauritania II expeditions collected 15 species of the known Plexauridae through the southern NE Atlantic Ocean, representing 62.5 % of the 24 described species known to occur in this area (Grasshoff 1977, 1986, 1992; Table 3). Only the genus *Dentomuricea* was not represented in these samples. This taxon is known from the Great Meteor complex of seamounts and its known biotopes in the Azores that were not visited by the Dutch expeditions. Nonetheless, some species are still missing a definite taxonomic status, meaning that so far only 12 of the 15 identified species can be used as reference records for future studies. If *Paramuricea* aff. *macrospina* is indeed *P. macrospina*, the most expressive extension of the geographical species is here reported. This species was known as endemic to the Mediterranean Sea and therefore this may represent its first report in the NE Atlantic at the Cape Verde archipelago (Carpine and Grasshoff 1975; Table 2, Figure 4).

New regional records were found in distinct Macaronesian archipelagos. While the easier taxonomic assignments were found in Azorean specimens, the most difficult were found in Cape Verdean specimens (Figures 3, 4). Easier taxonomic assignments were found in Azorean specimens due to the higher deep-sea exploration and the effort in octocoral taxonomy within the region (Sampaio et al. 2019). Nonetheless, difficult taxonomic assignments were found for the Cape Verdean specimens due to the lack of knowledge on octocoral diversity of that archipelago (Figures 3, 4). The sampling and research effort of Azorean octocorals is much higher than those in other southern areas of the NE Atlantic Ocean, like Cape Verde, which explains why the octocoral fauna of those areas is mostly unknown (Pérez et al. 2016; Sampaio et al. 2019). As expected based on previous knowledge for the area, Azorean CANCAP plexaurids have a high species and genus richness and have revealed a new record for the region (Sampaio et al. 2019). Paramuricea biscaya has its type locality in the Gulf of Biscaya, and was further mentioned to occur in Tenerife, Canary Islands, the Mid-Atlantic Ridge and the Gulf of Mexico (Grasshoff 1977, 1985; Brito and Ocaña 2004; Molodtsova et al. 2008; Thoma 2013). Therefore, we know now that more than 50% of the Plexauridae species of the NE Atlantic inhabit the Azorean marine waters (Sampaio et al. 2019). Herein, we also report the first record of *P. biscaya* for Selvagens Islands (Table 3; Figures 2, 3). In the Canary Islands we raise the number of plexaurid octocorals from seven to ten with three new records for the archipelago according to previous data (Brito and Ocaña 2004): Muriceides lepida, Placogorgia coronata and P. terceira (Table 3; Figure 3).

Despite some sparse records found in the taxonomic literature (e.g., *Acanella arbuscula* (Johnson, 1862)) and a vast number of gorgonians mentioned for the area, no thorough revision of Octocorallia of Cape Verde was completed at this point (Molodtsova et al. 2008; Raddatz et al. 2011; Hansteen et al. 2014). In this study we report the highest number of species of Plexauridae collected in this archipelago, reflecting the two *Tydeman* expeditions that exclusively explored this area: Cape Verde islands CANCAP VI and CANCAP VII (Table 3; Figure 4). Moreover, two newly recorded species are reported for the archipelago with certainty, *Muriceides lepida* and *M. paucituberculata*, and three are still considered uncertain records

Paramuricea aff. *macrospina*, *Placogorgia* aff. *graciosa* and *Placogorgia* cf. *graciosa*. Aditionally, in this archipelago, there are five species that seem to be new to science and are in need of further taxonomic investigation (Figures 2, 4; Table 3).

As undescribed marine species are commonly found in museum collections (Appeltans et al. 2012), also a sixth new species was discovered on the shelves of this NHMC (Sampaio et al., personal observation). After observing the samples and videos collected during the German expedition MSM 16/3 in 2010, the first author, in 2016, discovered that a new species of the genus *Swiftia* was preliminarily collected during the *Tyro* Mauritania II expedition in 1988 and identified until the genus level by the senior author (M.G.). Also from Mauritania, *Thesea talismani*, was reported as a new record for this location in 2016 based on the same German expedition and two Spanish expeditions Maurit-0911 and Maurit-1011 (Matos-Pita et al. unpublished data). However, it had been also sampled in 1988, identified and stored at NBC (Table 2; Figures 2a, 3).

Plexaurid species are commonly found forming coral ecosystems of high density (e.g., *Dentomuricea meteor* at the plateau of Great Meteor seamount) (Grasshoff 1977; Tempera et al. 2013). The existence of multiple colonies under a single museum collection number indicate that the colonies were collected during a single sampling event and may be present at the seafloor in high densities such as octocoral gardens. For example, 11 specimens of *Bebryce mollis* were collected at Punta de Jandia, South of Fuerteventura (Canary Islands) and 11 specimens of a new species of *Swiftia* sp. were sampled off Mauritania, potentially indicating coral garden communities dominated by these species in each area (Table 3).

Biogeography of NE Atlantic Plexauridae

Zoogeographical regions of the North Atlantic Ocean have clustered for deep-sea Scleractinia by Cairns and Chapman (2001) and were further adapted for deep-sea corals in general and octocorals in particular (Watling et al. 2011; Braga-Henriques et al. 2013). These studies cluster species known from the Mediterranean Sea with NE Atlantic species of the Lusitanian region which are denominated as Lusitanian-Mediterranean species. Therefore, the majority of the species of this study (twelve) would be considered exclusively Lusitanian-Mediterranean (IIIA) while three, *Paramuricea biscaya, Paramuricea grayi* and *Spinimuricea atlantica*, would inhabit also the New England and Corner seamounts, Bermuda (IIC) (Watling et al. 2011; Table 4). *P. biscaya* is also known from the Gulf of Mexico (Thoma 2013). This would be in accordance with the trend found for the Azorean Alcyonacea, where most species are Lusitanian-Mediterranean (Braga-Henriques et al. 2013).

Nonetheless, if we consider the regions defined by Grasshoff (1977) for the Paramuriceidae (now Plexauridae) and take into account the boundary he suggested between the gorgonians of the NE Atlantic Ocean and the Mediterranean Sea, then six species of the 12 known Plexauridae species identified here are exclusively inhabitants of the NE Atlantic Ocean (Table 4). *Muriceides paucituberculata* and *Placogorgia graciosa* are widespread and live from the temperate waters in Ireland to the tropical waters of the West coast of Africa. *Placogorgia terceira* occurs on the vicinity of the Tropic of Cancer, between temperate and tropical waters of the southern NE Atlantic Ocean, while two species are uniquely known from the Azores, namely *Paramuricea candida* and *Placogorgia intermedia*. *Thesea talismani* is exclusive to the west coast of Africa (Grasshoff 1977, 1986). All the new putative species are exclusively known to inhabit the southern NE Atlantic Ocean, with *Swiftia* sp. only found in the West of Africa.

Six plexaurid species from the CANCAP records live in the "natural whole" (Ekman, 1935), the NE Atlantic Ocean (Lusitanian, Moroccan, Mauritanian and Macaronesian territories) and Mediterranean region, representing all five species mentioned by Grasshoff (1977) plus *Paramuricea* aff. *macrospina*. Here this species is mentioned as being located in the NE Atlantic Ocean; however, this record needs to be considered carefully, as explained above. Moreover, *Paramuricea biscaya*, *P. grayi*, and *Spinimuricea atlantica* are amphi-Atlantic (Watling et al. 2011; Table 4).

The distribution of marine invertebrates is highly influenced by oceanographic conditions (Ansín-Agís et al. 2001). Several oceanic currents and different climates influence the Macaronesian archipelagos (Amorim et al. 2017). The Equatorial countercurrent, for example, seems to influence the distribution of scleractinian corals in the deep sea. Scleractinian corals at the Canary Islands, a warm temperate area, cluster together with corals from Cape Verde archipelago at the tropics. Additionally, Scleractinia from temperate areas like the Azores and Madeira archipelagos make up the large cluster of the Lusitanian Province (Cairns and Chapman 2001). However, NE Atlantic plexaurid octocorals seem to be more influenced by the climate. Further taxonomy

Species	Zoogeographical Affinity I	Zoogeographical Affinity II
Bebryce mollis	NEA & MS	IIIA
Muriceides lepida	NEA & MS	IIIA
Muriceides paucituberculata	NEA	IIIA
Paramuricea biscaya	AA	IIIA & IIC
Paramuricea candida	NEA	IIIA
Paramuricea grayi	AA	IIIA & IIC
Paramuricea aff. macrospina	NEA & MS	IIIA
Placogorgia coronata	NEA & MS	IIIA
Placogorgia cf. graciosa; P. aff. graciosa	NEA	IIIA
Placogorgia intermedia	NEA	IIIA
Placogorgia terceira; P. aff. Terceira	NEA	IIIA
Spinimuricea atlantica	AA	IIIA
Swiftia cf. dubia; Swiftia aff. dubia	NEA & MS	IIIA
Thesea talismani	NEA	IIIA
Villogorgia bebrycoides	NEA & MS	IIIA

Table 4. Zoogeographical affinities of the Plexauridae species from CANCAP and *Tyro* Mauritania II expeditions. Abbreviations: I based on Grasshoff (1977); AA: amphi-Atlantic, MS: Mediterranean Sea and NEA: Northeast Atlantic; II based on Cairns and Chapman (2001) and Watling et al. (2011); IIIA: Lusitanian-Mediterranean; IIC: New England and Corner Seamounts, Bermuda.

and biogeographical analyses need to be done in order to make conclusive comments. Notwithstanding, the plexaurid species of the Canary Islands are also present at the Madeira and Azores archipelagos, while the new putative plexaurid octocoral species of Cape Verde indicate a distinction between species in temperate cold deep-sea waters and those at cold deep-sea tropical climates.

Depth zonation of NE Atlantic Plexauridae

The present study has altered the known bathymetrical distribution ranges of a few plexaurid octocorals in the NE Atlantic (Figure 5). One species, Paramuricea aff. macrospina, had its depth range increased by 150 m and is now known from the upper mesophotic to the upper bathyal (40-350 m depth) (Grasshoff 1977). Spinimuricea atlantica (20–875 m), Villogorgia bebrycoides (63–845 m), Bebryce mollis (71–1250 m) and Muriceides lepida (80-1350 m), the last with its depth range increased by 650 m, inhabit the lower sublittoral down to the bathyal (Stiasny 1940; Tixier-Durivault and D'Hondt 1974; Carpine and Grasshoff 1975; Grasshoff 1977, 1985, 1992; Brito and Ocaña 2004). Species exclusively inhabiting the bathyal zone are Thesea talismani (462-1090 m), Placogorgia cf. graciosa (769-1300 m), which increased its depth range by 360 m, Placogorgia intermedia (800-1400 m), increasing its depth by 285 m, and *Paramuricea candida* with an additional 165 m (1069–1400 m depth) (Tixier-Durivault and d'Hondt 1974; Grasshoff 1977, 1985; Alvarez-Claudio 1993; Matos-Pita et al. unpublished data). Moreover, five species are eurybath having ranges from sublittoral or mesophotic depths until upper abyssal depths: Muriceides paucituberculata (51–2100 m), Paramuricea gravi (20–2195 m), Placogorgia coronata (50–2080 m), Swiftia aff. dubia (10–2400 m), and Placogorgia terceira (170–3200 m) (Grasshoff 1977, 1981, 1985, 1989; Altuna et al. 2010). Finally, the deepest plexaurid of the NE Atlantic is Paramuricea biscaya (1200-4152 m), an inhabitant of bathyal and abyssal depths (Brito and Ocaña 2004; Molodtsova et al. 2008).

The importance of natural history museum collections for deep-sea research

Natural history museum collections harbour long-term biodiversity collection data. Museum data collected over time are prone to being incomplete (e.g., by lacking geographic locality information) (Soberón and Peterson 2004; Ross et al. 2012). Therefore, NHMC data are often overlooked in marine biodiversity assessments. CANCAP geo-referenced records from the 1970s and 80s have a low position accuracy in comparison with precise records sampled with modern submersibles and remote operated vehicles (ROVs) (see for example Englebert et al. 2015; Hoeksema et al. 2017). Most samples from the Dutch expeditions were collected by dredges and trawls which operated through transects, while only a single point position was recorded for each sampling location, detailing coordinates exclusively in degrees and minutes (Table 3). While digitisation is improving museum data quality and standardisation, it is still essential to visit NHMC in order to have an accurate source of information on specific taxa (Roy and Gagnon 2016). Yet, even when having access to all the data available in NHMC, there are some problems to sort out. For example, among the octocorals deposited in NBC collected during CANCAP and *Tyro* Mauritania II expeditions, some specimens were not yet catalogued, other specimens were mixed with specimens from a different family of octocorals having the same catalogue number for different taxa and, a specimen of *Spinimuricea atlantica*, present on Bioportal, could not be located in the museum at present time.

Similar concerns can be raised by mapping published species records without checking the original record and its auxiliary information (Ross et al. 2012). Unvouchered records can be easily misidentified without proper local taxonomic knowledge or observable taxonomical characters essential to identify the species (Henry and Roberts 2013). In consequence, poor quality data can be used in studies that model distribution of species and may lead to overestimation of their putative distributions (Davies and Guinotte 2011; Bullimore et al. 2013; Henry and Roberts 2013). Unvouchered records in deep-sea ecology studies need to be identified with care, particularly if plexaurid octocorals are present. Plexaurids are extremely diverse and difficult to identify in video transects and in situ images, despite high definition and highly magnified imagery. Colony morphology is not the main distinctive taxonomic feature of most octocorals, including the Plexauridae. Consequently, some plexaurid species identification based on imagery can be easily mistaken as species of different families like Acanthogorgiidae and Gorgoniidae when the sclerome of the specimens is not analysed.

Even when a specimen is available, plexaurids have a remarkable and little studied variability of their sclerites, which hampers an easy identification and description of new species (Grasshoff 1977). Moreover, genetic markers currently used in the DNA barcoding of octocorals are not as effective as it would be desirable to discriminate at species level. Notwithstanding, currently it is important to consider genetics when describing new octocoral species and their cryptic diversity (Breedy and Guzman 2011; Reijnen et al. 2014). Museum specimens, when suitable for genetics, may be used to sequence vouchered reference DNA barcodes (Morín et al. 2019). Antique octocoral reference samples can be compared with recently collected samples like some of the CANCAP and *Tyro* Mauritania II Plexauridae, which were already sequenced with this goal.

Deep-sea exploration is expensive and constrained to specific areas of the vast, unexplored and difficult to sample deep sea. Likewise, deep-sea sampling cruises are limited to specific sampling gears and determined depth strata. Therefore, locations where well-curated deep-sea specimens are well identified and stored through decades, or even centuries, represent inestimable access to baseline knowledge on deep-sea biodiversity. NHMC with type and reference octocoral deep-sea specimens are money savers because they decrease the need of much new expensive and time-consuming fieldwork (Suarez and Tsutsui 2004). Museum records already proved to be useful for cold-water scleractinian reef building species off the southeastern United States and for Canadian Arctic marine benthos distribution based on online databases, selected publications and visits to museums (Ross et al. 2012; Roy and Gagnon 2016). Besides, CANCAP deep-sea plexaurids represent high standard accounts for this family because their identification was made by leading experts on taxonomy of gorgonians. Additionally, they increase the knowledge on Plexauridae, a neglected but important octocoral family, with many structural species which form vulnerable marine habitats. Therefore, visits to NHMC should be encouraged to greatly increase known biodiversity, to gather reference samples with credible taxonomic status and auxiliary data associated to specimens. Visits to museums are also essential to correct errors that are hampering the accessibility to this knowledge.

More value needs to be given to NHMC like the Octocorallia collection stored at NBC. Reliability on taxonomic knowledge, which is fundamental for the quality of the following biological knowledge, is dependent on NHMC (Suarez and Tsutsui 2004). Contemporary biodiversity studies rely on the 300 years of historical research deposited in museums to have accurate knowledge on species distribution and their changes under anthropogenic pressures and climate change (Roy and Gagnon 2016). This is particularly true for deep-sea invertebrates for which there is little taxonomical knowledge, especially in unexplored geographical areas. In some cases, like the Plexauridae from Cape Verde islands herein mentioned, NHMC store the unique existing data (Graham et al. 2004; Funk 2018).

Still, many countries have no or very limited funding for taxonomy, their natural history museums have limited personal to curate and investigate collections, there are shifts in the scientific focus of NHC towards molecular studies and a trend in the scientific community in publishing biodiversity studies based on unvouchered records (Kemp 2015; Troudet et al. 2018). This raises concerns on the reliability of identifications that cannot be verified (Costello et al. 2013). Moreover, taxonomic papers are published in low-citation indexed journals and NHMC are in high risk of not being preserved in the long run (Andreone et al. 2014). The consequence of a lack of taxonomical knowledge is the loss of irreplaceable sources of high-quality biodiversity data, and the proliferation of unvouchered misidentified records with poor or no auxiliary data which, in turn, results in a doubtful source of knowledge for future generations (Yesson et al. 2007; Funk 2018; Troudet et al. 2018). This trend is alarming, particularly in the light of a biodiversity extinction crisis.

A taxonomist-ecologist partnership would benefit museums and ecological studies improving long-term storage of ecological specimens and the quality and reproducibility of ecological studies (Ward et al. 2015). Therefore, collections-based research would complement field surveys in all biodiversity disciplines to achieve a more comprehensive understanding of the taxa under study and to discover biodiversity hotspots that can be considered priority for future conservation (Minton and Perez 2010).

Threats to biodiversity emphasise the need to decrease the Linnean shortfall by gathering information on known species based in specimen collection and also in describing new species, as rapidly as possible, to understand their vulnerability and to conserve them (Costello et al. 2015; Hortal et al. 2015; Ceríaco et al. 2016; Troudet et al. 2018). Henceforth, the understanding of the current state and future effects on the NE Atlantic Plexauridae relies on a complete data gathering exercise. Considering

the heterogeneous octocoral taxonomy effort in the Macaronesian archipelagos and West Africa, historical literature and specimen collection data have a great value to fill in gaps in areas where biodiversity is still unknown (e.g., at greater depths) (Sampaio et al. 2019). The present study has generated accurate baseline octocoral taxonomic status records reliable for species distribution, biodiversity and conservation studies. This Plexauridae museum database will be beneficial to decide future field surveys in geographic and taxonomic unexplored areas and for a better management of deep-sea areas where plexaurid species are rare or form vulnerable marine ecosystems (VMEs).

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RESEARCH ARTICLE



The first proven oxychilid land snail endemic to China (Eupulmonata, Gastrodontoidea)

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Abstract

A new and the first proven oxychilid species endemic to China is reported from Sichuan Province. *Sinoxychilus* **gen. nov.** is established based on this new species and has diagnostic traits of the sculptured protoconch, partial epiphallus wrapped by developed penis sheath, penial retractor muscle inserting on the top of penial caecum, spinelets on penial pilasters, absence of epiphallic papilla and perivaginal gland present on vagina and proximal bursa copulatrix duct. In light of shell morphology and through geometric morphometric analyses, *Zonites scrobiculatus scrobiculatus* Gredler and *Z. scrobiculatus hupeina* Gredler are proposed to be included in the new genus. A phylogenetic inference based on ITS2 gene indicates that the new genus is systematically close to *Oxychilus* Fitzinger, which is known from the Western Palearctic and the Southwestern Arabian Peninsula, regions that are geographically far from the distribution range of the new genus.

Chinese abstract

首次从四川青城山报道了璃螺科(Oxychilidae, 癞蜗牛总科Gastrodontoidea)的陆生软体动物。 依据胚螺具雕饰、交接器鞘包裹部分成荚器、交接器收缩肌着生于交接器盲囊顶端、交接器 内的壁柱具小棘、成荚器乳突阙如、雌道及纳精囊管基部具雌道周腺等特征,建立了由貊华 璃螺*Sinoxychilus melanoleucus* gen. nov. and sp. nov.为属模式种的华璃螺属*Sinoxychilus* gen. nov.。根 据贝壳特征及贝壳几何形态学分析,认为分别分布于湖南和湖北的*Zonites scrobiculatus scrobicula tus* Gredler, 1885 与*Z. scrobiculatus hupeina* Gredler, 1887当归于本新属。据ITS2序列重建的支序关 系揭示该属与广泛分布于古北区西部等地区的璃螺属(*Oxychilus* Fitzinger)具有较其它癞蜗牛 总科类群更近的系统发生关系。地理分布上,华璃螺为位于璃螺科连续分布区之外的一属。

Keywords

Geometric morphometric analysis, ITS2, new genus, Oxychilidae, phylogeny, Sichuan

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Introduction

The family Oxychilidae Hesse, 1927 is one of the three families under the superfamily Gastrodontoidea Tryon, 1866 (sensu Bouchet et al. 2017) and is distributed in the Western Palearctic and the Southwestern Arabian Peninsula (Neubert 1998; Schileyko 2003). The members of this family in China were believed to belong to the genus *Hyalina* A. Férussac, 1821 (= *Oxychilus* Fitzinger, 1833). Möllendorff reported a *Hyalina* sp. from the mountains at Kiukiang (= Jiujiang, Jiangxi) (1875a) and *H. fulva* Müller, 1774 from Po-chwa-schan (= Baihuashan, Beijing) (1875b).

Gredler (1881) proposed H. (Conulus) franciscana Gredler, 1881 and its subspecies H. (Conulus) franciscana planula Gredler, 1881 (Futschiazung, Hunan) (Gredler 1881a), and treated Helix rejecta L. Pfeiffer, 1859 (N and Central China, Guangdong) as a Hyalina species (Gredler 1881a, 1881b). Later, Gredler (1882) proposed two additional species, Hyalina (Conulus) spiriplana Gredler, 1882 (Fu-tschiao-zung, Hunan) and H. (Zonitoides?) loana Gredler, 1882 (Changsha, Hunan) (Gredler 1882a) and listed more than 10 species, namely H. politissima (L. Pfeiffer, 1853) (NE China, but originally described from Sri Lanka), H. superlita (Morelet, 1862) (Whampoa and Canton), H. rejecta (NE China, Hunan, Guangdong), H. moellendorffi (Reinhardt, 1877) (Peking), H. perdita (Deshayes, 1874) (Near Peking, Eastern Mongolia), H. (Conulus) franciscana, H. (Conulus) franciscana planula (Hunan), and H. (Conulus) fulva (Peking and the Eastern Mongolia) (Gredler 1882a, 1882b). Heude (1882) described 13 new species of Hyalina, namely H. planula (Ningguo, Anhui), H. rathouisii (near Shanghai), H. planata (Hunan), H. mamillaris (Hunan), H. sinensis, H. zikaveiensis (Shanghai), H. sekingeriana (Ningguo, Anhui), H. colombeliana (Yixing, Jiangsu), H. bambusicola (Ningguo, Anhui), H. spelaea (Guanyinmen, Nanjing, Jiangsu), H. castaneola (Qingyang, Anhui), H. imbellis (Ningguo, Anhui), and H. gredleriana (Hunan), and treated *Helix rejecta* and *Helix miliaria* Gredler, 1881 as species of *Hyalina*. Retaining H. politissima, H. planula, and H. zikaveiensis ("Likaveiensis" was a typographical error by Möllendorff 1883: 375) in Hyalina, Möllendorff (1883) arranged part of above mentioned species, most proposed by Heude (1882), into four genera, viz. H. superlita in Macrochlamys Benson, 1832; H. rejecta (synonym H. mamilaris), H. planata, H. moellendorffi, H. sinensis, H. colombeliana, H. sekingeriana, H. bambusicola, H. spelaea and H. castaneola in Microcystis? Beck, 1837; H. imbellis, H. franciscana and H. gredleriana in Kaliella? Blanford, 1863; and H. rathouisii in Nanina Grey, 1834.

Gredler (1885) proposed *H. crystallodes* Gredler, 1885. In the second series of the "Manual of Conconchology", Tryon (1886) included *H. gredleriana* as a subspecies of *H. franciscana*. He categorized the *Hyalina* species into seven genera (= sections), placing *H. franciscana*, *H. franciscana gredleriana*, and *H. imbellis* under *Kaliella*; placing *H. politissima*, *H. sinensis*, *H. superlita* Morelet, 1862 (Hongkong, Macao, Kuang-tung), and *H. rathouisii* in *Macrochlamys*, moving *H. zikaveiensis*, *H. planula*, *H. sekingeriana*, *H. colombeliana*, *H. spelaea*, *H. castaneola*, *H. bambusicola*, *H. ejecta*, *H. planata*, and *H. moellendorffi* to *Microcystis*; moving *H. mamillaris* and *H. perdita* to *Polita* Held, 1837, placing *H. loana* in *Zonitoides* Lehmann, 1864; and moving *H. spiriplana* and *H. fulva* to *Conulus* Fitzinger, 1833.

Then, Gredler transferred *H. franciscana*, *H. franciscana planula* Gredler (not Heude, 1882), and *H. spiriplana* to *Kaliella* and transfered *H. rathouisii* to *Nanina*; while retaining *H. politissima*, *H. planula* Heude, *H. zikaveiensis*, and *H. loana* in *Hyalina* (Gredler 1887a). Yen (1939) grouped *H. spelaea*, *H. sekingeriana*, and *H. franciscana* into *Kaliella* Blanford, 1863 and *H. zikaveiensis* (in Yen 1939: 118, "*sicaveiensis*" was a typographical error) into *Microcystina* Mörch, 1876; he placed *H. sinensis*, *H. planula*, *H. planata*, and *H. rejecta* in *Macrochlamys* and moved *H. rathouisii* to *Euplecta* Semper, 1870.

None of the above mentioned species was anatomically examined. Over-dependence on shell morphology caused many conflicts in the early classification of Chinese species of *Hyalina*. Furthermore, none of the above-mentioned species that had once been treated as *Hyalina* has been studied since Yen (1939), and the existence of true oxychilid species in China has been questioned. However, our recent work on the malacofauna of Sichuan, has found a species which meets the morphological definition of Oxychilidae Hess, 1927 but conchologically differs from above-mentioned *Hyalina* species. The close relationship of the new genus with the oxychilid *Oxychilus* is also supported by molecular data.

Materials and methods

Four living animals and three empty shells, all fully mature, were collected by hand from the type locality. The living specimens were relaxed by drowning in water before being transferred to 70% ethanol which was replaced with ethanol of the same concentration after three days. The sizes of shell and genitalia of each specimen were measured with calibrated digital Vernier callipers and from photos, both to the nearest 0.1 mm. The number of whorls was recorded with 0.125 whorl accuracy as described by Kerney and Cameron (1979). Soft parts were measured after the specimens were fixed in 70% ethanol.

Whole genomic DNA was extracted from a piece of pedal muscle of the ethanol-preserved specimens using Animal Genome Quick Extraction Kit (B518221, Sangon Biotech). Each 25 μ L PCR mixture consisted of 12.5 μ L cwbio 2× Es Taq MasterMix Dye, 9.5 μ L ddH₂O, 1 μ L template DNA, 1 μ L forward primer (10 μ L/L) (5'-CTAGCTGCGAGAATTAATGTGA-3', Wade and Mordan 2000) and 1 μ L reverse primer (10 μ L/L) (5'-ACTTTCCCTCACGGTACTTG-3'; Wade and Mordan 2000). The conditions for thermal cycling, performed on a Eastwin ETC811, was 2 min at 94 °C for pre-denaturing, 35 circles of 30 s at 94 °C, 30 s at 58 °C and 60 s at 72 °C. The amplicons were examined on a 1% agarose gel for quality and fragment size, then were purified and sequenced on an automated sequencer. Information of the outgroup in phylogenetic inference: *Pseudiberus liuae* Wu, 2017 (Camaenidae), 33.102N, 104.336E, Shijiba, Wenxian, Gansu Province, China; June 10, 2011; coll. Wu, M., Xu, Q. & Buhda, P., registered and DNA voucher no. HBUMM06758.

Chromatographs and sequences were examined and were initially compiled in Sequencher 4.5. The sequence alignment, the evolution model selection and the Maximum Likelihood inference were performed by MEGA 7.0.26 (Kumar et al. 2016). After the data set of internal transcribed spacer 2 (ITS2) were examined by Gblocks 0.91b (Castresana 2000), 58% of the original 950 positions was retained for the final phylogenetic analyses. The Bayesian inference was conducted using MrBayes 3.1 (Ronquist et al. 2012).

Shell morphological variation study was performed in the tps series software including tpsUtil32 (Rohlf 2004), tpsDig32 (Rohlf 2005), using the geometric morphometric (GM) methods based on the landmarks (LMs) and semi-landmarks on the contour of the shell in aperture view (Schilthuizen et al. 2012). The designs of the landmarks and semi-landmarks are as follows: LM1, the columella insertion; LM2, the right insertion of peristome onto body whorl; LM3, the intersection point of right contour and suture of the last whorl; LM4 and LM8, respective right and left extremities on suture; LM5 and LM7, the right and left extremities on suture above LM4 and LM8, respectively; LM6, apex of shell; LMs 9-26, 18 semi-landmarks on the left contour between LM8 and the intersection point of left contour with peristome, by length; LMs 27-44, 18 semi-landmarks on peristome between LM1 and LM2, by length (Fig. 7; the number on landmarks transferred from semi-landmarks are not shown). The landmarks and the semi-landmarks were treated indiscriminately. The geometric morphometric analysis employed photos of 32 shells in aperture view, including five type specimens of the new species described in this paper, 10 Indian Ariophanta species randomly selected from Raheem et al. (2014), and 15 oxychiline species randomly selected from Sysoev and Schileyko (2009). Full Procrustes fitting, covariance matrix generating, and subsequent canonical variate analysis (CVA) were conducted using MorphoJ (version 1.05f; Klingenberg 2011).

Directions used in descriptions: proximal = towards the genital atrium; distal = away from the genital atrium.

Abbreviations: At - atrium; BC - bursa copulatrix; BCD - bursa copulatrix duct; Ep - epiphallus; fma - fully mature animal(s); FO - free oviduct; HBUMM - Mollusc collection of the Museum of Hebei University, Baoding, China; OE - orifice of epiphallus; P - penis; PC - penial caecum (this part is judged here as penial caecum rather than flagellum as termed in some works because the flagellum, if present, is located at the distal end of epiphallus); PP - penial pilaster; PR - penial retractor muscle; PS - penis sheath; PVG - perivaginal gland; Va - vagina; VD - vas deferens.

Systematics

Gastrodontoidea Tryon, 1866 Oxychilidae Hesse, 1927 Oxychilinae Hesse, 1927

Sinoxychilus gen. nov. http://zoobank.org/C90C05C0-17A9-4D50-BC87-25688D997E07

Type species. Sinoxychilus melanoleucus gen. nov. and sp. nov.

Diagnosis. Protoconch with intercrossing radial wrinkles and spiral grooves. Penis sheath developed, more or less wrapping partial epiphallus. Tubercles of broken longitudinal penial pilasters bearing spinelets. Penial retractor muscle inserting on the top of penial caecum. Neither flagellum nor epiphallic papilla present. Perivaginal gland present on vagina and proximal bursa copulatrix duct.

Description. Shell depressed; thin; opaque; of about 4.5 whorls. Umbilicus moderately wide. Protoconch with intercrossing radial wrinkles and spiral grooves. Teleoconch with spiral furrows. Aperture somewhat sinuate at peristome. Aperture toothless, unexpanded.

Sole tripartite. Caudal foss or caudal horn absent. Jaw oxygnathous, with median projection.

Penis sheath present; wrapping partial epiphallus. Penis moderately long and thick; externally simple. Sarcobelum absent. Penial caecum present, having no external demarcation between it and penis. Penial retractor muscle inserting on top of penial caecum. Flagellum absent. Epiphallus thin. Penial caecum internally with transversal ridges near epiphallic pore. Epiphallic papilla absent. Penis internally with developed pilasters. Penial pilasters broken into connected tubercles that each bearing a very short spinelet. Vagina short, internally simple, and without papilla or verge. Perivaginal gland well developed on the surface of vagina and proximal part of bursa copulatrix duct.

Distribution. China (Sichuan, Hunan, Hubei).

Etymology. The generic name is a compound of Greek "sino" (= China) and *Oxychilus* which is a genus of the family Oxychilidae.

Molecular phylogenetic analyses. The examined ITS2 sequences are from Gen-Bank and this study. According to Hausdorf (2000), Gastrodontoidea is made up of six families, namely Pristilomatidae Cockerell, 1891, Chronidae Thiele, 1931, Euconulidae H.B. Baker, 1928, Trochomorphidae Möllendorff, 1890, Gastrodontidae Tryon, 1866, and Oxychilidae. After searching for ITS2 sequences from these six families in NCBI (https://www.ncbi.nlm.nih.gov/), 21 ITS2 haplotypes of *Euconulus* spp. (Euconulidae), *Oxychilus* spp. (Oxychilidae), and one *Vitrea* species (Pristilomatidae) were added to our analyses (Table 1). After eliminating poorly aligned positions and divergent regions of the alignment, a dataset of 25 × 552 bp was used for the subsequent analyses. The "T92 (Tamura 3-parameter) + G" model was chosen as the best nucleotide substitution model because of the lowest AIC score (lnL = -1746.871, AICc = 3594.112). The phylograms produced by the Maximum Likelihood Inference and the Bayesian Inference are topologically identical (Fig. 8). The obtained phylogenetic inference shows *Sinoxychilus* gen. nov. forms a sister group with the genus *Oxychilus*, and both genera are well embedded in the Gastrodontoidea clade (Fig. 8).

Taxonomic remarks. Morphologically, this group belongs to the family Oxychilidae based on the presence of a tripartite sole, oxygnathous jaw, penis sheath, and perivaginal gland and the absence of a caudal horn and sarcobelum, by which *Sinoxychilus* gen. nov. can be promptly distinguished from Gastrodontidae and Pristilomatidae, the other two families of Gastrodontoidea (sensu Bouchet et al. 2017). The new genus and *Oxychilus* have many characteristics in common, such as a developed penial caecum, connection

Family	Species	Genbank Accession No. of ITS2
Euconulidae	Euconulus alderi (J.E. Gray, 1840)	MK299689, MK299710
	E. chersinus (Say, 1821)	MK299741
	E. dentatus (Sterki, 1893)	MK299732, MK299739
	E. fulvus (O.F. Müller, 1774)	MK299691, MK299693, MK299695, MK299702, MK299723, MK299724, MK299737, MK299738
	E. trochulus (Reinhardt, 1883)	MK299730-31
	E. polygyratus (Pilsbry, 1899)	MK299747
Pristilomatidae	Vitrea crystalline (O.F. Müller, 1774)	AY014113
Oxychilidae	Oxychilus alliarius (Miller, 1822)	JF837183, AY014114
	O. cellarius (O.F. Müller, 1774)	AY014116
	O. helveticus (Blum, 1881)	AY014115
	Sinoxychilus melanoleucus gen. nov. & sp. nov.	MN056416, MN056417
Camaenidae (Outgroup)	Pseudiberus liuae Wu, 2017	MN056414, MN056415

Table 1. The species and ITS2 sequences used for phylogenetic study.

of some part of epiphallus + vas deferens and distal penis sheath by connective tissue, as in the European *Oxychilus mortilleti* (L. Pfeiffer, 1859) (Manganelli and Giusti 1998: figs 5, 10, 13, 14) and in the Asian *Araboxychilus sabaeus* (Martens, 1889) (Colville and Riedel 1998: fig. 7). However, *Sinoxychilus* gen. nov. differs from *Oxychilus* in having an opaque shell with a delicately sculptured protoconch, and in bearing short spinelets on the penial pilasters. The new genus also shows an unusual shell shape, which differs from shells of *Ariophanta* Desmoulins, 1829 and some other oxychiline genera (Fig. 7).

Zonites scrobiculatus scrobiculatus Gredler, 1885 and Z. scrobiculatus hupeina Gredler, 1887 are included in the new genus although they are only known conchologically (see Taxonomic remarks below).

Riedeliconcha Schileyko, 2003 and *Vitrinoxychilus* Riedel, 1963 are two oxychilid genera which also have spines on the penis inner wall. The new genus differs from them in possessing well-developed penial caecum, penis sheath, and epiphallus, a long bursa copulatrix, and conchologically, an opaque shells with a sculptured protoconch.

Sinoxychilus melanoleucus gen. nov. & sp. nov.

http://zoobank.org/E4075613-A987-471A-A095-D058CBDA466F Figures 1–10, Table 1

Type material. Holotype, 1 fma (HBUMM08236 specimen-1), Qingchengshan Mt., humid forest, in litter (Fig. 9); Sichuan Province, China; 30.919N, 103.494E; 24 March 2018; coll. Liu, Zhengping & Ma, Hongwen. **Paratypes**, 3 fma (HBUMM08236; specimens 2–4) and 2 fully mature empty shells (HBUMM08236; specimens 6, 7), collection data as holotype. One empty shell specimen (HBUMM08236; specimen 5) was broken accidentally after measurement and as a result is not included as a paratype. From each of type specimens with soft parts (HBUMM08236; specimens 1–4) a piece of foot (HBUMM08236a; specimens 1–4) was cut and preserved in 99.7% ethanol at –20 °C.

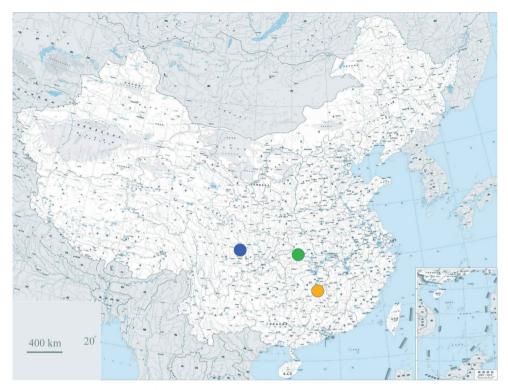


Figure 1. Distribution map of Sinoxychilus melanoleucus gen. nov and sp. nov. (blue dot), Zonites scrobiculatus scrobiculatus Gredler, 1885 (orange dot), and Zonites scrobiculatus hupeina Gredler, 1887 (green dot).

Description. Shell (Figs 2, 3). Dextral; clearly depressed; very thin and fragile; opaque. Whorls convex. Suture impressed. Umbilicus moderately wide. Basal-umbilicus transition gentle. Columella arched to oblique. Columellar lip not dilated, never covering umbilicus. Protoconch with intercrossing radial wrinkles and spiral grooves (Fig. 3A). Teleoconch with regularly, densely distributed spiral furrows (Fig. 3B). Growth lines fine, distinct. Aperture large, oblique, somewhat sinuate at peristome. Body whorl straight. Adult shell neither hairy nor scaly. Body whorl of adult shell very bluntly angulate at periphery, with base convex. Aperture toothless, unexpanded. Peristome rather thin. Callus indistinct. Shell in uniformly greenish yellow, spiral band absent (Fig. 2). Measurements (n = 6): shell height = 6.7-8.1 (7.7 ± 0.55) mm, shell breadth = 12.6-13.8 (13.2 ± 0.51) mm, aperture height = 4.9-5.7 (5.3 ± 0.31) mm, aperture width = 2.2-2.6 (2.4 ± 0.16) mm, embryonic shell whorls = 1.38-1.63 (1.50 ± 0.079) mm, whorls = 4.25-4.63 (4.41 ± 0.151) mm, shell height/breadth ratio = 0.53-0.62 (0.58 ± 0.030) mm.

General anatomy. Sole tripartite. Caudal foss or caudal horn absent. Eversible head wart between ommatophore insertions absent. Tentacles and dorsum leadenblack. After preservation in 70% ethanol, black pigments on animal become faint. Lower sides and sole creamy white (Figs 4A, 10). Jaw oxygnathous, with an evidently median projection (Fig. 4B).

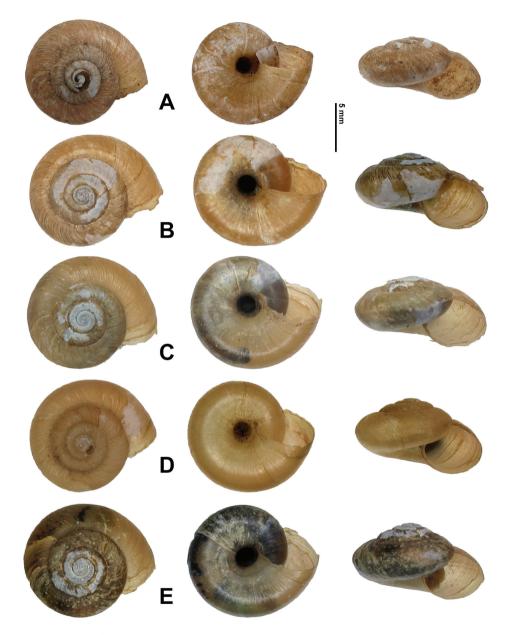


Figure 2. *Sinoxychilus melanoleucus* gen. nov. and sp. nov. shells. **A** Holotype, HBUMM08236 specimen 1 **B–E** paratypes, HBUMM08236 specimens 2–4, 6.

Genitalia (Figs 4C, 5, 6). Penis sheath about half length of penis, in holotype and two paratypes wrapping about 1/3 central epiphallus (Figs 4C, 6), but in one specimen (HBUMM08236; specimen 2) median part of epiphallus loosely joined to distal penis sheath by connective tissue (Fig. 5A). Penis more or less long, moderately thick, surface simple. Sarcobelum absent. Penial caecum present (Figs 4C, 5A, 5B, 6), having no ex-

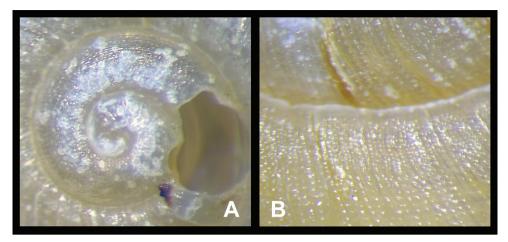


Figure 3. *Sinoxychilus melanoleucus* gen. nov. and sp. nov. HBUMM08236 specimen 4, paratype **A** magnified embryonic shell **B** surface of teleoconch, magnified.

ternal demarcation between it and penis (Figs 4C, 5A, 6). Penial retractor muscle inserting on top of penial caecum. Flagellum absent. Epiphallus thin, but 2–3 times thicker than vas deferens (Figs 4C, 5A, 6). Distal part of epiphallus attached at lateral side of penis by connective tissue before entering it. Penial caecum internally with three pairs of symmetrically arranged low transversal ridges near epiphallic pore which is surrounded by several very fine pilasters (Fig. 5B). Epiphallic papilla absent. Penis internally with a thickened, 'M'-shaped median pilaster which has two arms branching into several narrow pilasters and the median pilaster running to the most proximal part of penis where it extends and forming a transversal ridge (Fig. 5B). The 'M'-shaped median pilaster consists of connected tubercles, the apex of each bearing a very short spinelet that without exception points to atrium (Fig. 5C). Vagina short, internally simple, without papilla/verge. Perivaginal gland well developed on surface of vagina and proximal part of bursa copulatrix duct (Figs 4C, 5A). Measurements of holotype: P = 5.0 mm; Ep = 8.4 mm; VD = 6.5 mm; PR = 2.3 mm; Va = 2.3 mm; BC + BCD = 11.8 mm.

Distribution. The new species is known only from its type locality.

Etymology. The species is named for the clear demarcation between the leaden black ommatophores and dorsum and the remaining creamy white body, which is reminescent of the giant panda, *Ailuropoda melanoleuca* by having the color pattern of clear-cut patches of black and white (Fig. 10).

Ecology. The new species was found living in extremely humid environment at type locality. In the laboratory, below 100% relative humidity, animals became active at the relatively lower temperature of 5 °C (Fig. 10) before they were totally inactive at room temperature (ca. 25 °C).

Taxonomic remarks. This new species can be distinguished from all other Chinese *Hyalina* species in the measurements of its shells (Table 2) and other features. This species, however, as kindly pointed out by Dr Barna Páll-Gergely, is obviously close to *Zonites scrobiculatus* Gredler, 1885, which was usually treated

Species	Whorls	Diam. maj. (mm)	Height (mm)	Distribution
Hyalina fulva O.F. Müller, 1774	5–6	4	3.5*	Beijing, E Mongolia
H. politissima (L. Pfeiffer, 1853)	4.5	24	11	Sri Lanka, NE China
H. rejecta (L. Pfeiffer, 1859)	6	3.5	3	Hunan, Guangdong, NE China
H. superlita (Morelet, 1862)	5-5.5	16.5-21	10-11.5	Guangdong, Macao
H. perdita (Deshayes, 1874)	4	3	1.5*	Beijing, E Mongolia
H. moellendorffi (Reinhardt, 1877)	5.5	10	5.5	Beijing
H. (Conulus) franciscana Gredler, 1881	6	3.5	3	Hunan
H. (Conulus) f. planula Gredler, 1881	6	3.5	2	Hunan
H. (Conulus) spiriplana Gredler, 1882	4.5-5	3	1 ³ / ₄	Hunan
H. (Zonitoides?) loana Gredler, 1882	5	4 ³ / ₄ -5	2	Hunan
H. bambusicola Heude, 1882	5	3.5-4	3.5	Anhui
H. castaneola Heude, 1882	6	3-4	3	Anhui
<i>H. colombeliana</i> Heude, 1882	6	4.5-5	3.5	Jiangsu
<i>H. gredleriana</i> Heude, 1882	6	2.5-3	3.5	Hunan
H. imbellis Heude, 1882	5.5	3.5-33/4	3	Anhui
<i>H. planula</i> Heude, 1882	4.5	6–7	3	Anhui
<i>H. planata</i> Heude, 1882	4	9-10	3.5	Hunan
H. rathouisii Heude, 1882	7	6	3.5	Shanghai
<i>H. sekingeriana</i> Heude, 1882	6	3.5-33/4	3.5	Anhui
H. sinensis Heude, 1882	4	5–6	3.5	Yangtze River Valley
H. spelaea Heude, 1882	6	4-4.5	3	Jiangsu
H. zikaveiensis Heude, 1882	4	2	1	Shanghai
<i>H. crystallodes</i> Gredler, 1885	5-5.5	5	2	Hunan

Table 2. Shell measurements and distribution of Chinese species once grouped in *Hyalina* A. Férussac,1821, with synonyms excluded.

* Measured from two figures in Tryon (1886: pl. 53).

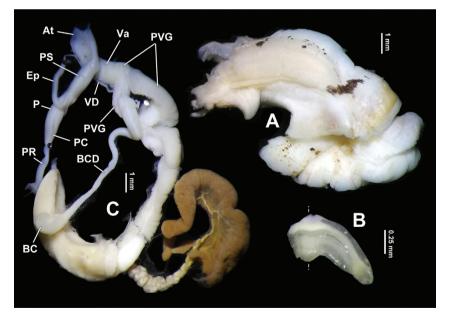


Figure 4. *Sinoxychilus melanoleucus* gen. nov. and sp. nov., holotype, HBUMM08236 specimen 1 **A** partial soft part **B** partial jaw. Dotted line indicating axis line **C** genitalia in general view. At-atrium; BC-bursa copulatrix; BCD-bursa copulatrix duct; Ep-epiphallus; P-penis; PC-penial caecum; PR-penial retractor muscle; PS-penis sheath; PVG-perivaginal gland; Va-vagina; VD-vas deferens.

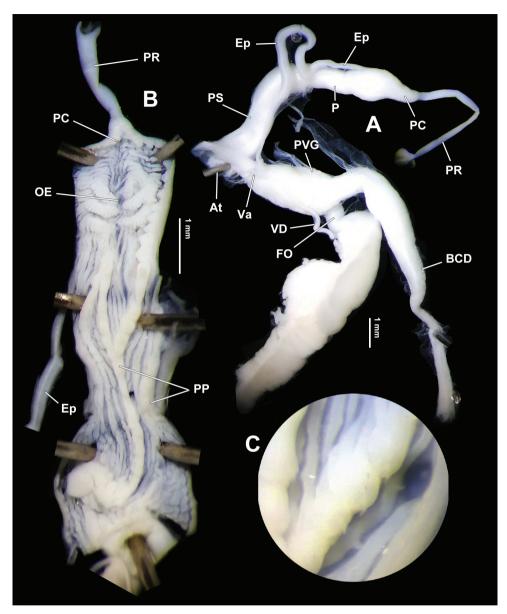


Figure 5. *Sinoxychilus melanoleucus* gen. nov. and sp. nov. **A** Genitalia in general view, paratype, HBUMM08236 specimen 2, showing the median section of epiphallus is not wrapped inside the penis sheath **B**, **C** holotype, HBUMM08236 specimen 1 **B** interior view of penis **C** a section of magnified penial pilaster, showing apical spinelet on each tubercle consisting the penial pilaster. At-atrium; BCD-bursa copulatrix duct; Ep-epiphallus; FO-free oviduct; OE-orifice of epiphallus; P-penis; PC-penial caecum; PP-penial pilaster; PR-penial retractor muscle; PS-penis sheath; PVG-perivaginal gland; Va-vagina; VD-vas deferens.

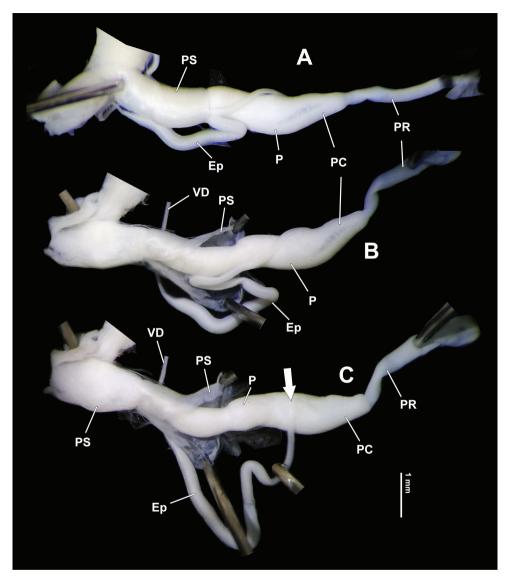


Figure 6. *Sinoxychilus melanoleucus* gen. nov. and sp. nov., HBUMM08236 specimen 2, paratype **A–C** indicating that the median part of epiphallus was dissecting out from the penis sheath **C** arrow indicates epiphallus insertion. Ep-epiphallus; P-penis; PC-penial caecum; PR-penial retractor muscle; PS-penis sheath; VD-vas deferens.

as a species in the bradybaenine genus *Coccoglypta* Pilsbry, 1895 (Páll-Gergely in press). The species can be promptly distinguished from *Z. scrobiculatus*, which has two subspecies, namely *Z. scrobiculatus scrobiculatus* [Zonites scrobiculatus Gredler, 1885a: 220–221, pl. 6, fig. 2; Tryon 1886: pl. 53, figs 12–14; Bachmann and Gredler 1894: 416 (radula); *Retinella? scrobiculata* Kobelt 1899: 918, pl. 241, figs 10, 11; *Coccoglypta scrobiculata scrobiculata* Yen 1939: 153, pl. 15, fig. 62; *Coccoglypta scrobiculata* Zilch 1974: 211; *Coccoglypta (Coccoglypta) scrobiculata*

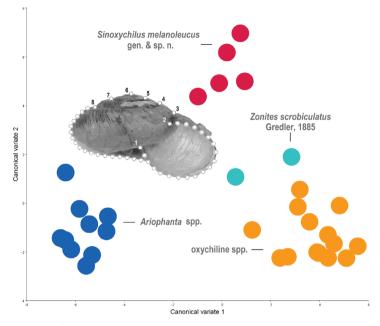


Figure 7. Scatter plot of canonical variate 1 against canonical variate 2 (yielded by canonical variate analysis), showing morphological relationship among *Sinoxychilus melanoleucus* gen. nov. and sp. nov. (red dots), *Zonites scrobiculatus scrobiculatus* Gredler, 1885 and *Zonites scrobiculatus hupeina* Gredler, 1887 (light blue dots), Indian *Ariophanta* spp. (Raheem et al. 2014) (dark blue dots) and oxychiline spp. (Sysoev and Schileyko 2009) (orange dots). A diagram showing design of landmarks (numbered) and semi-landmarks (not numbered) is provided.

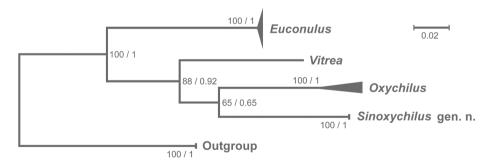


Figure 8. Maximum likelihood tree based on ITS2 gene (-ln likelihood = -1746.99). Ingroups: *Euconulus* Reinhardt, 1883 (Euconulidae), *Vitrea* Fitzinger, 1833 (Pristilomatidae), *Oxychilus* Fitzinger, 1833 (Oxychildae), and *Sinoxychilus* gen. nov. (Oxychildae). This ML tree shares the same topology with the Bayesian Inference tree. Numbers on branches indicate maximum likelihood and Bayesian posterior probabilities.

scrobiculata Zilch 1968: 180] and Z. scrobiculatus hupeina Gredler, 1887 [Zonites (Nanina?) scrobiculatus var. hupeina Gredler 1887b: 344–345; Coccoglypta scrobiculata hupeina Yen 1939: 153, pl. 15, fig. 63; Zilch 1974: 199; Coccoglypta (Coccoglypta) scrobiculata hupeina Zilch 1968: 180], by having a distinctly smaller shell, with fewer whorls, and a particular shell shape which is sharply divergent from that of



Figure 9. Habitat of Sinoxychilus melanoleucus gen. nov. and sp. nov. Qingchengshan, Sichuan.

Z. scrobiculatus (Fig. 7). Sinoxychilus melanoleucus is also geographically distant from the geographic range of Z. scrobiculatus (Fig. 1). Nevertheless, we are inclined to believe that based on shell morphology Z. scrobiculatus should belong to Sinoxychilus, although anatomical and molecular evidence is unavailable.

With respect to the genitalia, *Sinoxychilus melanoleucus* is similar to the Japanese *Urazirochlamys doenitzii* (Reinhardt, 1877) (Helicarionidae sensu Azuma 1995 and Schileyko 2002) in having the apical insertion of penial retractor and the absence of



Figure 10. *Sinoxychilus melanoleucus* gen. nov. and sp. nov. Active animals. The photo was taken in laboratory rather than from the original habitat.

flagellum (Schileyko 2002: fig. 1600). *Sinoxychilus* and *Urazirochlamys* Habe, 1946 also share a characteristically spirally sculptured protoconch. However, the latter genus has a caudal horn (Azuma 1995: pl. 28, fig. 339), which suggests that *Urazirochlamys* does not belong to the Oxychilidae.

With the exception of two genera distributed in the southwestern part of the Arabian Peninsula, oxychilid snails are only known from the Western Palearctic (Neubert 1998; Schileyko 2003). The new species described herein, and its congeners, are undoubtedly the easternmost representatives of Oxychilidae, which suggests that *Sinoxychilus* might be an isolated group in China, remote from the main distribution area of the family.

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RESEARCH ARTICLE



Re-description of the type species of the genera Ganesella Blanford, 1863 and Globotrochus Haas, 1935; with description of a new Ganesella species from Thailand (Eupulmonata, Camaenidae)

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Abstract

The taxonomy of the speciose genus *Ganesella* W.T. Blanford, 1863 and the endemic genus *Globotrochus* Haas, 1935 is unclear since the anatomical characters of the the type species of these two genera have never been reported before. Therefore, the present paper provides the first anatomical descriptions of the reproductive apparatus, pallial system and radula of *Helix capitium* Benson, 1848 and *Helix onestera* Mabille, 1887, the respective type species of *Ganesella* and *Globotrochus*. In addition, *Ganesella rhombostoma* (Pfeiffer, 1861) and *Ganesella carinella* (Möllendorff, 1902) from Thailand are re-described, and a new species, *Ganesella halabalah* Sutcharit & Panha, **sp. nov.**, from southern Thailand is described. This new species differs from all others by having a larger shell, an obtuse apex and an aperture lip with a prominent beak-like deflection.

Keywords

anatomy, Cerastidae, Indochina, Orthurethran, Southeast Asia, synonym, systematics, tree snail

Introduction

The Camaenidae is one of the most speciose pulmonate snail families in Asia, and shows an astonishing diversity of taxa with different shell shapes, sizes and ecological characteristics (e.g., Pilsbry 1895, Solem 1959, Richardson 1985). Hitherto, camaenid taxonomy and classification has relied heavily on the shell morphology and, to a far lesser extent, on the reproductive anatomy. However, pulmonate shell characters are poor taxonomic markers as they often show convergent evolution and/or plastic features. The Camaenidae of Southeast Asia, including eastern India, Japan, Taiwan and southern China, are ground-dwelling or arboreal snails with relatively small to medium-sized, dextral or sinistral, trochoid shells. Traditionally, they were all assigned to the genus *Ganesella* W.T. Blanford, 1863.

The (sub)generic name *Ganesella* was first coined without any description or definition to accommodate *Helix capitium* Benson, 1848 and *Helix hariola* Benson, 1856 (Blanford 1863). As such, the definition of this (sub)genus has remained unclear (Zhou et al. 2011), the more so as the genital anatomy of *Helix capitium* was unknown until now (Schileyko 2003). Hence, the name *Ganesella* has been applied to a heterogeneous assemblage of what appears now to be at least four nominal subgenera (Thiele 1931, Zilch 1960, Richardson 1985). Unfortunately, there is little, if any, anatomical information on these (sub)genera.

The first data on the genital apparatus of *Ganesella* were published by Pilsbry (1895) for Helix japonica Pfeiffer, 1847, the type species of the genus Satsuma Adams, 1868. This genus was considered for a long time as a junior synonym of Ganesella (Pilsbry 1895, Thiele 1931, Zilch 1960). Yet, subsequent anatomical and molecular evidences have confirmed that Satsuma is to be treated as a distinct genus (Azuma 1995, Schileyko 2003, Wu et al. 2008), and is comprised of the species from Japan, Taiwan and southern China that were formerly assigned to Ganesella. As a consequence, the current interpretation of Ganesella confines this genus geographically to east of India and Southeast Asia. However, a general and consistent delimitation of Ganesella in terms of its genital features is still lacking, not in the least because the genital anatomy of its type species, Helix capitium was unknown until now (see below). Hence, species were assigned to Ganesella on the basis of shell characters only, and this has led to several misclassifications. A case in point is Ganesella brevibarbis (Pfeiffer, 1859) from China, which, after anatomical study, appeared to belong to the genus Plectotropis Martens, 1860 in the family Bradybaenidae (Albers 1860, Zhou et al. 2011).

The recent revision of the Camaenidae by Schileyko (2003) has raised several subgenera of *Ganesella* to full genus rank (*Liocystis* Mörch, 1872, *Coliolus* Tapparone-Canefri, 1887, *Coniglobus* Pilsbry & Hirase, 1906 and *Globotrochus* Haas, 1935), but this was still based only on shell characters. Hence, the first step towards a sound taxonomic revision of *Ganesella* in Indochina is to provide comparative anatomical data of the type species of the different genus-level taxa involved. The present study does so for the nominal genera *Ganesella* and *Globotrochus*, with their respective type species *Helix capitium* and *Helix onestera* Mabille, 1887. In addition, *Ganesella rhombostoma* (Pfeiffer, 1861) and *Ganesella carinella* (Möllendorff, 1902) from Thailand are re-described, and a new species from southern Thailand is described.

Materials and methods

Shells and living specimens were collected from various localities in Thailand and Vietnam. Live specimens were drowned in water and then fixed in 70% (v/v) ethanol for anatomical examination. Specimens were primarily identified using the publications of Benson (1848, 1856), Pfeiffer (1853), Pilsbry (1891, 1895) and Möllendorff (1898), and were also compared with the relevant type material in museum collections (see below). To study anatomy, three to ten specimens were dissected under a stereomicroscope. Drawings were made with a camera lucida. Adult shells were used to measure the shell height (\mathbf{h}) and shell width (\mathbf{w}), and to count the number of whorls. Radulae were examined under scanning electron microscopy (SEM; JEOL, JSM-5410 LV).

Anatomical conventions and abbreviations

In the descriptions of the genitalia, the term 'proximal' refers to the region closest to the genital orifice, while 'distal' refers to the region furthest away from the genital orifice. The following abbreviations were used as defined by Pilsbry (1891, 1895) and Solem (1993): **a**, anus; **ag**, albumen gland; **at**, atrium; **au**, auricle; **e**, epiphallus; **fl**, flagellum; **fo**, free oviduct; **gd**, gametolytic duct; **gs**, gametolytic sac; **hd**, hermaphroditic duct; **hg**, hermaphroditic gland; **i**, intestine; **k**, kidney; **l**, lung; **mc**, mantle collar; **ov**, oviduct; **p**, penis; **pn**, pneumostome; **pp**, penial pilaster; **pr**, penial retractor muscle; **puv**, pulmonary vein; **pv**, penial verge; **r**, rectum; **ur**, ureter; **v**, vagina; **vd**, vas deferens; **ve**, ventricle; **vp**, vaginal pilaster.

Institutional abbreviations

CUMZ, Chulalongkorn University, Museum of Zoology, Bangkok; **FMNH**, Field Museum of Natural History, Chicago; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **NHMUK**, The Natural History Museum, London; **NHMW**, Naturhistorisches Museum, Wien; **RBINS**, Royal Belgian Institute of Natural Sciences, Brussels; **SMF**, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; **UMZC**, University Museum of Zoology Cambridge, Cambridge; **ZMB**, Museum für Naturkunde, Humboldt University, Berlin.

Systematics

Family Camaenidae Pilsbry, 1895

Genus Ganesella Blanford, 1863

Helix (Ganesella) W.T. Blanford, 1863: 86.

- *Trochomorphoides* Nevill, 1878: 80. Type species: *Helix acris* Benson, 1859, by original designation.
- *Darwininitium* Budha & Mordan in Budha et al. 2012: 21. Type species: *Darwininitium shiwalikianum* Budha & Mordan in Budha et al. 2012, by original designation. New synonym.

Type species. *Helix capitium* Benson, 1848 by subsequent designation (Pilsbry 1895: 168).

Description. Shell more or less trochoid, moderately thin to solid, with 4–6 convex whorls. Last whorl rounded to angular, with or without a peripheral keel, a little descending in front. Colour light monochrome or with a few dark bands and/or spots and streaks. Embryonic shell smooth. Post apical whorls with irregular, thin, radial ridges and spiral lines (smooth below peripheral angle or keel). Aperture widely ovate, moderately oblique with variously reflected margins. Umbilicus narrow, but open, rarely closed. Shell height ranged from 4.5 to 25.0 mm and shell width ranged from 5.5 to 27.0 mm.

Genitalia typical of camaenids, without accessory organs on penis or vagina. Penis short to long, with small to large penial verge, but no penial appendix; epiphallus and flagellum short.

Radular teeth triangular to spatulate, central tooth unicuspid, lateral and marginal teeth tricuspid.

Remarks. The genus *Ganesella* s.s. differs from *Satsuma* s.s by having a penial verge, but no penial appendix. In contrast, *Satsuma* has a short to long penial appendix on the distal part of the penis, but lacks a penial verge. In addition, *Satsuma* occurs from Japan to Taiwan and southern China, while *Ganesella* occurs from South to Southeast Asia, including Japan (Azuma 1995, Schileyko 2003, Wu et al. 2008).

Darwininitium shiwalikianum Budha & Mordan, 2012, the type species of the monotypic genus *Darwininitium* Budha & Mordan, 2012, appears conchologically identical to *Helix capitium*, the type species of *Ganesella* (see also Budha et al. 2016). Therefore, the genus *Darwininitium*, which was originally described from central Nepal, is here tentatively regarded as a junior subjective synonym of the camaenid genus *Ganesella*. If this is confirmed, then *Darwininitium* was erroneously assigned to the family Cerastidae and as such, its pallial system with a long kidney and s-shape ureter would point to a sigmurethrous condition and not to a case of pseudosigmure-thry within the Orthurethra (sensu Solem 1959 and see also Budha et al. 2016). These taxonomic conclusions appear to be supported by DNA sequence data (Budha et al. 2016).

Figs 2A, B, 8

Helix capitium Benson, 1848: 160. Hanley and Theobald 1870: 7, pl. 14, fig. 5. Tryon 1887: 74, pl. 14, fig. 99.

Helix (Planispira) capitium: Nevill 1878: 78.

Trochomorpha capitium: Morlet 1889: 124, 125.

Ganesella capitium: Pilsbry 1895: 170, pl. 55, fig. 18. Blanford 1903: 278. Gude 1914: 196, 197. Zilch 1960: 610, fig. 2140. Zilch 1966: 202. Richardson 1985: 132, 133.

Darwininitium shiwalikianum Budha & Mordan in Budha et al. 2012: 21–23, figs 2–4. Type locality: Kasara near Tamor Lake, Chitwan National Park, Central Nepal. New synonym.

Type locality. Sicrigali province Bahar Indiae Orientalis [Bihar State, India].

Material examined. Type specimens. Three syntypes of *Helix capitium* are in Benson's collection. The specimen that closely matched with the measurement in the original description is designated here as the lectotype UMZC I.102385/1 (Fig. 2A, height 13.3 mm, width 13.5 mm), and the other two as paralectotypes UMZC I.102385/2–3 (2 shells; Fig. 2B, height 14.4 mm, width 13.8 mm).

Additional material. Bahar Province, India: ZMB ex. Albers coll. 1 lot (1 shell). South India: NHMUK ex. Godwin-Austen coll. no. 501 (2 shells).

Remarks. Budha et al. (2012) described *Darwininitium shiwalikianum* from Chitwan National Park, Nepal. The holotype has a trochoid, brownish shell with irregular opaque white spots. As such, it appears to be identical to the type specimens of *Ganesella capitium*. In addition, the type localities of *D. shiwalikianum* and *G. capitium* are geographically quite close to each other. Hence, in line with our earlier conclusions about the genus *Darwininitium*, we tentatively regard *D. shiwalikianum* as a junior subjective synonym of *G. capitium*.

Shell and genitalia have been described in detail by Budha et al. (2012). The unique and distinctive characters of *G. capitium* are its small, relatively elevated, trochoid shell. Aperture open sublaterally. Whorls slightly convex with wide and shallow suture. Last whorl angular with weak peripheral keel. Shell colour brownish with whitish-opaque, irregular, spots or streaks. Genitalia with short atrium; cylindrical, short penis, about half as long as the vagina, and proximally with blackish, spongy tissue. Epiphallus and flagellum together short, about as long as the penis, but flagellum longer than epiphallus. Internal wall of penis with numerous longitudinal pilasters.

Ganesella hariola (Benson, 1856)

Figs 2C–E, 8

Helix hariola Benson, 1856: 251. Pfeiffer 1860: 123, pl. 36, figs 21, 22. Hanley and Theobald 1870: 7, pl. 14, fig. 6.

Helix capitium var. hariola: Tryon 1887: 74, pl. 14, fig. 100.

Helix (Ganesella) hariola var. *carinata* Godwin-Austen, 1888: 242. Type locality: Khagan on Irrawaddy, and Hlindet, 1200 feet.

Ganesella capitium var. hariola: Pilsbry 1895: 170. Gude 1914: 197.

Type locality. Thyet-Myo, prope ripas Irawadi fluvii [near the banks of the River Irrawaddy in Thayetmyo, Magway Region, Myanmar].

Material examined. Type specimens. To stabilize the name, the syntype from Benson's collection that most closely matched with the features and measurements of the original description is here designated as the lectotype UMZC I.104370/1 (Fig. 2C, height 11.6 mm, width 14.4 mm) of *Helix hariola* Benson, 1856. The other shells from the same lot hence become the paralectotypes UMZC I.104370/2–4 (3 shells; Fig. 2D, height 13.8 mm, width 16.2 mm).

Additional material. MYANMAR: Thungadan, North Ava, Burma: syntype of *Helix hariola* var. *carinata* NHMUK 1906.2.2.176 (4 shells). Burma: NHMUK 1906.2.2.276. Pegu: NHMUK Salisbury coll. ex. Beddome (1 shell). North Chin Hills, Upper Burma: NHMUK 1893.12.6.30–4 (5 shells). Thyet-myo, Pegu, Burma: NHMUK 1906.2.2.109 (4 shells). Pegu, Burma: ZMB Paetel coll. (2 shells), Dunker coll. (1 shell). Pyintha, Mandalay, Burma: ZMB Notling coll. (3 shells). Popa View Point Resort, about 50 km southeast of Bagan (20°55'19.1"N, 95°12'41.9"E), Kyaukpandaung Township, Nyaung-U District, Mandalay Region: CUMZ 5134 (1 shell; Fig. 2E).

Description. Shell small, dextral, thin and with a depressed trochoid. Apex acute; embryonic shell smooth with brownish colour. Whorls 5-6, increasing regularly, convex; suture wide and deep. Shell surface smooth or with fine growth lines. Last whorl large, very weekly angular to rounded; beneath convex; last whorl with brownish peripheral band. Shell brownish and translucent, with whitish-opaque, irregular streaks on upper and lower periphery. Aperture ovate; lip whitish and expanded; parietal callus transparent. Umbilicus rimate; columella whitish and expanded, overhanging umbilicus.

Remarks. The shells of *Ganesella hariola*, *G. carinella* and *G. capitium* have a trochoid shape, but the shell of *G. capitium* is clearly more elevated than the shells of the two other species. The shell of *G. hariola* differs further from that of *G. capitium* and *G. carinella* in having a deep suture and a rounded last whorl with a brownish spiral band on the periphery. In contrast, the shells of *G. capitium* and *G. carinella* have a shallow suture and an angular to keeled last whorl without a brownish peripheral band.

Ganesella carinella (Möllendorff, 1902)

Figs 1A, B, 2F-H, 3A, B, 5A-D, 7A-C, 8

Eulota (Ganesella) hariola carinella Möllendorff, 1902: 158, 159. Zilch 1966: 202.
Ganesella capitium [non Benson 1848]: Pilsbry 1895: 170, 360, pl. 55, fig. 18. Blanford 1903: 278. Gude 1914: 196, 197. Zilch 1960: 610, fig. 2140. Zilch 1966: 202. Richardson 1985: 132, 133. Schileyko 2003: fig. 1958.

Type locality. Siam, Muoklek and Kanburi [Thailand: Muaklek District, Saraburi Province and Kanchanaburi Province].

Material examined. Type specimens. Lectotype SMF 27534a (Fig. 2F, height 14.8 mm, width 18.5 mm) and paralectotype SMF 27534b (1 shell; Fig. 2G, height 17.6 mm, width 18.2 mm) from Siam [Thailand].

Additional material. CAMBODIA: Cambodia: NHMUK Cuming coll. ex Mouhot (2 shells). THAILAND: Siam: NHMUK 1902.9.17.30-31 (2 shells). Tam Barijinda, Chom Thong District, Chiangmai Province: CUMZ 4153, 4193, 4165 (Fig. 3B), 5123. Wat Tham Rakung, Sri Samrong District, Sukhothai Province: CUMZ 4937. Tam Lom-Tam Wang, Sri Samrong District, Sukhothai Province: CUMZ 4938. Tam Pha Thaphol, Nern Maprang District, Phitsanuloke Province: CUMZ 4195, 5127. Tam Wang Daeng, Nern Maprang District, Phitsanuloke Province: CUMZ 4932, 4939, 5113, 5126. Wat Chuek Charoentham, Ban Rai District, Uthaithani Province: CUMZ 4935. Wat Sri Uthumporn, Muang District, Nakhonsawan Province: CUMZ 4940. Tam Phet-Tam Thong, Takhi District, Nakhonsawan Province: CUMZ 4173, 4943, 5121, 5133 (Fig. 2H). Tam Poon Sawan, Srithep District, Phetchabun Province: CUMZ 4284. Tam Sombat Chomphol, Lomsak District, Phetchabun Province: CUMZ 4934, 5115, 5125. Khao Samokorn, Tha Wung District, Lopburi Province: CUMZ, 4218, 4279, 4282 (Fig. 3A), 4933. Wat Bandai Samsaen, Banmee District, Lopburi Province: CUMZ 4280. Tam Santisuk, Kok Samrong District, Lopburi Province: CUMZ 4931. Tam Tam-bon, Chaibadan District, Lopburi Province: CUMZ 5116. Muak Lek Waterfall, Muak Lek District, Saraburi Province: CUMZ 4186, 4172, 4941. Tam Dao Khaokaeo, Muak Lek District, Saraburi Province: CUMZ 4197. Tam Singha Ratde-cho, Kaeng Khoi District, Saraburi Province: CUMZ 4164, 4178, 5122. Tam Sriwilai, Chaloem Phrakiat District, Saraburi Province: CUMZ 4187, 4930. Wat Thep Pitak, Pakchong District, Nakhon Ratchasrima Province: CUMZ 4199. Wang Takrai Waterfall, Muang District, Nakhon Nayok Province: CUMZ 4942. Wat Khao Chakan, Khao Chakan District, Srakaeo Province: CUMZ 4159, 4182, 4213, 5114. Ta Praya District, Srakaeo Province: CUMZ 4283. Tam Phet Phothong, Klonghad District, Srakaeo Province: CUMZ 5120. Tam Kaeo Sawanbandan, Pong Namron District, Chanthaburi Province: CUMZ 4165.

Description. Shell. Shell small, dextral, thin and depressed trochoid. Apex acute; embryonic shell smooth with brownish colour. Whorls 5-6, increasing regularly, slightly convex and slightly shouldered near suture; suture wide and shallow. Shell surface smooth or with fine growth lines. Last whorl large, angular with strong keel; beneath convex. Shell brownish and translucent, with wide, whitish-opaque, irregular spiral band on upper and lower side. Aperture ovate; lip slightly expanded and whitish; parietal callus transparent. Umbilicus rimate with small hole; columella whitish and expanded overhanging umbilicus.

Genital organs. Atrium (at) short (N = 10) and proximally with blackish tissues. Penis (p) cylindrical, about as long as the vagina; proximally blackish; distally slightly enlarged at penial verge. Epiphallus (e) and flagellum (fl) very short, approximately one-third of penis length. Vas deferens (vd) long and narrow, extends from free oviduct

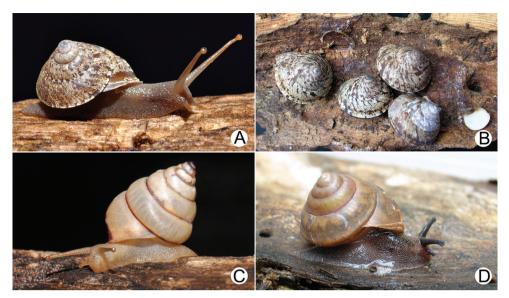


Figure 1. A, B *Ganesella carinella* from Keng-khoy, Saraburi (shell width about 15 mm) **A** live snail and **B** snails aestivated under loose tree bark, and with white epiphrams attached on substrate **C** *Ganesella rhombostoma* from Klong Had, Srakeo (shell height about 15 mm) **D** *Globotrochus onestera* from Cuc Phuong, Vietnam (shell width about 15 mm).

and terminates at distal epiphallus. Penial retractor muscle (pr) long and thin. Flagellum short, as long as or longer than epiphallus (Fig. 5A).

Penial verge (pv) small, conical, and with smooth surface. Penial wall ribbed, forming a series of swollen longitudinal pilasters (pp); middle wall with very thin pilasters. Pilasters swollen in the distal portion of penial chamber (Fig. 5B).

Vagina (v) long, cylindrical and proximally with blackish tissues. Gametolytic duct (gd) short; proximally wider; distally tapering to small tube and terminated with gametolytic sac (gc). Free oviduct (fo) short; oviduct (ov) enlarged with curled lobules. Albumen gland (ag) curved ligulate. Hermaphroditic duct (hd) convoluted and connected to hermaphrodic gland (hg) (Fig. 5A).

Internal wall of vagina with smooth, longitudinal, vaginal pilasters (vp); with slightly deep crenulated ridges throughout vaginal chamber (Fig. 5B).

Radula. Teeth arranged in nearly straight rows, each row containing 74 (37-(4-6)-1-(4-6)-36) teeth. Central tooth monocuspid with spatulate and truncate cusp. Lateral teeth larger than central tooth; teeth no. 1-3 monocuspid, no. 4-6 bicuspid, endocone spatulate and ectocone very small with pointed cusp (Fig. 7A, B). Marginal teeth start from teeth no. 6-7. Inner marginal teeth tricuspid, endocone and ectocone very small with pointed cusp and mesocone large and spatulate. Outermost teeth (near radula edge) tricuspid, endocone and ectocone with two or more pointed cusps, and mesocone large with curved cusp (Fig. 7B, C).

Jaw crescent, with anterior convex cutting margin. Vertical ribs prominent, and variable in number and size (Fig. 5D).



Figure 2. A, B *Ganesella capitium* **A** lectotype UMZC I.102385/1 and **B** paralectotype UMZC I.102385/2–3 **C–E** *Ganesella hariola* **C** lectotype UMZC I.104370/1 **D** paralectotype UMZC I.104370/2–4 and **E** shell from Popa Mountain, Myanmar CUMZ 5134 **F–H** *Ganesella carinella* **F** lectotype SMF 27534a **G** paralectotype SMF 27534b and **H** shell from Takhli, Nakhonsawan CUMZ 5133.

Pallial system. Typical sigmurethran; heart (au and ve) located left of kidney (on right in Fig. 5C). Pulmonary cavity approximately 5× longer than wide. Pulmonary vein (puv) and venation on lung roof (l) distinct and well developed. Kidney (k) long, slender and extending from posterior side to approximately the middle of pulmonary

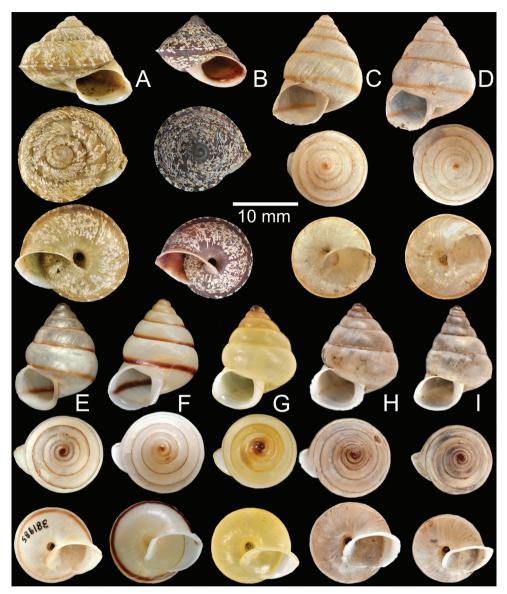


Figure 3. A, B *Ganesella carinella* A shell from Lopburi CUMZ 4282 and B shell from Tam Brichinda, Chiangmai CUMZ 4165 C–I *Ganesella rhombostoma* C lectotype NHMUK 20130215/1 D paralectotype NHMUK 20130215/2-3 E shell of "*harryleei* Thach, 2017" from Cambodia FMNH 381985 F shell from Klonghad, Srakeo CUMZ 5132 G shell from Chachoengsao CUMZ 5130 H shell from Sirisophon, Cambodia CUMZ 5131 and I shell from Srakaeo CUMZ 4286.

cavity. Ureter (ur) is a sigmoid, closed tube arising from apex of kidney, extending along right side of kidney, recurving near rectum (r). Rectal opening adjacent to anus (a) and pneumostome (pn) (Fig. 5C).

Distribution. *Ganesella carinella* is widely distributed in Thailand: northern area in Chiangmai, Phitsanuloke; northeastern area in Loei, Phetchaboon, Nakhonratchas-

rima; central area in Saraburi, Lopburi; eastern area in Srakeow, Chanthaburi; western area in Kanchanaburi.

Remarks. Hitherto, *Ganesella carinella* was regarded as a junior synonym of *G. capitium*. However, after Budha et al. (2012) described the genital apparatus of conchologically typical *G. capitium*, it became clear that *G. carinella* differs from the type species not only by having a more depressed shell with a strong peripheral keel but also by its longer penis and epiphallus, and its shorter vagina. In contrast, *G. capitium* has a more elevated trochoid shell, an angular last whorl, a shorter penis and epiphallus, and a longer vagina.

Ganesella carinella shows considerable variation in shell shape and colour. For example, specimens from Lopburi (Fig. 3A) tend to be paler and have a more descending aperture than specimens from Saraburi. Specimens from Chiangmai (Fig. 3B) tend to have more whitish spots on their shell than specimens from Lopburi and Saraburi. Yet, this conchological variation is not matched by consistent genital differences. Therefore, we conclude that the shell variation within this widely-distributed species only involves intraspecific polymorphism.

Ganesella rhombostoma (Pfeiffer, 1861)

Figs 1C, 3C-I, 5E-G, 7D-F, 8

Bulimus rhombostomus Pfeiffer, 1861: 194, 195. Pfeiffer 1868: 33.

Amphidromus rhombostomus: Pfeiffer and Clessin 1881: 214. Morlet 1889: 127. Morlet 1890: 121, 122, pl. 3, figs 6, 6a, b. Fischer and Dautzenberg 1904: 407.

Buliminus rhombostomus: Dautzenberg and Fischer 1906: 366, 367.

Buliminus rhombostomus var. *pupoidea* Dautzenberg and Fischer 1906: 367. Type locality: Hong-Chon, Cochinchine.

Giardia rhombostoma: Schileyko 2011: 46.

Pseudobuliminus harryleei Thach, 2017: 54, 55, figs 756–760. Type locality: Suburb of Battambang City, Battambang Province, Northwest Cambodia. New Synonym

- Pseudobuliminus tuongvyae Thach, 2017: 56, figs 751–755. Type locality: Ha Tien, Kien Gaing Province, Southwest Vietnam. New Synonym
- *Pseudobuliminus huberi* Thach, 2017: 55, figs 759–760. Type locality: 20 km of Kampong Trach District, Kampot Province, Northwest Cambodia. New Synonym

Type locality. Camboja [Cambodia].

Material examined. Type specimens. Three syntypes of *Bulimus rhombostomus* Pfeiffer, 1861 in H. Cuming collection, the shell that best matches with the original description is designated here as the lectotype NHMUK 20130215/1 (Fig. 3C, height 16.7 mm, width 11.5 mm) to stabilize the name; the other two shells from the same lot become the paralectotypes NHMUK 20130215/2-3 (2 shells; Fig. 3D, height 18.4 mm, width 13.2 mm).

Additional material. VIETNAM: Ha Tien, Kien Gaing Province, Southwest Vietnam: holotype of *Pseudobuliminus tuongvyae* Thach, 2017 MNHN-IM-2000-33203. **CAMBODIA:** Suburb of Battambang City, Battambang Province, Northwest Cambodia: holotype of *Pseudobuliminus harryleei* Thach, 2017 FMNH 381985 (Fig. 3E). Wat Thammaban Khiri, Sirisophon Town, Banteay Meanchey Province (13°37'58.1"N, 102°56'38.0"E): CUMZ 5131 (Fig. 3H). **THAILAND:** Tam Leoum, Klonghad District, Srakaeo Province: CUMZ 4286 (Fig. 3I). Tam Pha Pheung, Klonghad District, Srakaeo Province: CUMZ 5124. Tam Srithong, Klonghad District, Srakaeo Province: CUMZ 4070, 5118, 5132 (Fig. 3F). Tam Phet Phothong, Klonghad District, Srakaeo Province: CUMZ 4600, 5119. Khoa Phlapphueng Thong, Wang Somboon District, Srakaeo Province: CUMZ 4069. Wat Khao Maka, Muang District, Srakaeo Province: CUMZ 4071, 4598, 4599, 5130 (Fig. 3G). Tam Kaeo Sawanbandan, Pong Namron District, Chanthaburi Province: CUMZ 4285.Tam Rad, Tha Takiep District, Chachoengsao Province: CUMZ 5117.

Description. Shell. Shell small, sinistral, thin and trochoid. Apex acute with blackish colour; embryonic shell smooth. Whorls 5-6, increasing regularly, convex; suture wide and shallow. Shell surface smooth or with fine growth lines. Last whorl large, well rounded, keeled near aperture; with or without brownish spiral band. Shell monochrome white, yellow to light brownish and translucent. Aperture semi-ovate, open subventrally; lip expanded and whitish; parietal callus transparent. Umbilicus rimate; columella wide and whitish.

Genital organs. Atrium (at) short (N = 10). Penis (p) cylindrical, long and may be as long as the vagina. Epiphallus (e) and flagellum (fl) each about half as long as the penis. Vas deferens (vd) long and narrow, extending from free oviduct and connected to distal part of epiphallus. Penial retractor muscle (pr) long and slightly thickened (Fig. 5E).

Penial verge (pv) small, conical, and with smooth surface. Penial wall ribbed, forming a series of irregular, smooth longitudinal pilasters (pp) that encircle penial verge (Fig. 5F).

Vagina (v) large, cylindrical about as long as penis. Gametolytic duct (gd) short, cylindrical, gradually tapering towards gametolytic sac (gs). Free oviduct (fo) short, about half as long as vagina; oviduct (ov) enlarged with curled lobules. Albumen gland (ag) curved ligulate. Hermaphroditic duct (hd) convoluted and connected to hermaphrodic gland (hg) (Fig. 5E).

Vaginal wall with several smooth, longitudinal pilasters; vaginal wall itself with strong longitudinal ridges through the vaginal chamber (Fig. 5F).

Radula. Teeth arranged in nearly straight rows, each row containing 58 (29-(6-9)-1-(7-9)-28) teeth. Central tooth triangular, symmetric monocuspid with dull cusp. Lateral teeth asymmetric, teeth no. 1-6 monocuspid and no. 7-10 bicuspid with very small ectocone (Fig. 7D, E). Marginal teeth start from teeth no. 9-10, tricuspid, endocone very small to absent, mesocone large triangular, and ectocone very small with pointed cusp. Outermost marginal teeth (near radula edge) tricuspid, endocone small, mesocone large with curved cusp, and ectocone with one, two or more pointed cusps (Fig. 7E, F).

Jaw crescent, with anteriorly convex cutting margin. Vertical ribs thin, and variable in number and size (Fig. 5G).

Distribution. This species was formerly known from its type locality in Cambodia (Morlet 1889, 1890) and some inaccurate localities recorded from Vietnam (Schileyko 2011). In Thailand, it is known from several localities in Chachoengsao, Srakeo and Chanthaburi Provinces.

Remarks. Ganesella rhombostoma has long been overlooked and its taxonomic status has been unclear. The species has been erroneously assigned to Amphidromus Albers, 1850 and Giardia Ancey, 1907 (see Dautzenberg and Fischer 1906, Schileyko 2011). Yet, its trochoid shell and sub-ventrally opening aperture show that it belongs to neither of these genera, since Giardia (type species Bulimus siamensis Redfield, 1853) and Amphidromus (type species Helix perversus Linnaeus, 1758) have an elongate, ovate shell, a non-deflected last whorl, an ovate and laterally opening aperture, and a narrowly opened umbilicus (see also Schileyko (2003) and Sutcharit and Panha (2006) for further comparisons). Moreover, the anatomical evidence presented here suggests that this species rather belongs to Ganesella. However, the relationships between Ganesella and Giardia needs further investigation by molecular analysis.

Specimens from isolated limestone outcrops at Khao Maka, Chacheongsao are smaller and have a more ovate shell without a brownish spiral band on of the last whorl (Fig. 3G). However, anatomically they are indistinguishable from typical *G. rhombostoma* and, therefore, they are considered conspecific.

Ganesella halabalah Sutcharit & Panha, sp. nov. http://zoobank.org/65AC036B-D3B7-4AE4-A363-5496D1F42146 Figures 4A–C, 8

Type material. Holotype CUMZ 2608 (Fig. 4A, height 22.6 mm, width 23.3 mm, 5¾ whorls), paratypes CUMZ 2599 (3 shells; Fig. 4B, height 22.0 mm, width 22.1 mm) from the type locality. Paratype ZMB 53120 (1 shell; Fig. 4C) ex. Waterstradt coll. from Gunung Tahan, Kelantan, Malaysia.

Type locality. Sirindhorn Waterfall, Hala-Bala Wildlife Sanctuary, Waeng District, Narathivat Province, Thailand.

Diagnosis. The dextral, large, trocoid shell with pale green to yellow colour, obtuse apex and apertural lip with prominent beak-like deflection.

Description. Shell. Shell medium-sized (height 23.6 mm, width 25.1 mm), thin, dextral and trochoid. Apex obtuse; embryonic shell smooth and black. Whorls 5-6, increasing regularly, smooth; suture wide and shallow; shell surface with thin growth lines. Last whorl large, with well-developed peripheral keel and blunt at lower periphery. Shell colour pale green or yellow to monochrome creamy; earlier whorls paler; with or without brown spiral band on peripheral keel and lower periphery. Periostracum thin corneous, brownish and translucent. Aperture relatively large, semi-ovate; parietal callus transparent; columella wide and whitish. Apertural lip expanded, whitish, and angled with prominent beak-like deflection at peripheral keel. Umbilicus rimate and partially obscured by lower apertural lip.

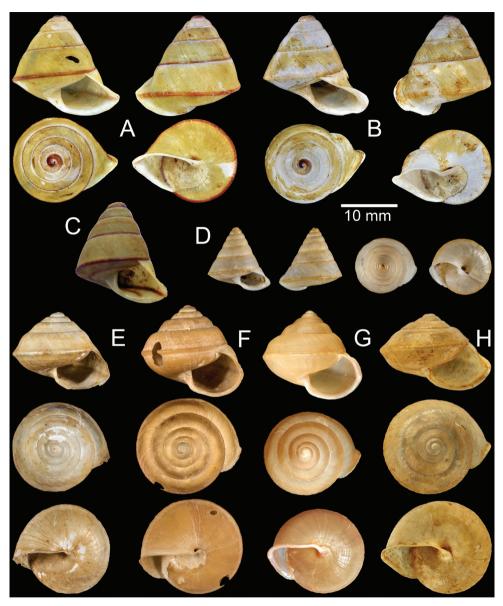


Figure 4. A–C *Ganesella halabalah* sp. nov. **A** holotype CUMZ 2608 **B** paratype CUMZ 2599 from the type locality and **C** paratype ZMB 53120 from Kelantan, Malaysia **D** *Ganesella perakensis*, syntype MNHN-IM-2000-1964. **E–G** *Globotrochus onestera* **E** lectotype MNHN-IM-2000-32456 **F** holotype of *"simonei* Thach & Huber, 2017" MNHN-IM-2000-33206 and **G** specimen from Vietnam CUMZ 5218 **H** *Globotrochus mellea*, holotype RBINS/MT/ 525051.

Etymology. The specific name is derived from the type locality Hala-Bala Wildlife Sanctuary, Narathivat, Thailand.

Distribution. This new species is currently known from the type locality (in Narathivat, Thailand) and Gunung Tahan, Kelantan, Malaysia, which is about 150 km

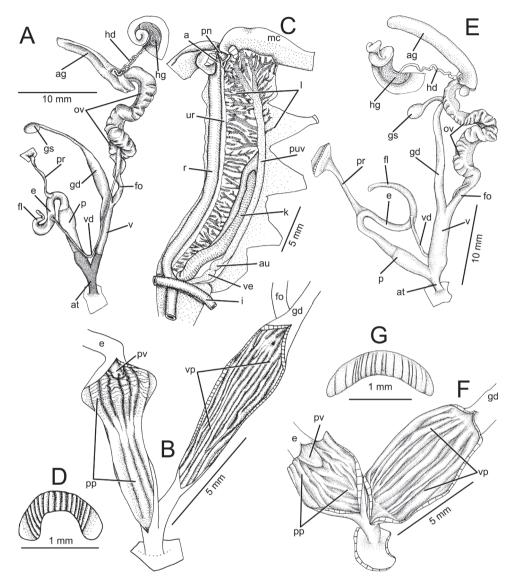


Figure 5. A–D *Ganesella carinella* from Saraburi **A** general view of genital system **B** internal structure of penis and vagina **C** pallial system and pulmonary cavity and **D** jaw **E–G** *Ganesella rhombostoma* from Srakaeo **E** general view of genital system **F** internal structure of penis and vagina and **G** jaw.

south of the type locality. The latter shell (Fig. 4C) was collected in 1901 in a tropical rain forest. This shell is in all aspects identical to the unique name-bearing type.

Remarks. Even though *Ganesella halabalah* sp. nov. is described from empty shells, its unique features mean that it cannot be confused with any other camaenid species from the area. Yet, with its trochoid shell and its prominent, beak-like apertural rostrum, *G. halabalah* sp. nov. does resemble a Papuininae phenotype. However, the geographic distribution of the Papuininae is largely restricted to New Guinea, Australia

and Melanesia (Schileyko 2003), though excluding the Greater Sunda Islands and Indochina. Given that the Malay Peninsula is a remote area for land snail dispersal between Australasia and Indochina (Hausdorf 2000), further anatomical and molecular evidence is needed to assess an eventual relationship with Papuininae.

This new species clearly differs from all *Ganesella* and other land snail species known in Indochina. The most similar species is *Ganesella perakensis* (Crosse, 1879) from Malaysia, which has a much smaller (average shell height < 10 mm), thin shell, and a simple apertural lip (Fig. 4D). *Ganesella halabalah* sp. nov. has a larger shell (average shell height > 20 mm), an obtuse apex and an aperture lip with a typical, prominent beak-like deflection.

The new species also differs from all *Kenyirus* Clements & Tan, 2012 species from Malaysia by having a conical spire, yellowish shell and narrower umbilicus. While *K. sodhii* Clements & Tan, 2012 has a depressed spire, long spout-like apertural rostrum on the peripheral keel, and 3-4 brownish spiral bands on the last whorl. In comparison *K. sheema* Foon et al., 2015 has subglobose shell, an angular last whorl, and with two brownish spiral bands below the periphery; while *K. balingensis* Tan et al., 2017 has a smaller and brownish shell.

Genus Globotrochus Haas, 1935

Ganesella (*Globotrochus*) Haas, 1935: 47. Zilch 1960: 611. Zilch 1966: 210. *Globotrochus*: Schileyko 2003: 1519. Schileyko 2011: 46.

Type species. Helix onestera Mabille, 1887, by monotypy.

Description. Shell trochoid, thin, translucent, 4-6 slightly convex whorls. Last whorl angulated or carinated, slightly descending in front. Colour light yellowish-brown. Embryonic shell smooth. Post apical whorls with irregular, thin, radial ridges and spiral line (smooth below peripheral angle or keel). Aperture ovate, moderately oblique, with slightly expanded and reflexed margins. Umbilicus closed. Shell height ranged from 16 to 17 mm and shell width ranged from 21 to 22 mm.

Genitalia typical of camaenids, but with thin (small size and fully functional) male genital organs (penis and epiphallus).

Radular teeth triangular and tricuspid.

Remarks. The weak development of male genitalia in *Globotrochus* is unusual among the Indochinese taxa, but is common in papuinid genera, such as *Papustyla* Pilsbry, 1893, *Letitia* Iredale, 1941, *Papunella* Clench & Turner, 1959 and *Wahgia* Clench & Turner, 1959 (Schileyko 2003). However, Papuininae are geographically confined to New Guinea, Australia and Melanesia (Schileyko 2003), and have never been recorded in Indochina. Therefore, it seems as if 'weak male genital parts' is an autapomorphy of *Globotrochus*.

Globotrochus differs from all other camaenid genera in Indochina (i.e., Chloritis, Satsuma, Ganesella and Neocepolis) by its weakly developed male genital organs. In contrast, the genera Chloritis, Ganesella and Neocepolis have typical camaenid genitalia, with well-developed male genital organs, including a relatively short to long penis, an epiphallus and penial verge, and a short to long flagellum. Furthermore, *Ganesella* has no penial appendix. *Satsuma* has a fully-developed male genital organ, with a short to long penial appendage, but without a penial verge (Solem 1993, Schileyko 2003, 2004, Sutcharit et al. 2007, Sutcharit and Panha 2010).

Currently, only two nominal species are assigned to *Globotrochus*. Based on the literature, museum specimens and recent field surveys, it seems as if *Globotrochus* is restricted to the north of Vietnam (Vermeulen and Maassen 2003, Schileyko 2003, 2011). However, an ambiguous locality record from Elephant Mountain, Laos (sensu Schileyko 2011: 46) needs verification.

Globotrochus onestera (Mabille, 1887)

Figs 1D, 4E–G, 6, 7G–I, 8

- *Helix onestera* Mabille, 1887a: 3. Mabille 1887b: 89, 90, pl. 2, figs 4, 5. Dautzenberg and Fischer 1908: 184, 185. Haas 1935: 46, 47. Fischer and Dautzenberg 1904: 404.
- Ganesella (Globotrochus) onestera: Zilch 1960: 611, fig. 2143. Zilch 1966: 210.
- Ganesella onestera: Richardson 1985: 140.
- *Globotrochus onestera*: Schileyko 2003: 1519, fig. 1959. Schileyko 2011: 46. Inkhavilay et al. 2019: 152, fig. 60c.
- *Diastole simonei* Thach & Huber in Thach 2017: 34, 35, figs 418–420. Type locality: Nho Quan District, Ninh Binh Province, North Vietnam. New Synonym.

Type locality. Tonkin [north Vietnam].

Material examined. Type material. This species was described on the basis of shells from the Balansa coll. Mabille (1887b: 89, 90, pl. 2, figs 4, 5) re-published the description of the species with an illustration of a shell. The MNHN-Malacologie collection contains two lots with syntypes. The first lot is from the Balansa coll. and consists of two shells with an original label giving the taxon name, collection locality and marked with the word "M. Balansa 1887. Type". One of the two shells is not damaged and its size closely matches the measurements in the original description and the illustration of Mabille (1887b: pl. 2, figs 4, 5). This shell is, therefore, here designated as the lectotype MNHN-IM-2000-32456/1 (Fig. 4E, height 15.1 mm, width 20.5 mm, 5 whorls). The second shell is broken up into three pieces and becomes the paralectoype MNHN-IM-2000-32456/2 (1 shell). The second lot MNHN-IM-2000-2073 consists of a shell with the marking "Type" on its label. Yet, this lot does not belong to the Balansa collection and was subsequently labeled as "*H. onestera* J. Mab. var.". Therefore, we exclude this lot from the type series of this nominal species (ICZN 1999: Art. 72.4.1).

Other material. VIETNAM: Nho Quan, District, Ninh Binh Province, North Vietnam: holotype of *Diastole simonei* Thach & Huber, 2017 MNHN-IM-2000-33206 (1 shell; Fig. 4F). Buc-Kan, Tonkin: NHMUK Kennard coll. (1 shell), MNHN (1 juvenile shell). Haiphong, Tonkin: NHMUK 1893.12.8.21–22 (2 shells), NHMUK Salisbury ex Beddome coll. (2 shells), SMF 27512 (3 shells), SMF 297452 (2 shells),

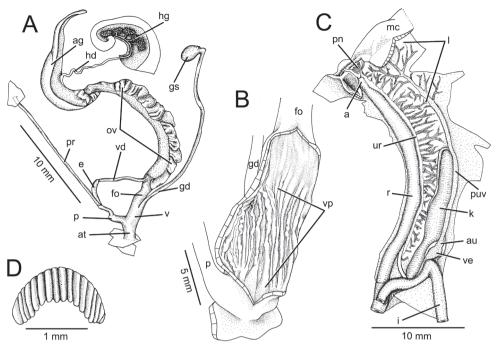


Figure 6. Anatomy of *Globotrochus onestera* from Cuc Phuong, Vietnam. **A** general view of genital system **B** internal structure of vaginal chamber **C** pallial system and pulmonary cavity and **D** jaw.

ZMB 47931 (1 shells), NHMW 23331 (1 shell). Nin-Cho, Nga Ba Tha, Tonkin: SMF 297450 (3 shells), NHMW 11734 (2 shells), NHMW 50818 (2 shells), NHMW Rusnov coll. (2 shells). Da-Bac, Tonkin: SMF 297451 (3 shells). Cuc Phuong National Park, Nho Quan District, Ninh Binh Province (20°14'59.0"N, 105°42'52.3"E): CUMZ 5128 (Fig. 4G), 5129.

Description. Shell. Shell medium-sized, dextral, thin and trochoid. Apex acute; embryonic shell smooth with brownish colour. Whorls 5-6, increasing regularly, slightly convex and slightly shouldered near suture; suture wide and shallow. Shell surface smooth or with fine growth lines. Last whorl large, angular with strong keel, beneath slightly convex. Shell monochrome, light brownish and translucent. Aperture semi-ovate; lip slightly expanded and brownish; parietal callus thin. Umbilicus closed; columella small and whitish.

Genitalia. Male genital organ (N = 3) thin (small size and fully function). Atrium (at) short, about as long as penis. Penis (p) short, proximally cylindrical, distally like a short, but wider tube. Penial sheath and penial verge absent. Epiphallus (e) small, as long as penis; flagellum absent. Vas deferens (vd), short, narrow, extending from free oviduct to tip of epiphallus. Penial retractor muscle (pr) relatively thin and long (Fig. 6A).

Vagina (v), cylindrical, short, size and shape similar to atrium. Gametolytic duct (gd) long and narrow; distally terminating at gametolytic sac (gs). Free oviduct (fo) relatively long; oviduct widened by curled lobules. Albumen gland (ag) curved lingu-

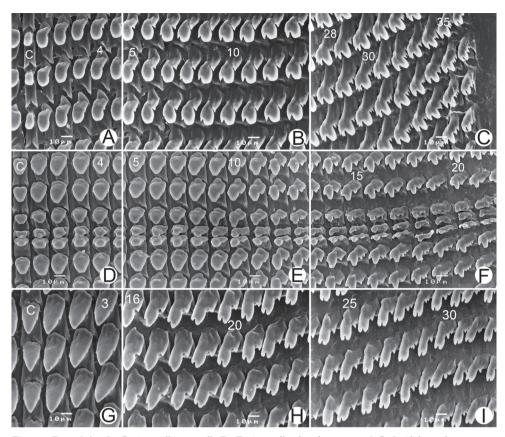


Figure 7. Radula. **A–C** *Ganesella carinella* **D–F** *Ganesella rhombostoma* and **G–I** *Globotrochus onestera* **A, D, G** central tooth with the first to the second lateral teeth **B, E, H** lateral teeth with the tricuspid marginal teeth transition **C, F, I** outermost marginal teeth. Numbers indicate order of lateral and marginal teeth. Central tooth indicated by 'C'.

late. Hermaphroditic duct (hd) convoluted and located between hermaphrodic gland (hg) (Fig. 6A).

Internal walls of vagina with several smooth surfaces of longitudinal pilasters (vp). Vaginal wall itself with strong longitudinal ridges through the vaginal chamber (Fig. 6B).

Radula. Teeth arranged in anteriorly pointed, nearly straight rows, each row containing about 79 (39-1-39) teeth. Central tooth symmetric tricuspid, mesocone large with pointed cusp, ectocone very small and located in the middle of tooth. Lateral and marginal teeth undivided. Inner teeth (no. 1-14) asymmetric tricuspid, endocone and ectocone small, and mesocone large with pointed cusp (Fig. 7G, H). Outermost teeth tricuspid, endocone small and located close to apex of teeth; mesocone relatively large with curved cusp, and ectocone located at base and cusps sometimes split into two pointed cusps (Fig. 7H, I).

Jaw crescent, with anteriorly convex cutting margin. Vertical ribs prominent, variable in number and size (Fig. 6D).

Pallial system. Typical sigmurethran; heart (auricle and ventricle) located left of kidney (on right in Fig. 6C). Pulmonary cavity approximately 5× longer than wide. Pulmonary vein and venation on lung roof distinct and well developed. Kidney elongated, slender and extending from posterior side of cavity to approximately half of pulmonary cavity. Ureter sigmoidal, closed tube arising from apex of kidney, extending along right side of kidney, recurving adjacent to rectum. Rectal opening adjacent to anus and mantle collar (Fig. 6C).

Distribution. This species is known from the type locality and recent records from Cuc Phuong National Park, Ninh Binh, and Nui Con Vui near Hai Phong, in northern Vietnam (Schileyko 2011).

Remark. Live specimens of this species were collected for the first time in 2006 at Cuc Phuong, Vietnam. This is a very humid area with tropical forest patches and limestone karst. The snails were collected on small shrubs, suggesting that it may be an arboreal species.

Recently, Thach (2017) described a new species from Vietnam under the southern Pacific Islands endemic genus *Diastole* Gude, 1913 (see Schileyko 2002). The species *Diastole simonei* Thach & Huber, 2017 was described from the same geographical area as *Globotrochus onestera*, the original description of which did not mention this species. The type specimens of *Globotrochus onestera* and *Diastole simonei* are identical in all characters. Hence, we treat *Diastole simonei* Thach & Huber, 2017 as a junior subjective synonym of *Globotrochus onestera*.

Globotrochus mellea (Bavay & Dautzenberg, 1915)

Figs 4H, 8

Helix (Ganesella?) mellea Bavay & Dautzenberg, 1915: 147, 148, pl. 5, figs 1–3. Ganesella mellea: Richardson 1985: 139. Globotrochus mellea: Schileyko 2011: 46.

Type locality. Nui-Ba-Dinh, Phu-Ha, and Phu-Ly [Vietnam].

Material examined. Type material. Only a single shell was available, viz. the syntype RBINS/MT/ 525051 ex. Dautzenberg collection (1 shell; Fig. 4H, height 18.4 mm, width 26.3 mm).

Description. Shell. Shell medium-sized, dextral, thin and depressed trochoid. Apex acute; embryonic shell smooth. Whorls 5-6, increasing regularly, slightly convex and slightly shouldered near suture; suture wide and shallow. Shell surface with fine growth lines. Last whorl large, angular with strong peripheral keel; slightly convex beneath. Shell monochrome, light brownish and translucent. Aperture semi-ovate; lip slightly expanded and brownish; parietal callus thin. Umbilicus closed; columella small and whitish.

Remark. *Globotrochus mellea* is similar to *Globotrochus onestera* in almost all shell characters, except for its larger last whorl, strong angular peripheral keel and more depressed trochoid shell. Therefore, we provisionally retain *Globotrochus mellea* as a distinct species.

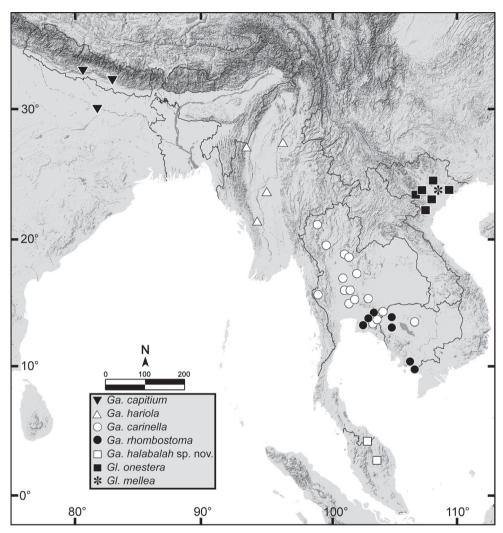


Figure 8. Geographic distribution of *Ganesella* spp. and *Globotrochus* spp.

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RESEARCH ARTICLE



Further study of two Chinese cave spiders (Araneae, Mysmenidae), with description of a new genus

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Abstract

The current paper expands knowledge of two Chinese cave spider species originally described in the genus *Maymena* Gertsch, 1960: *M. paquini* Miller, Griswold & Yin, 2009 and *M. kehen* Miller, Griswold & Yin, 2009. With the exception of these two species, the genus *Maymena* is endemic to the western hemisphere, and new evidence presented here supports the creation of a new genus for the Chinese species, which we name *Yamaneta* gen. nov. The male of *Y. kehen* is described for the first time. Detailed illustrations of the habitus, male palps and epigyne are provided for these two species, as well as descriptions of their webs. DNA sequences are provided for both *Yamaneta* species. We build on a previously published phylogenetic analysis of Mysmenidae to assess the phylogenetic position of *Yamaneta* and its relationship to true *Maymena*.

Keywords

China, Gaoligong Mountains, Maymena, new genus, phylogeny, symphytognathoids, troglobite

Introduction

The genus *Maymena* Gertsch, 1960 was established in the context of a taxonomic paper describing several American spiders of the family Symphytognathidae Hickman, 1931. At that time, the concept of Symphytognathidae was broader than it is today;

the taxa described therein are currently distributed among four families (Symphytognathidae, Mysmenidae Petrunkevitch, 1928, Anapidae Simon, 1895 and Theridiosomatidae Simon, 1881). The world's Symphytognathidae were reviewed and redefined by Forster and Platnick (1977), and several symphytognathid genera were transferred to other families, including *Maymena* to the Mysmenidae. Gertsch's (1960) original description included observations of several characteristics of *Maymena* but did not provide diagnostic characters for separating the genus from its close relatives. It was not until the recent publication of Lopardo and Hormiga (2015) that a rigorous and convincing diagnosis of *Maymena* was finally published.

Miller et al. (2009) described several symphytognathoid spiders from the Gaoligong Mountains, Southwest China. Two species from caves were placed in the genus *Maymena: M. paquini* Miller, Griswold & Yin, 2009 and *M. kehen* Miller, Griswold & Yin, 2009, the latter species being known only from females. The genus *Maymena* currently contains 13 described species (World Spider Catalog 2019). Except for the two Chinese species, all are known from the western hemisphere, from the USA south through Mexico, Central America, the Caribbean, and Peru. In addition, two undescribed taxa in Lopardo et al. (2011) considered to belong to *Maymena* (Lopardo and Hormiga 2015) were from Argentina. Most *Maymena* species are clearly associated with caves, although a few species are occasionally or typically found in surface habitats (Gertsch 1960, 1971, Brignoli 1974, Baert 1990, Eberhard et al. 1993).

In August 2008, students and professors of Sichuan University carried out a collecting survey in the Gaoligong Mountains. Both males and females of Miller et al.'s Chinese *Maymena* species were collected from their type localities and their web structures were discovered and photographed. In addition to new detailed morphological data and the description of the previously unknown male of *M. kehen*, multiple individuals of both species were sequenced for five loci. To test the relationships of Chinese *Maymena* to western *Maymena* and other Mysmenidae, we added this DNA sequence data to the molecular phylogenetic dataset of Lopardo et al. (2011).

Material and methods

Specimens were acquired by hand from the dark zone of caves and preserved in 95% ethanol. They were examined using a Leica M205 C stereomicroscope. Further details were studied under an Olympus BX43 compound microscope. Male palps and epigynes were examined and photographed after dissection. Epigynes were treated in lactic acid before being embedded in Arabic gum to take the photos of the vulva. To reveal the course of the spermatic ducts, male palps were also clarified using lactic acid and subsequently mounted in Hoyer's Solution. The left palp was photographed and described. Photos were taken with a Canon EOS 60D wide zoom digital camera (8.5 megapixels) mounted on an Olympus BX 43 compound microscope. The images were montaged using Helicon Focus 3.10 (Khmelik et al. 2006) image stacking software. All measurements are in millimeters. Leg measurements are given as follows: total length (femur, patella, tibia, metatarsus and tarsus). Tissue samples were taken from eight individual specimens of Chinese *Maymena* representing both known species. Whole genomic DNA was extracted from tissue samples with TIANamp Micro DNA Kit (TIANGEN) following the manufacturer's protocol for animal tissues. Five gene fragments were amplified in 25μ L reactions: mitochondrial large-subunit ribosomal RNA (16S), nuclear small-subunit ribosomal RNA (18S), nuclear large-subunit ribosomal RNA (28S), cytochrome *c* oxidase subunit I (COI), and histone H3 (H3). Primer pairs and PCR protocols are given in Table 1. Raw sequences were edited and assembled using BioEdit v.7.2.5 (Hall 1999). New sequences generated for this study were deposited in GenBank; accession numbers are reported in Table 2. All molecular vouchers and examined materials are deposited in the Natural History Museum of Sichuan University in Chengdu (**NHMSU**), China.

The most recent molecular phylogeny of Mysmenidae was Lopardo et al. (2011). Lopardo supplied alignments of the six genes used in their analysis (the five above plus the mitochondrial small-subunit ribosomal RNA 12S). Taxonomic determinations were updated according to notes in Lopardo and Hormiga (2015). The COI sequence "Mysmena-MYSM-018-MAD" (GU456888) was omitted because it was flagged on GenBank as removed at the submitter's request because of possible contamination. We used the MAFFT version 7 online service (https://mafft.cbrc.jp/alignment/server/add sequences.html) with the following settings to add the Chinese Maymena sequences to the existing alignments of the five shared loci (Strategy: Auto, scoring matrix for nucleotide sequences: 200PAM/k=2, Gap opening penalty: 1.53, offset value: 0.0; Katoh et al. 2017). Alignments of all six loci were concatenated in Geneious version 8.1.8 (https://www.geneious.com). The final alignment consisted of 6038 positions (Suppl. material 1). Uncorrected pairwise distances between terminals in the expanded alignment were calculated using MEGA X (Kumar et al. 2018) and are included as Suppl. material 2. We did not build on the morphological data matrix of Lopardo et al. (2011) or the expansion of this dataset in Lopardo and Hormiga (2015), and these data were not used in our analysis. This is because DNA sequence datasets are relatively simple to expand with additional data; it would be difficult for us to do the same for the large and complex morphological dataset without risking the introduction of errors and artifacts.

The most parsimonious tree was found using 1000 replicates of random taxon addition and TBR (Tree-Bisection-Reconnection) branch swapping using MEGA X (Kumar et al. 2018). To assess support, bootstrap values were calculated using MEGA X (Kumar et al. 2018) with 1000 bootstrap replicates, each consisting of 1000 replicates of random taxon addition and TBR branch swapping. Departing from the approach of Lopardo et al. (2011), gaps/missing data were treated as ambiguities, not as a 5th character state.

The Bayesian phylogenetic inference was performed using MrBayes version 3.2.6 (Ronquist and Huelsenbeck 2003) through the Cipres Science Gateway (Miller et al. 2010). Partitions and models followed Lopardo et al. (2011; table 4). A total of 10 partitions were defined (three independently modeled regions each for the nuclear ribosomal genes 18S and 28S, single model for each of the remaining four loci). The Bayesian search consisted of 50,000,000 generations using four chains, with the chain sampled every 1000 generations (see Suppl. material 1). Tracer version 1.7.1 (Rambaut et al. 2018) was used to establish the appropriate level of burn-in, which was set at 5000.

ALE	anterior lateral eyes	РС	paracymbium
AME	anterior median eyes	PLE	posterior lateral eyes
BC	base of cymbium	PME	posterior median eyes
BH	basal haematodocha	S	spermathecae
CA	cymbial apophysis	SD	spermatic duct
CD	copulatory ducts	Sp	scape
CS	clasping spine on leg I	Т	tegulum
Су	cymbium	Ti	tibia
CyC	cymbial conductor	TiS	setae on palpal tibia
CyFs	setae on cymbial fold	TS	tibial spine on leg I
E	embolus	TTr	trichobothria on tibia
FD	fertilization ducts		

Abbreviations appearing in text and figures are as follows:

Institutional acronyms:

NHMSU Natural History Museum of Sichuan University, Chengdu, China

Locus	Annealing temperature/time	Direction	Primer	Sequence 5'→3'	Reference
	48.5°/30s	F	LR-J-12864	CTCCGGTTTGAACTCAGATCA	Hormiga et al. 2003
16S	46.37308	R	LR-J-13360	GTAAGGCCTGCTCAATGA	This study
105	45°/30s	F	LR-J-12964	AACTCAGATCATGTAATAATT	This study
	437308	R	LR-J-13360	GTAAGGCCTGCTCAATGA	This study
18S	54.9°/30s	F	18S-1F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al. 1996
185	54.9750s	R	SSU rRNA reverse	GTGGTGCCCTTCCGTCAATT	Balczun et al. 2005
285	53.1°/30s	F	28Sa	GACCCGTCTTGAAACACGGA	Rix et al. 2008
203	55.17508	R	LSUR	GCTACTACCACCAAGATCTGCA	Rix et al. 2008
	46°/30s	F	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
COI	40 / 505	R	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
COI	45°/30s	F	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
	437508	R	C1-N-2191 (Nancy)	CCCGGTAAAATTAAAATATAAACTTC	Simon et al. 1994
	46°/30s	F	H3aF	ATGGCTCGTACCAAGCAGACVGC	Colgan et al. 1998
H3	407308	R	H3aR	ATATCCTTRGGCATRATRGTGAC	Colgan et al. 1998
115	49.4°/30s	F	H3nF	ATGGCTCGTACCAAGCAGAC	Colgan et al. 1998
	47.47308	R	H3nR	ATRTCCTTGGGCATGATTGTTAC	Colgan et al. 1998

Table 1. The loci, primer pairs, and PCR protocols used in this study.

Table 2. GenBank accession numbers for new DNA sequence data provided here.

Species	Identifier	Sex/Stage	165	185	28S	COI	H3
Yamaneta kehen	GlgMY14	Male	MK908789	MK908805	MK908797	MK895530	MK895538
	GlgMY14	Female	MK908790	MK908806	MK908798	MK895531	MK895539
	GlgMY14	Juvenile	MK908791	MK908807	MK908799	MK895532	MK895540
	GlgMY15	Male	MK908792	MK908808	MK908800	MK895533	MK895541
	GlgMY15	Female	MK908793	MK908809	MK908801	MK895534	MK895542
Yamaneta paquini	GlgMY16	Male	MK908794	MK908810	MK908802	MK895535	MK895543
	GlgMY16	Female	MK908795	MK908811	MK908803	MK895536	MK895544
	GlgMY16	Juvenile	MK908796	MK908812	MK908804	MK895537	MK895545

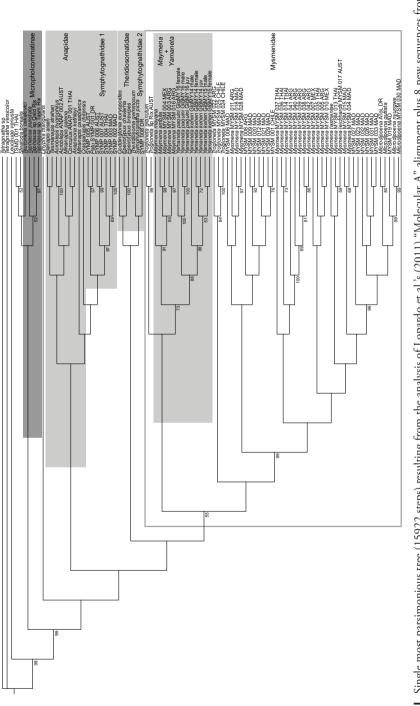
Results

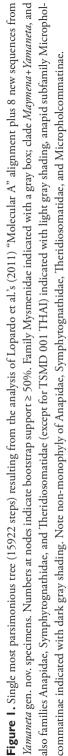
Parsimony analysis of the expanded sequence alignment recovered a single most parsimonious tree (Fig. 1). This tree features a monophyletic, but weakly supported, Mysmenidae. Western hemisphere and Chinese *Maymena* are reciprocally monophyletic, with moderate bootstrap support. The two Chinese species are coherent. Few clades, especially along the backbone of the phylogeny, have high bootstrap support, and relationships among outgroup taxa are complicated. The low support values seem in part to be attributable to a number of unstable taxa. *Maymena* (western and Chinese) and *Trogloneta* Simon, 1922 together form a paraphyletic complex, with one branch of *Trogloneta* sister to *Maymena* (western and Chinese) and the other *Trogloneta* branch sister to the remaining Mysmenidae.

After 50,000,000 generations of Bayesian analysis, the average deviation of split frequencies fell below 0.05. The combined effective sample sizes of the two MCMC chains were 7425.9 and 7654.5 (12,520.9 combined), comfortably above the recommended minimum of 200 (Lanfear et al. 2016). The Bayesian topology (Fig. 2) features a monophyletic Mysmenidae, which in contrast to the parsimony analysis enjoys high support from posterior probability. As in the parsimony analysis, western and Chinese *Maymena* are reciprocally monophyletic with high support, and the two Chinese species are coherent. However, branch lengths suggest a long separation between the Chinese and western lineages. The Bayesian analysis also indicates complicated relationships among the outgroup taxa. *Maymena* (western and Chinese) and *Trogloneta* together form a paraphyletic complex similar to that found in the parsimony analysis; one branch of *Trogloneta* is sister to all other Mysmenidae, and the other branch of *Trogloneta* is sister to the remaining Mysmenidae, except for *Maymena* (western and Chinese).

Discussion

Monophyly of and relationships between the so-called symphytognathoid families (including Mysmenidae, Anapidae, Theridiosomatidae and Symphytognathidae) are complicated and inconsistent across various analyses. Early attempts based on morphological data (e.g., Griswold et al. 1998) proposed a "symphytognathoid" clade composed of monophyletic families, but Schütt (2003) warned that some of this could be based on a syndrome of parallel reductions and simplifications related to the evolution of small size. DNA sequences initially seemed promising as a source of phylogenetic data independent of morphology, where homology assessment could be confused with parallel evolution. The analysis of Rix et al. (2008) tested the relationships of Anapidae and Micropholcommatidae (currently considered part of Anapidae; Schütt 2003, Lopardo et al. 2011, World Spider Catalog 2019), with representatives of several other relevant families, based on DNA sequence data from two nuclear ribosomal loci. Results concerning the primary focal group of the study, the Micropholcommatidae, were fairly robust and consistent.





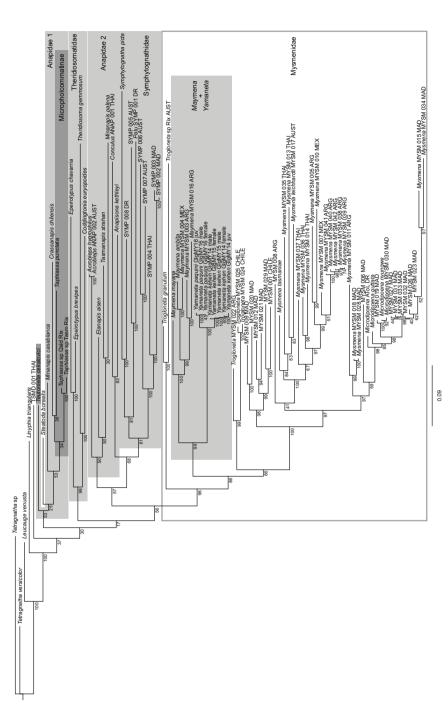


Figure 2. Topology from Bayesian mixed model analysis based on Lopardo et al.'s (2011) "Molecular A" alignment plus 8 new sequences from *Yamaneta* gen. nov. specimens. Numbers at nodes indicate percent posterior probabilities; other conventions as in Fig. 1. Note diphyly of Anapidae, nesting of most Micropholcommatinae within "Anapidae 1", and placement of *Teutoniella cekalovici* outside other micropholcommatines.

However, results regarding the Anapidae and key outgroup taxa were generally of poor resolution and inconsistent across tree-building methods. This despite being built upon what was, for the time at least, a rigorous and sophisticated analytical approach. The results of the analyses reported in Lopardo et al. (2011) were similarly sensitive to changes in analytical parameters. This analysis was based on an expanded set of loci compared to Rix et al. (2008), plus a set of morphological characters, and many permutations of data partitions and phylogenetic optimization methods were employed. The monophyly of Mysmenidae was relatively robust to permutations of the analysis, but the inclusion of morphological data had a tendency to support the monophyly of outgroup families, which sometimes collapsed in analyses based on molecular sequences alone. A series of studies by Dimitrov et al. (2012, 2016) used roughly the same set of loci with a progressively expanded sample of taxa to explore deep questions of spider relationships. These consistently recovered two clades of anapids and never found support for the monophyly of symphytognathoid families. The phylogenetic analysis of Wheeler et al. (2017) further expanded the taxon sample, but not the selection of loci. Anapidae (including a monophyletic Micropholcommatinae), Symphytognathidae, and Mysmenidae were each monophyletic and moderately well supported; Theridiosomatidae was monophyletic only after the pruning of one problematic taxon, and still presented with low support. The four symphytognathoid families together were found to be closely related but not monophyletic.

The parsimony and Bayesian phylogenies presented here disagree about outgroup relationships in several important ways, including the monophyly of Anapidae, its relationship to Micropholcommatinae, and the sister clade to Mysmenidae. Such results are not surprising, because previous studies relying on the same limited set of reliable loci have seen similar results for nearly a decade, and also because taxon sampling outside Mysmenidae in this study and its predecessors (Lopardo et al. 2011, Lopardo and Hormiga 2015) is very limited.

Recent phylogenomic approaches have finally expanded the volume of DNA sequence data used to investigate spider phylogeny (Bond et al. 2014, Fernández et al. 2014, 2018, Garrison et al. 2016), but only Fernández et al. (2018) has achieved the taxon sampling necessary to address some of the longstanding symphytognathoid questions. Their study, based on ca 2500 genes, found monophyletic Theridiosomatidae (4 terminals), Mysmenidae (3 terminals) and Anapidae (2 terminals; Symphytognathidae was not represented); none of the symphytognathoid families present were found to be sister taxa. We look forward to further studies with greatly expanded DNA sequence coverage and the taxon sample necessary to address longstanding symphytognathoid questions.

Lopardo and Hormiga (2015) noted that the placement of the several mysmenid species and genera described by Miller et al. (2009) had yet to be tested phylogenetically; here we have begun to rectify this. Both parsimony and Bayesian analyses found the Chinese *Maymena* species formed a clade sister to the remaining *Maymena*. This suggests that placing the Chinese species in *Maymena* was defensible. However, multi-

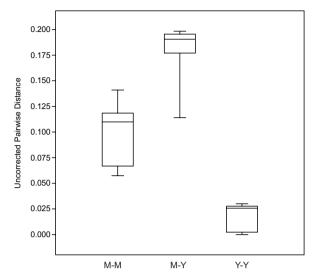


Figure 3. Box plot of uncorrected pairwise distances between terminals representing *Maymena* (M-M), *Yamaneta* gen. nov. (Y-Y), and between *Maymena* and *Yamaneta* (M-Y). See Suppl. material 2 for complete distance matrix.

ple lines of available evidence seem sufficient to justify the creation of a new genus to accommodate the Chinese species. The two Chinese *Maymena* are the only members of the genus known from beyond the western hemisphere. Although the Chinese *Maymena* resemble and share several characters with those from the west (e.g., aspects of the genital morphology, trichobothria on the male palpal tibia, troglophily, web architecture), they also express distinguishing features (e.g., elongate male palpal tibia and patella, relatively long and setose epigynal scape). Bayesian branch lengths (Fig. 2) and uncorrected pairwise distances based on our alignment (Fig. 3) both indicate a degree of distinctness between the Chinese and western *Maymena*.

Taxonomy

Mysmenidae Petrunkevitch, 1928

Genus Yamaneta Miller & Lin, gen. nov. http://zoobank.org/5383A9BC-F125-4D4B-8603-BDA44B06163D

Type species. Maymena paquini Miller, Griswold & Yin, 2009.

Etymology. Formed from *Yama*, the figure in Chinese mythology who oversees the realm of the dead, and *-neta* ($-\nu\dot{\eta}\tau\eta\varsigma$), an element in several spider names conventionally taken to mean 'spinner' (Cameron 2005). The gender is masculine.

Diagnosis. Distinguished from other mysmenid genera except *Maymena* by the presence of a modified spatulate seta on the PLS (Miller et al. 2009: fig. 57D, F; Lo-

pardo and Hormiga 2015: fig. 11G, H), the proximal position of the male metatarsus I clasping spur (more proximal in Maymena than Yamaneta; Miller et al. 2009: fig. 53A; Lopardo and Hormiga 2015: fig. 16G), the shape of the apical part of the cymbium, which appears to form a functional conductor (Miller et al. 2009: fig. 55A; Lopardo and Hormiga 2015: fig. 10D, G) that interacts with the embolus. The presence of trichobothria on the male palpal tibia is a rare character in Mysmenidae, occurring in such genera as Maymena, Yamaneta, Trogloneta, Mysmenopsis Simon 1898 and Isela Griswold, 1985. Distinguished from Maymena by the elongate male palpal tibia and patella, long and setose epigynal scape, by the absence of a modified seta with a long row of branches near the major ampullate gland spigot on the anterior lateral spinnerets (Miller et al. 2009: fig. 57B), and by the clustered arrangement of male epiandrous fusules (Miller et al. 2009: fig. 56D; dispersed in Maymena: Lopardo and Hormiga 2015: figs 12B, 16A). The type species Maymena mayana (Chamberlin & Ivie, 1938) has been described as having a small rounded scape (Gertsch 1960), although this is a glabrous structure (setose in Yamaneta), and M. mayana is coded as absent for a scape in phylogenetic data matrices (Lopardo et al. 2011, Lopardo and Hormiga 2015: character 60). There are also similarities in the female reproductive path shared between M. mayana and Yamaneta, such as the fertilization ducts arising from the copulatory ducts rather than the spermathecae (Lopardo and Hormiga 2015: fig. 128B); internal female reproductive structures and spinneret spigot morphology have been documented for only a few Maymena species.

Description. Relatively large mysmenids (>2 mm). Femoral spots on legs I and II in female, leg I only in male. Legs with macrosetae on the femora, tibiae, and metatarsi, especially in the anterior legs. Male clasping spurs arise from distal part of tibia I and basal third of metatarsus I. Leg formula IV-I-II-III. Carapace subovate, ocular area slightly raised. Eight eyes in two rows. AME black and with dark base, others reflective. ALE and PLE contiguous. ARE procurved, PRE straight (Fig. 4). Clypeus moderately high, inclined from anterior lip to eye region. Cervical groove and thoracic fovea indistinct. Thoracic region flat, smooth, nearly hairless except for the eye region and midline. Chelicerae strong, deeper color than carapace. Endites nearly rectangular. Labium rectangular, fused to sternum. Sternum heart-shaped, flat, hirsute, posterior corner sharp (Figs 4B, E, 7B, E). Abdomen globular dorsally, ovate laterally, mottled light to medium gray or tan, sparsely covered with black setae. Spinnerets distinctly sclerotized, the anteriors larger than the posteriors; colulus small, with two tiny setae; anal tubercle pale yellow (Figs 4, 7). Male palpal patella and tibia elongate, palpal tibia with at least one trichobothrium. Hook-like apophysis on prolateral face of cymbium (Miller et al. 2009: fig. 55C). Cymbium folded distally, forming functional conductor. Tegular conductor absent. Embolus long and filiform arising from proximal part of palpal bulb. Epigyne with setose scape extending nearly to the tracheal spiracle (Figs 4E, F, 7E, F). Scape with notched lateral margins (Figs 6D, 9D), profile distinctly curved at dorsum (Figs 6B, 9B). Spermathecae globular, copulatory ducts arise from mesal part of spermathecae, loop near base of scape, terminate in paired openings near

middle of scape (Figs 6C, D, 9C, D). Fertilization ducts arise from copulatory ducts rather than spermathecae (Figs 6D, 9D). Male epiandrous fusules with clustered arrangement (Miller et al. 2009: fig. 56D). PLS with modified spatulate seta (Miller et al. 2009: fig. 57D, F; Lopardo and Hormiga 2015: fig. 11G, H).

Composition. *Yamaneta kehen* (Miller, Griswold & Yin, 2009) comb. nov., *Yamaneta paquini* (Miller, Griswold & Yin, 2009) comb. nov.

Distribution. Gaoligong Mountains, Yunnan, China.

Affinity with Maymena. Lopardo and Hormiga (2015) highlighted several key morphological characteristics of Maymena and discussed their status as putative synapomorphies and utility as diagnostic characters. These observations were based on a selection of western species, but many of the characteristics discussed are consistent with Yamaneta. The modified spatulate seta on the PLS (Lopardo and Hormiga 2015: fig. 11G, H) is present in Yamaneta paquini (Miller et al. 2009: fig. 57D, F [indicated by arrow]). The variable shape of the aciniform gland spigots on both pairs of posterior spinnerets and in both sexes (Lopardo and Hormiga 2015: fig. 11F-H, 13F, G) is visible in Yamaneta paquini (Miller et al. 2009: fig. 57C-F). However, the modified seta with a long row of branches near the major ampullate gland spigot on the anterior lateral spinnerets (Lopardo and Hormiga 2015: fig. 11E, 13C, 16B) is not visible in Yamaneta paquini (Miller et al. 2009: fig. 57B). The presence of macrosetae on the femora, tibiae, and metatarsi, especially on the anterior legs (Lopardo and Hormiga 2015: figs 140M, 141C), is shared by Maymena, Yamaneta (Miller et al. 2009: fig. 53A, B, see also text), and the kleptoparasitic clade Mysmenopsinae. A roughly cylindrical palpal tibia (i.e., distal width less than two times proximal width; Lopardo and Hormiga 2015: fig. 10A) is difficult to discern in Yamaneta, which have the palpal tibia elongated and modified in shape compared to Maymena species (Figs 5, 8). Like Maymena, males of Y. paquini and Y. kehen have a femoral spot on femur I, a clasping spur in a proximal position on male metatarsus I (Miller et al. 2009: fig. 53A; Lopardo and Hormiga 2015: fig. 16G), and lack a tegular conductor. Also consistent across Maymena and Yamaneta is the presence of macrosetae on the female palpal tarsus (Miller et al. 2009: fig. 53B; Lopardo and Hormiga 2015: figs 13A, 15A). Unlike the Maymena species studied by Lopardo and Hormiga (2015: fig. 10H), Yamaneta species do not appear to have a deeply grooved embolic rim. As in the Maymena species studied by Lopardo and Hormiga (2015), described as having the primary cymbial conductor apically bent over the ventral side (Lopardo and Hormiga 2015: figs 10D, G, 14D), the cymbium of Yamaneta species has a complex, almost helical shape, with the embolus and cymbium interacting distally (Figs 5, 8; Miller et al. 2009: figs 54, 55A, B). Unlike Maymena (Lopardo and Hormiga 2015: figs 12B, 16A), where the epiandrous fusules are arranged in a dispersed row, those of *Y. paquini* are arranged in a few rough clusters (Miller et al. 2009: fig. 56D). Lopardo and Hormiga (2015: 778) report that the respiratory system of Maymena distinguishes it from other mysmenids, but this has not been investigated for Yamaneta.

Yamaneta kehen (Miller, Griswold & Yin, 2009) comb. nov.

Figs 4-6, 10A

Material examined. CHINA • $2\sqrt[3]{}, 25\text{}\Circlelee}$ multiple juveniles; Yunnan Province, Nujiang Lisu Autonomous Prefecture, Fugong County, Shiyueliang Town, Lishadi Village, 3.9 km E of Yamu River Fork, "a nameless cave"; 27.12818N, 98.86014E; 1500 m a.s.l.; 18 Aug. 2018; Y.C. Li, Y. Li, Y.F. Shu & Y.C. Lin leg.; NHMSU • $1\sqrt[3]{}$; same data as for preceding; GenBank: MK908789, MK908805, MK908797, MK895530, MK895538; GlgMY14 male • 1; same data as for preceding; GenBank: MK908790, MK908806, MK908798, MK895531, MK895539; GlgMY14 female • 1 juvenile; same data as for preceding; GenBank: MK908791, MK908807, MK908799, MK895532, MK895540; GlgMY14 juv. • $1\sqrt[3]{}$; same data as for preceding; GenBank: MK908793, MK895541; GlgMY15 male • $1\]$; same data as for preceding; GenBank: MK908793, MK895541; GlgMY15 male • $1\]$; same data as for preceding; GenBank: MK908793, MK895542; GlgMY15 female.

Diagnosis. *Yamaneta kehen* can be distinguished from its congener *Y. paquini* by having only a single proximal-dorsal trichobothrium (TTr) and a single long distalventral setae (TiS) on the male palpal tibia, but 2 of each in *Y. paquini* (Fig. 5A, B vs. Fig. 8A, B); and by the form of the epigyne in the female, which features a basally wider and shorter scape (Fig. 6C vs. Fig. 9C), a distinctly notched lateral margin of the scape (Fig. 6D vs. Fig. 9D), and a more strongly curved profile of the dorsal surface of the scape (Fig. 6B vs. Fig. 9B). Lateral margins of scape proximal to notches are nearly parallel in *Y. paquini* (Fig. 9C, D), converging in *Y. kehen* (Fig. 6C, D).

Description. Male. Somatic coloration and characters see Fig. 4A-C.

Measurements: Total length 2.19. Carapace 1.13 long, 1.12 wide. Clypeus 0.26 high. Sternum 0.57 long, 0.58 wide. Abdomen 1.09 long, 1.10 wide. Length of legs: I 6.98 (2.13, 0.66, 1.77, 1.27, 1.15); II 5.92 (1.83, 0.57, 1.46, 1.12, 0.94); III 3.93 (1.28, 0.39, 0.86, 0.74, 0.66); IV 4.25 (1.42, 0.40, 0.97, 0.83, 0.63).

Male palp (Fig. 5A–F): Femur long, curved mesially (Fig. 5E, F); patella elongate, with a distal-dorsal spine (Fig. 5E, F); tibia swollen, longer than patella, bears cluster of stiff dorsal setae and a dorsal trichobothrium proximally, with a long ventral setae distally (Fig. 5B: TiS). Cymbium broad, covers ventral part of bulb, dorsal part exposed (Fig. 5A–C). Paracymbium with long thick setae (Fig. 5C). Cymbial apophysis small hooked, sclerotized, on prolateral surface of cymbium (Fig. 5A–C). Cymbial conductor translucent, falcate, bearing dense cluster of long setae on prolateral face (Fig. 5C). Tegulum smooth, without process; spermatic duct long, twisted on base of embolus (Fig. 5D). Embolus long, wire-like, with proximal origin (Fig. 5B, D).

Female. See Fig. 4D–F. Somatic characters as in male, but larger in size.

Measurements: Total length 2.48. Carapace 1.12 long, 1.10 wide. Clypeus 0.25 high. Sternum 0.64 long, 0.63 wide. Abdomen 1.43 long, 1.30 wide. Length of legs: I 6.46 (1.95, 0.63, 1.65, 1.21, 1.02); II 5.55 (1.66, 0.61, 1.38, 1.05, 0.85); III 3.82 (1.22, 0.42, 0.84, 0.73, 0.61); IV 4.09 (1.44, 0.40, 0.93, 0.75, 0.57).

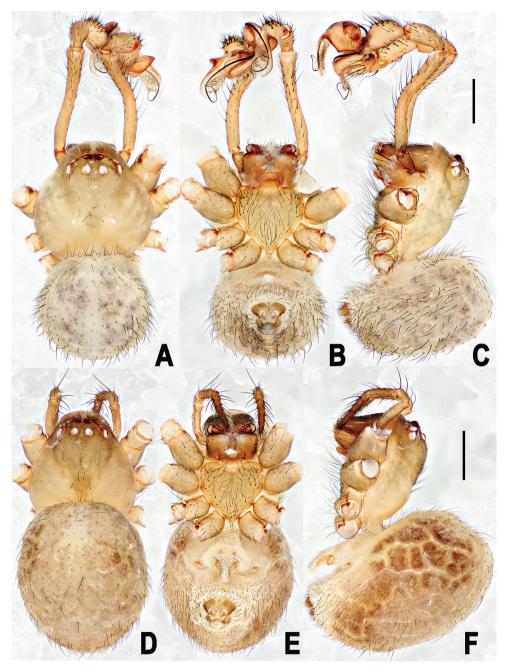


Figure 4. *Yamaneta kehen* (Miller, Griswold & Yin, 2009) comb. nov. from Fugong Co., Lishadi, "a nameless cave" **A–C** Male habitus **D–F** female habitus **A, D** dorsal **B, E** ventral **C, F** lateral. Scale bars: 0.50 mm.

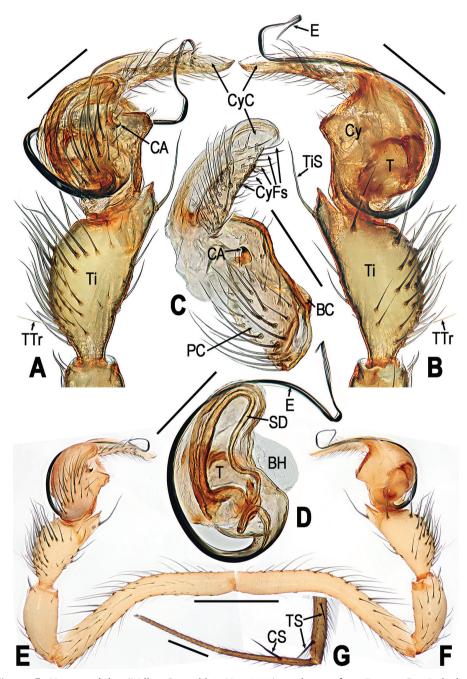


Figure 5. *Yamaneta kehen* (Miller, Griswold & Yin, 2009) comb. nov. from Fugong Co., Lishadi, "a nameless cave", male **A**, **B**, **E**, **F** Left palp **C** cymbium **D** palpal bulb **G** partial leg I **A**, **E**, **G** prolateral **B**, **F** retrolateral **C** prolateral **D** retrolateral. Abbreviations: **BC** base of cymbium; **BH** basal haematodocha; **CA** cymbial apophysis; **CS** clasping spine on leg I; **Cy** cymbium; **CyC** cymbial conductor; **CyFs** setae on cymbial fold; **E** embolus; **PC** paracymbium; **SD** spermatic duct; **T** tegulum; **Ti** tibia; **TS** tibial spine on leg I; **TTr** trichobothrium on tibia; **TiS** setae on palpal tibia. Scale bars: 0.50 mm.

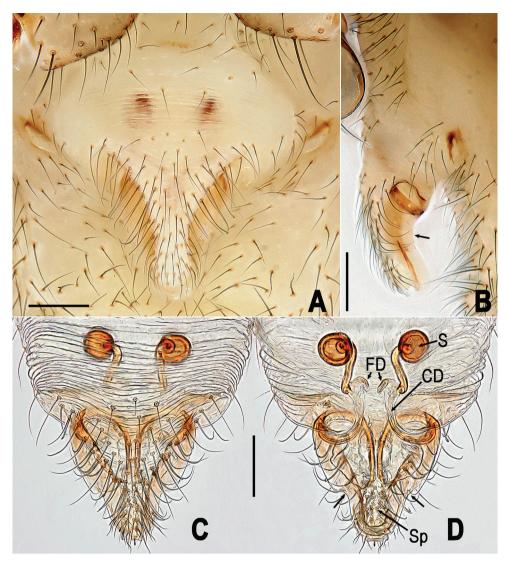


Figure 6. *Yamaneta kehen* (Miller, Griswold & Yin, 2009) comb. nov. from Fugong Co., Lishadi, "a nameless cave", female genitalia **A**, **B** Epigyne **C–D** vulva (lactic acid treated) **A**, **C** ventral **B** lateral **D** dorsal. Unlabeled arrow in **B** indicates curved profile of dorsal surface of scape, in **D** indicates notched lateral margin of scape. Abbreviations: **CD** copulatory ducts; **FD** fertilization ducts; **S** spermathecae; **Sp** scape. Scale bars: 0.10 mm.

Vulva (Fig. 6A–D): Scape relatively wide basally (Fig. 6A, C), with distinctly notched lateral margins (Fig. 6D) and strongly curved dorsal profile (Fig. 6B). Lateral margins of scape proximal to notches are converging (Fig. 6C, D).

Distribution. Known from a single cave in Yunnan, China.

Natural history and web architecture. This species lives in the dark zone of the cave. They build a web typical of *Maymena* (e.g., Eberhard 1986, Lopardo and Hor-

miga 2015: fig. 147D, E). Aerial lines extend upwards from web radii and hub and are attached to frame lines or the substrate above. The web is under tension and the hub is lifted. The catching spiral is dense and nearly horizontal. Above the catching spiral is an irregular network of horizontal and angled lines under tension (Fig. 10A). The spider usually hangs in the irregular area above the catching spiral.

Yamaneta paquini (Miller, Griswold & Yin, 2009) comb. nov.

Figs 7–9, 10B

Material examined. CHINA • 23322 juveniles; Yunnan Province, Nujiang Lisu Autonomous Prefecture, Lushui County, Daxingdi Town, Walayaku [cave]; 26.13198N, 98.86149E; 940 m a.s.l.; 24 June 2016; Y.C. Li leg.; NHMSU • 2332022 multiple juveniles; same data as for preceding; 18 Aug. 2018; Y.C. Li, Y. Li, Y.F. Shu & Y.C. Lin leg.; NHMSU • 13; same data as for preceding; GenBank: MK908794, MK908810, MK908802, MK895535, MK895543; GlgMY16 male • 12; same data as for preceding; GenBank: MK908795, MK908811, MK908803, MK895536, MK895544; GlgMY16 female • 1 juvenile; same data as for preceding; GenBank: MK908796, MK908812, MK908804, MK895537, MK895545; GlgMY16 juv.

Diagnosis. See Y. kehen.

Description. Male. Somatic characters see Fig. 7A–C, and Miller et al. 2009: 56. *Measurements*: Total length 2.22. Carapace 1.10 long, 1.00 wide. Clypeus 0.25 high. Sternum 0.58 long, 0.60 wide. Abdomen 1.13 long, 0.99 wide. Length of legs: I 6.95 (2.10, 0.66, 1.79, 1.25, 1.15); II 5.88 (1.82, 0.57, 1.45, 1.12, 0.92); III 3.96 (1.31, 0.39, 0.86, 0.74, 0.66); IV 4.24 (1.42, 0.40, 0.96, 0.83, 0.63).

Male palp (Fig. 8A–F): Femur long, curved mesially (Fig. 8E, F); patella elongate, with a distal-dorsal spine (Fig. 8E, F); tibia swollen, longer than patella, bearing dense stiff dorsal setae and 2 dorsal trichobothrium proximally, 2 long ventral setae distally (Fig. 8A: TiS). Cymbium broad, covers ventral part of bulb, dorsal part exposed (Fig. 8A–C). Paracymbium with long thick setae (Fig. 8C). Cymbial apophysis small hooked, sclerotized, on prolateral surface of cymbium (Fig. 8A–C). Cymbial conductor translucent, falcate, bearing dense cluster of long setae on prolateral face (Fig. 8C). Tegulum smooth, without process; spermatic duct long, twisted on base of embolus (Fig. 8D). Embolus long, wire-like, with proximal origin (Fig. 8B, D).

Female. Somatic characters see Fig. 7D–F, and Miller et al. 2009: 56.

Measurements: Total length 2.48. Carapace 1.16 long, 1.12 wide. Clypeus 0.25 high. Sternum 0.64 long, 0.63 wide. Abdomen 1.43 long, 1.30 wide. Length of legs: I 6.66 (1.96, 0.64, 1.64, 1.31, 1.11); II 5.81 (1.73, 0.62, 1.36, 1.13, 0.97); III 3.98 (1.27, 0.40, 0.85, 0.78, 0.68); IV 4.69 (1.50, 0.66, 1.03, 0.85, 0.65).

Vulva (Fig. 9A–D): Scape relatively narrow basally (Fig. 9A, C), with gently notched lateral margins (Fig. 9D) and moderately curved dorsal profile (Fig. 9B). Lateral margins of scape proximal to notches are nearly parallel (Fig. 9C, D).

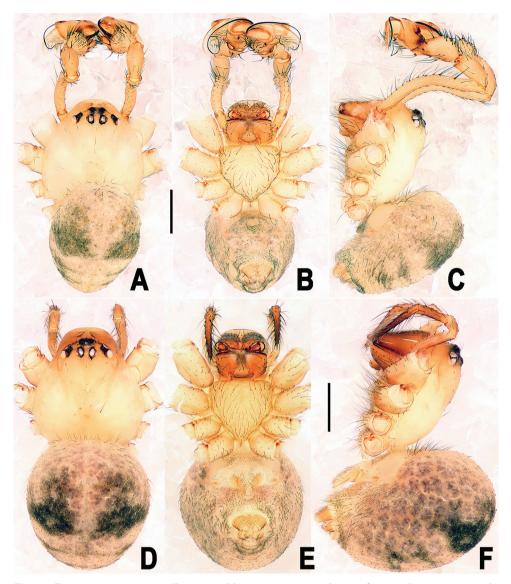


Figure 7. Yamaneta paquini (Miller, Griswold & Yin, 2009) comb. nov. from Lushui Co., Daxingdi, Walayaku [cave], male and female A-C Male habitus D-F female habitus A, D dorsal B, E ventral C, F lateral. Scale bars: 0.50 mm.

Distribution. Known from a single cave in Yunnan, China.

Natural history and web architecture. This species lives in the dark zone of the cave. The web documented in Fig. 10B resembles that of *Y. kehen*, except that it is under less tension, causing lines in the superstructure to bow. The occupant of this web was observed below the catching spiral.

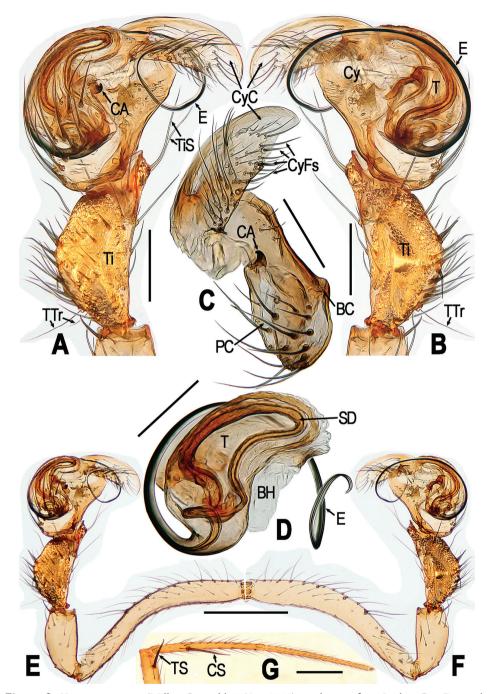


Figure 8. *Yamaneta paquini* (Miller, Griswold & Yin, 2009) comb. nov. from Lushui Co., Daxingdi, Walayaku [cave], male **A**, **B**, **E**, **F** Left palp **C** cymbium **D** palpal bulb **G** partial leg I **A**, **E**, **G** prolateral; **B**, **F** retrolateral; **C** prolateral; **D** retrolateral. Abbreviations: **B**C base of cymbium; **BH** basal haematodocha; **CA** cymbial apophysis; **CS** clasping spine on leh I; **Cy** cymbium; **CyC** cymbial conductor; **CyFs** setae on cymbial fold; **E** embolus; **PC** paracymbium; **SD** spermatic duct; **T** tegulum; **Ti** tibia; **TS** tibial spine on leg I; **TTr** trichobothria on tibia; **TiS** seta on palpal tibia. Scale bars: 0.50 mm.

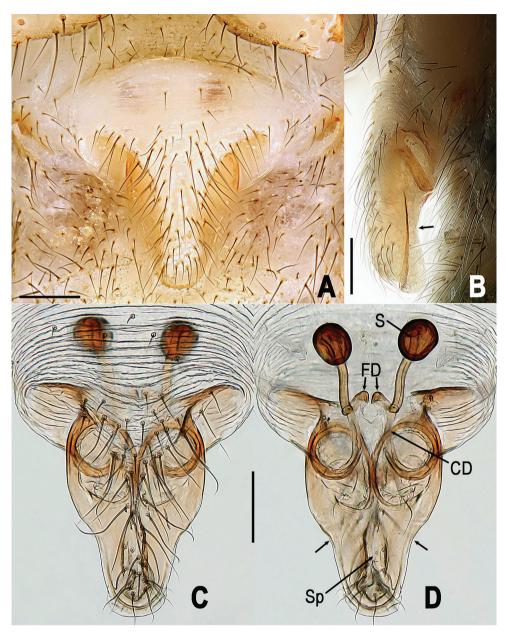


Figure 9. *Yamaneta paquini* (Miller, Griswold & Yin, 2009) comb. nov. from Lushui Co., Daxingdi, Walayaku [cave], female genitalia **A**, **B** Epigyne **C–D** vulva (lactic acid treated) **A**, **C** ventral **B** lateral **D** dorsal. Unlabeled arrow in **B** indicates curved profile of dorsal surface of scape, in **D** indicates notched lateral margin of scape. Abbreviations: **CD** copulatory ducts; **FD** fertilization ducts; **S** spermathecae; **Sp** scape. Scale bars: 0.10 mm.

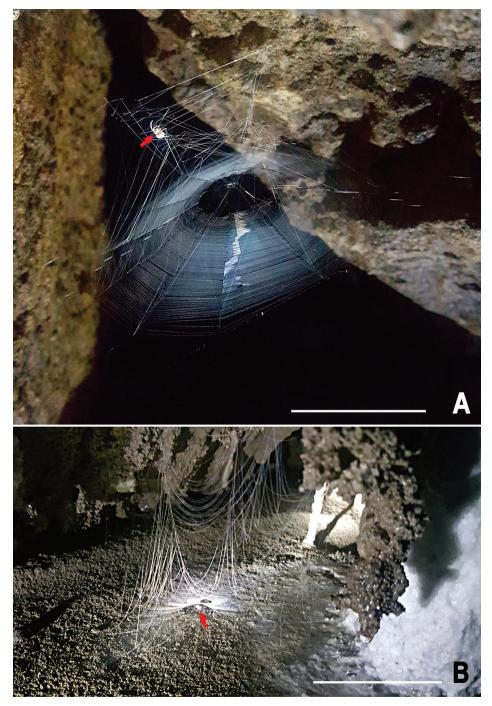


Figure 10. Webs of *Yamaneta* spiders in the Gaoligong Mountains **A** *Yamaneta kehen* (Miller, Griswold & Yin, 2009) comb. nov. from Fugong Co., Lishadi, "a nameless cave", female **B** *Yamaneta paquini* (Miller, Griswold & Yin, 2009) comb. nov. from Lushui Co., Daxingdi, Walayaku [cave], female. Red arrows indicate location of spider. Scale bars: 20.0 mm.

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Supplementary material I

Alignment of DNA sequence data used in phylogenetic analyses

Authors: Chengcheng Feng, Jeremy A. Miller, Yucheng Lin, Yunfei Shu Data type: molecular data

- Explanation note: Contains plain alignments in Fasta (FengetalAlignment.fas) and Nexus formats (FengetalAlignment.nex), plus the Nexus file used for data partition and tree search in MrBayes (FengetalAlignmentMrB.nex).
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.870.35971.suppl1

Supplementary material 2

Uncorrected pairwise distances based on full alignment

Authors: Chengcheng Feng, Jeremy A. Miller, Yucheng Lin, Yunfei Shu Data type: molecular data

- Explanation note: Contains uncorrected pairwise distances among all terminals as calculated using Mega X (Kumar et al. 2018).
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

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RESEARCH ARTICLE



New data on the western Balkan leuciscids Alburnoides and Alburnus (Teleostei, Leuciscidae) from the Vjosa River, Albania

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Abstract

The first voucher-confirmed record of *Alburnus scoranza* and the first morphological description of *Alburnoides* for the Vjosa River system in Albania are reported with a brief discussion of the diagnostic morphological traits and taxonomic assignment of both species.

Keywords

Biodiversity, freshwater fish, range extension, southeastern Adriatic ecoregion

Introduction

The Vjosa River (Aoos in Greece) belongs to the South Adriatic-Ionian zoogeographical division of Economidis and Bănărescu (1991) and is the southernmost river drainage of the Southeastern Adriatic ecoregion of Zogaris and Economou (2017). It originates in western Greece, flows through Albania, and drains into the southern Adriatic Sea. Some genera of the Greek (e.g., Economidis 1989, Durand et al. 1999, Economou et al. 2007, Geiger et al. 2014, Barbieri et al. 2017, Koutsikos et al. 2019) and the Albanian sections of the Vjosa/Aoos River (e.g., Šanda et al. 2008, Marková et al. 2010, Stierandová et al. 2016) were investigated mostly within wider phylogenetic studies, and summarising lists of fish species in the Albanian section have been also published

(Ahnelt and Elvira 1991, Rakaj and Flloko 1995, Shumka et al. 2010, Graf et al. 2017, Meulenbroek et al. 2018, Shumka et al. 2018a,b, Weiss et al. 2018). However, any new data on morphology and distribution of the Vjosa fishes could help for further research, especially in taxonomically difficult groups or species complexes.

Herein, we report the first voucher-confirmed records of *Alburnoides* based on a historical sample and the Scoranza bleak *Alburnus scoranza* Bonaparte, 1845 present in the middle and lower part of the Vjosa River drainage in Albania; we also present first morphological data for the Albanian Vjosa populations of these two cyprinids. Their species-level identifications are discussed based on some morphological comparisons.

Materials and methods

The Natural History Museum in Vienna (**NMW**) houses two small collections of freshwater fishes from the lower and middle course of the Vjosa River, from Selenica and Tepelena, respectively. These fishes were sampled in 1894 at the lower course of the Vjosa River near the town of Selenica (Selenicë) (Ahnelt and Elvira 1991) and in 1914 in the Bença River, a tributary of the Vjosa, near the village of Bença. No ecological data were available for either collection.

For methods and terminology of measurements and counts, and the comparative material, see Bogutskaya et al. (2010).

Results

Taxonomy

Alburnoides cf. *devolli* (a member of the *Alburnoides prespensis* complex of Stierandová et al. (2016)

Fig. 1

New record. NMW 55706, 40 specimens, SL 36.5–52.8 mm (mean 45.0 mm); Albania: Vjosa River drainage, Bença River at Bença village, ca. 6 km upstream of confluence with tVjosa (ca. 40°18'22"N, 20°1'29"E), collector(s) unknown, collected in July 1914, donated to NMW by F. Steindachner.

Identification. Based on 40 specimens except for numbers of pharyngeal teeth and measurements as specified below. Dorsal-fin branched rays 8½; anal-fin branched rays 10½-12½ (mode 11½, mean 11.3½); scales in lateral series 45–51 (mean 48.1); total lateral-line scales 43–50 (mean 46.8); later-line scales to posterior margin of hypurals 43–49 (mean 45.8); ventral keel (n = 20) from completely to 1/3 scaled, commonly ³/₄ scaled; mouth with a fleshy snout protruding lower jaw; gill-rakers 7–9 (mode 8, mean 8); total vertebrae 39–41 (mode 40, mean 40.4) with abdominal vertebrae 20–21 (mode 20, mean 20.5), predorsal abdominal 13–15 (mode 14, mean 13.70) and caudal vertebrae 19–21



Figure 1. *Alburnoides* cf. *devolli* (member of *A. prespensis* complex of Stierandová et al. (2016), NMW 55706. External appearance of **a** male SL 50.5 mm and **b** female 47.9 mm, and **c** radiograph of same specimen as **a**.

Table 1. Morphometric data of *Alburnoides* cf. *devolli* (member of *Alburnoides prespensis* complex of Stierandová et al. (2016) from river Bença (Vjosa drainage, Albania) deposited at NMW.

Alburnoides cf. devolli	NMW 55706: 1	55706: 2	55706: 3	55706: 4
Standard length (mm)	50.5	51.7	52.2	52.8
Percent of standard length	· · ·			
Body depth at dorsal-fin origin	28.5	30.1	29.8	29.9
Body width at dorsal-fin origin	10.9	13.7	11.9	13.0
Predorsal length	54.6	55.7	57.2	56.4
Postdorsal length	37.9	36.3	35.8	37.5
Prepelvic length	49.5	50.7	50.9	48.7
Preanal length	66.9	68.7	69.3	65.2
Pectoral – pelvic-fin origin length	23.6	24.1	25.4	24.0
Pelvic – anal-fin origin length	19.0	18.3	15.4	17.3
Caudal peduncle length	23.9	21.8	22.9	24.3
Caudal peduncle depth	12.3	13.2	12.6	12.3
Caudal peduncle width	8.9	9.0	9.1	8.9
Dorsal-fin base length	11.6	12.3	11.4	11.7
Dorsal-fin depth	22.5	20.7	21.3	20.9
Anal-fin base length	13.6	14.5	14.6	13.3
Anal-fin depth	18.6	16.8	15.3	17.1
Pectoral fin length	21.0	20.4	20.2	20.5

Alburnoides cf. devolli	NMW 55706: 1	55706: 2	55706: 3	55706: 4
Head length	26.4	26.5	25.6	24.9
Head depth at nape	18.8	19.2	18.2	18.8
Head width (maximum)	12.7	12.6	12.4	12.7
Snout length	7.6	7.4	7.5	7.5
Eye diameter (horizontal)	7.6	7.2	6.8	7.6
Postorbital distance	13.0	12.7	13.1	12.2
Interorbital width	8.8	8.3	8.8	8.8
Length of upper jaw	8.9	8.6	8.7	8.9
Length of lower jaw	11.3	11.1	10.0	11.3
Percent of head length	· · ·			
Head depth at nape	71.1	72.4	76.0	73.0
Head width (maximum)	48.3	47.3	49.7	49.9
Snout length	28.7	28.1	29.4	30.0
Eye diameter (horizontal)	28.9	27.2	29.4	27.4
Postorbital distance	49.6	45.8	50.9	51.2
Interorbital width	33.5	31.3	33.6	35.2
Length of upper jaw	33.8	32.5	35.0	35.1
Length of lower jaw	42.7	41.9	43.2	40.3
Depth of operculum	40.3	39.9	38.2	40.5
Percent of caudal peduncle length				
Depth of caudal peduncle	51.3	60.7	53.2	52.0
Percent of interorbital distance				
Eye diameter (horizontal)	86.1	86.9	87.3	77.8

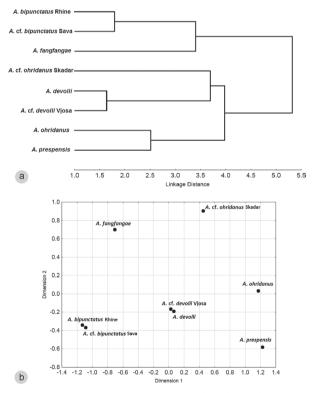


Figure 2. a Cluster analysis **b** multidimensional scaling results for *Alburnoides* samples of North, Black, and Adriatic basins from Rhine southwards to Vjosa in Albania based on data for counts and coded qualitative characters as in Table 3. Adriatic samples of *Alburnoides prespensis* complex named as presumed species.

Table 2. Diagnostic characters for examined Alburnoides samples of North, Black, and Adriatic basins from the Rhine southwards to Vjosa in Albania. Modal values are in bold.

Identification sensu Stierandová et al. (2016)	Our identifications, including	Total lateral line scales	Anal fin branched rays	Total vertebrae	Abdominal vertebrae	Caudal vertebrae	Predorsal abdominal vertebrae	Most frequent vertebral formulae	Most frequent states of the ventral keel development as part of keel length covered by scales
A. bipunctatus	A. bipunctatus,	45-51; 48-50 ;	45-51; 48-50 ; 13½-17½; 14½- 40-42; 41 ; 41.4	40-42; 41 ; 41.4	20-21; 20 ; 20.2	20-22; 21 ; 21.2	13-15; 14; 14.2	20+21	1/2 to 3/4 scaled
Lineage I	Rhine $(n = 22)$	48.4	15¹/2 ; [14.5] ¹ /2					_	
Alburnoides sp.	A. cf. bipunctatus,	45-54; 49-50 ;	121/2-151/2; 131/2;	40-42; 41; 41.1	20-21; 20 ; 20.3	20-22; 21; 20.8	13-15; 14; 13.9	20+21, 21+21	2/3 scaled
Lineage IV	Sava, upper	48.9	[13.3] ^{1/2}						
	Danube $(n = 50)$							_	
A. obridanus	A. obridanus, Ohrid		42-46; 44; 43.9 10 ^{1/2} -13 ^{1/2} ; 11 ^{1/2} ; 38-40; 39 ; 39.0 19-21; 20 ; 20.0	38-40; 39 ; 39.0	19–21; 20 ; 20.0	18–20; 19 ; 18.9 12–14; 13 ; 12.8	12-14; 13; 12.8	20+19	1/2 to 3⁄4 scaled
Lineage VII	L. $(n = 33)$		[11.4] ^{1/2}						
	A. cf. ohridanus,	42-47; 44; 44.3	121/2-151/2;	39-41; 40; 39.9	20-21; 20 ; 20.3	19–20; 20 ; 19.7 13–14; 14 ; 13.8	13-14; 14; 13.8	20+20	1/4 to 1/3 scaled
	Skadar L. $(n = 19)$		121/2-131/2;						
			[12.8]1/2						
A. prespensis	A. prespensis Prespa	42-44; 43.0	101/2-111/2; 101/2;	39 ; 39.0	20 ; 20.0	19 ; 19.0	13 ; 13.0	20+19	3⁄4 to completely scaled
complex Lineage IX			[10.3] ^{1/2}						
A. prespensis	A. fangfangae (n	6-53; 48-49;	111/2-141/2; 121/2;	40-42; 40-41 ;	20-21; 20 ; 20.5	19-21; 20; 20.1	13-14; 14 ; 13.8	20+20, 21+20,	1/3 to 0 scaled (=completely
complex *	= 44)	48.3	[12.1]1/2	40.6				20+21	scaleless)
A. prespensis	A. devolli $(n = 15)$	44-48; 47; 46.2	111/2-131/2; 121/2;	40-41; 40; 40.3	20-21; 20 ; 20.5	19-20; 20; 19.8	12-13; 13; 12.7	20+20	3⁄4 to completely scaled
complex *			[12.1]1/2					_	
A. prespensis	A. cf. devolli Vjosa	43-50; 44-49;	10 ¹ / ₂ -12 ¹ / ₂ ; 11 ¹ / ₂ ;	39-41; 40 ; 40.4	20-21; 20 ; 20.5	19-21; 20; 19.9	13-15; 14; 13.7	20+20; 21+20	1/2 to 3/4 scaled
complex Lineage	(NMW 55760, n	46.8	[11.3] ^{1/2}						
VIII	= 40)								

* Assignment to any lineage of Stierandová et al. (2016) cannot be determined without examination of voucher specimens.

(mode 20, mean 19.9); most frequent vertebral formulae 20+20 and 21+20; pharyngeal teeth 2.5–4.2 (n = 5). Measurements for four specimens with SL over 50 mm see Table 1.

For a morphological comparison with close species (and presumptive species) see Table 2 and Fig. 2.

Identification of the sample as *Alburnoides* cf. *devolli* is based on statistical analyses (Fig. 2). See Discussion for the taxonomy of *A. devolli* Bogutskaya, Zupančič et Naseka, 2012.

Colouration (preserved). The body is pale fawn, the back darker than the ventral side. A distinct, black to dark grey stripe extends from the posterior margin of the orbit to the base of the caudal fin. The ventral side of the belly and of the tail is unpigmented. The lateral line is lined dorsally and ventrally by pigment along its entire length, most distinct in its anterior half to about below the origin of the dorsal fin. The fins are hyaline with tiny melanophores lining the dorsal and caudal fin rays, the anterior rays of the anal and the dorsal rays of the pectoral fins.

Alburnus scoranza Bonaparte, 1845

Fig. 3

New record. NMW 87654, 1 specimen, SL 70.8 mm; Albania: Vjosa River system: Selenica (40°32'N, 19°38'E); collected by Pola Expedition, Franz Steindachner, 4 July 1894. - NMW 87658-87659, 3 specimens, SL 90.8–125.6 mm; same data as NMW 87654.

Identification. Measurements see Table 3. Dorsal-fin branched rays 8½; anal-fin branched rays 14½ (1 specimen) or 15½ (3 specimens); anal-fin origin behind base of 5th (2), 6th (1; Fig. 3c) or 7th (1) branched dorsal-fin ray; mouth upturned, mouth cleft straight, tip of mouth about at level with upper margin of pupil; keel between pelvic fins and anus completely exposed, variably sharp; scales in lateral series 47–51 (mean 48.8); total lateral-line scales 45–51 (mean 48.3); later-line scales to posterior margin of hypurals 45–48 (mean 46.0); gill rakers 22–25 (23.5); total vertebrae 41 (22+19, 3 specimens) or 42 (22+20, 1 specimen) with predorsal abdominal vertebrae 15 (3 specimens) or 16 (1 specimen).

Sexual dimorphism. Though only few specimens were examined, we may report on pronounced sexual dimorphism: the pectoral fin is longer while the pectoral-pelvic distance is shorter in males and the pectoral fin reaches behind the origin of the pelvic fin (Fig. 3a, b). Also, the pectoral fin is markedly rounded with a slightly convex outer margin and the first two branched rays of about similar length forming the apex of the fin in males vs. a clearly pointed fin with a slightly concave outer margin and the first branched ray which is clearly longer than the second one forming the apex of the fin in females. The male NMW 87659:2 has prominent nuptial tuberculation: tubercles densely cover the entire dorsal and lateral head surface down to the lower margin of the interoperculum and the branchiostegal rays, anterior back along the scale margins and on the upper surface of the pectoral fin along all its rays.

Colouration (preserved). The dorsal part of the head and the body is dark grey. The flank and the abdomen are silvery. The fins are hyaline.



Figure 3. *Alburnus scoranza*, NMW 87659. **a** Female 106.9 mm SL **b** male 98.2 mm SL; NMW 87658 **c** radiograph, male 90.8 mm SL.

Discussion

As the knowledge of the biodiversity in general and of the fish fauna in particular within the Vjosa River system in Albania is very scarce (Rakaj and Flloko 1995, Shumka et al. 2018b), descriptions of fishes from this river system are commonly based on the study of Rakaj (1995). However, the Rakaj's data were mostly based on material from Prespa, Ohrid, and Skadar lakes and their tributaries. This author did not give data for specimens of the Vjosa just indicating the occurrence of a species in this river.

Recent faunal lists mentioned the occurrence of an *Alburnoides* Jeitteles in the Vjosa River drainage under the names either *A. bipunctatus* (Bloch, 1782) (Meulenbroek et al. 2018, Shumka 2018b) or *A. prespensis* (Karaman, 1928) (Shumka et al. 2018a). Morphological (Coad and Bogutskaya 2009, Bogutskaya et al. 2010) and molecular (Geiger et al. 2014, Stierandová et al. 2016) data ruled out the occurrence of *A. bipunctatus* in the Vjosa/Aoos River (Barbieri et al. 2015, 2017). Mentioning *A. prespensis* in the Vjosa River in Albania, Shumka et al. (2018a) just refer to previous authors, e.g., Rakaj (1995), Kottelat and Freyhof (2007), Bogutskaya et al. (2010) or Geiger et al. (2014). Whereas Rakaj (1995) and Kottelat and Freyhof (2007) do not give records of *A. prespensis* outside of the Prespa lakes and their tributaries, the other authors just refer to records in the Greece part (Aoos) of the Vjosa River drainage.

Alburnus scoranza	NMW 55700:1	55700:2	87654	87658	87659:1	87659:2
	female	female	female	male	female	male
Standard length (mm)	125.6	93.4	70.8	90.8	106.9	98.2
Percent standard length						
Body depth at dorsal-fin origin	23.3	18.2	19.9	24.0	22.9	23.8
Body width at dorsal-fin origin	10.8	8.7	8.5	7.8	8.2	8.5
Predorsal length (% SL)	57.8	57.6	58.4	54.9	56.0	54.0
Postdorsal length (% SL)	35.0	33.0	30.7	36.2	33.9	35.0
Prepelvic length (% SL)	47.7	48.9	45.7	43.6	47.1	46.1
Preanal length (% SL)	68.5	69.1	65.0	64.3	68.2	66.1
Pectoral – pelvic-fin origin length	24.5	23.6	23.0	20.9	23.8	21.1
Pelvic – anal-fin origin length	21.7	20.8	19.8	20.1	21.4	20.0
Caudal peduncle length	20.2	20.5	21.2	19.0	19.2	18.3
Caudal peduncle depth	9.6	8.5	10.3	11.0	10.6	10.0
Caudal peduncle width	7.0	5.6	5.7	5.1	5.5	5.7
Dorsal-fin base length	10.5	11.7	12.2	11.5	10.8	12.5
Dorsal-fin depth	16.4	18.8	20.5	20.9	19.6	21.1
Anal-fin base length	14.8	14.0	16.3	20.0	16.2	18.9
Anal-fin depth	12.7	15.3	13.4	14.9	12.4	15.5
Pectoral-fin length	18.1	20.2	20.3	21.9	21.5	22.6
Pelvic-fin length	13.8	15.9	14.4	17.6	15.8	18.3
Head length	23.8	24.7	25.5	23.7	24.4	25.1
Head depth at nape	15.1	15.5	16.9	15.6	15.7	17.7
Head width (maximum)	11.0	10.5	11.5	11.3	11.1	12.5
Snout length	5.3	6.3	6.6	6.3	6.9	7.0
Eye diameter (horizontal)	6.2	6.7	7.8	6.7	6.8	6.8
Postorbital distance	12.7	12.6	11.9	12.1	12.2	10.6
Interorbital width	6.7	6.6	7.3	7.4	7.5	7.4
Length of upper jaw	6.0	6.4	7.7	7.2	7.5	6.9
Length of lower jaw	8.4	9.3	9.4	9.6	9.2	9.6
Percent head length						
Head depth at nape	63.3	62.7	66.1	65.9	64.2	70.3
Head width (maximum)	46.2	42.3	44.9	47.6	45.3	49.7
Snout length	23.3	25.5	25.9	26.6	28.2	27.9
Eye diameter (horizontal)	25.9	27.0	30.7	28.3	28.0	27.2
Postorbital distance	50.5	50.8	46.5	51.2	46.5	48.5
Interorbital width	28.3	26.5	28.4	31.0	30.7	29.6
Length of upper jaw	25.1	25.8	30.0	30.2	30.8	27.4
Length of lower jaw	35.2	37.5	37.6	39.5	37.6	38.3
Depth of operculum	36.9	37.2	38.2	37.3	36.5	37.0
Percent caudal peduncle length	1		L		1	
Depth of caudal peduncle	47.3	41.3	44.0	48.6	52.2	54.6
Percent interorbital distance						
Eve diameter (horizontal)	91.5	101.6	107.8	91.3	91.1	91.9

Table 3. Morphometric data of *Alburnus scoranza* from the Vjosa River at Selenize (Albania) and Montenegro (formerly considered syntypes, see text for discussion) deposited at NMW.

Limited mitochondrial (cytb) data of Perea et al. (2010) – only one specimen from Prespa Lake and one from the Aoos were studied – showed a very close position of the two specimens. Results of Geiger et al. (2014) clearly demonstrated that the CO1 marker did not provide resolution in many groups of conventional species in the subfamily Leuciscinae (Geiger et al. 2014: table S1-C). This table lists at least 17 complexes of "closely related" leuciscine species, which include clearly morphologically distinct species, e.g., *Delminichthys ghetaldii* (Steindachner, 1882), *D. jadovensis* (Zupančič et Bogutskaya, 2002) and *D. krbavensis* (Zupančič & Bogutskaya, 2002) or *Squalius tenellus* Heckel, 1843 and *S. microlepis* Heckel, 1843. *Alburnoides prespensis, A. devolli* and *A. fangfangae* Bogutskaya, Zupančič & Naseka, 2012 were not distinguished by COI barcode either: *A. devolli* and *A. fangfangae* from the Seman drainage were closely related to *A. prespensis* from Prespa Lake and the position of this cluster was a nearest sister to *A. ohridanus* (Karaman, 1928) (Skadar material was not examined) (Geiger et al. 2014). A study using a set of both nuclear (ß-actin, RAG1 and S7) and mitochondrial (cytb) markers (Stierandová et al. 2016) supported the divergence of the "*prespensis+devolli+fangfangae*" cluster from *A. ohridanus* (lineage VII) but subdivided most part of the Albanian samples into three lineages (VII, IX and X) naming them "*A. prespensis* species complex". This term has been in use since then (e.g., Juladeh Roudbar et al. 2016, Barbieri et al. 2017).

In the publication by Stierandová et al. (2016), the *A. ohridanus* lineage included the Ohrid Lake sample and some individuals from the Mat, Ishëm and Erzen Rivers -Adriatic drainages south of the Ohrid-Drin-Skadar basin. The range of the *A. prespensis* species complex embraces Prespa Lake and five Adriatic drainages in the south of Erzen – Shkumbin, Seman, Vjosa/Aoos, Dukati, and Borshi. The internal structure of the *A. prespensis* complex based on combined data (cytb, ß -actin and S7) (Stierandová et al. 2016: fig. 1) cannot be interpreted from either taxonomic or zoogeographic aspects. As any morphological diagnostic characters of the voucher samples used for the genetic research have not been published, a clear taxonomic assignment of the Aoos (Greek) *Alburnoides* as well as of the two Albanian species from the Seman River drainage (geographically closest to the Vjosa/Aoos) is still uncertain.

Our morphological data (Table 2, Fig. 2) is not congruent with the molecular data: *A. ohridanus* is located inside the *A. prespensis* complex and the whole set of samples that belong to the latter demonstrates a high degree of morphological divergence within the group in general and between some presumptive species, in particular. However, as it can be seen from Table 3 summarising our data for samples out of the *A. prespensis* complex, they are all different in key diagnostic characters indicating a considerably high morphological diversity of the complex. Our sample is similar to samples from the Aoos in Greece (Barbieri et al. 2017) in having a poorly developed ventral keel which is commonly almost or completely scaled, and 43–49, mean 45.8, lateral-line scales to posterior margin of hypurals (45–50, mean 46.3 in Barbieri et al. (2017). However, the number of branched anal-fin rays is lower, commonly 11½, mean 11.2[½] (vs. commonly 12½, mean 11.8[½] in Barbieri et al. (2017).

The entire *A. prespensis* complex needs a thorough revision, especially with regard to the southern river drainages of Albania (Bogutskaya et al. 2010, Stierandová et al. 2016, Barbieri et al. 2017). The data presented in this study are a first step towards resolving the phylogenetic and taxonomic position of the Vjosa/Aoos *A. cf. devolli* populations.

The Vjosa population of *A. scoranza* in Albania was documented as *Alburnus alburnus* (Linnaeus, 1758) by Ahnelt and Elvira (1994). The Aoos population of *A. scoranza* in Greece was also first reported as *A. alburnus* by Economou et al. (2007a) and then as *A. cf. scoranza* (Economou et al. 2007b). *Alburnus scoranza* is supposedly distributed in the western Balkans from the Drin drainage, including Skadar and Ohrid lakes, south to the Aoos in Greece where it is restricted to a short section of the middle section of the river within the Konitsa plateau downstream to the Albanian border (Barbieri et al.

2015). Based on COI barcodes, Geiger et al. (2014) showed that *A. scoranza* (material from Ohrid and Skadar lakes and the Aoos in Greece) is not included in the Adriatic *Alburnus* clade but is the closest neighbour to a wide group of *Alburnus* species spread from Portugal and France to Central Anatolia. Mangit and Yeril (2018) included some GenBank-available CO1 sequences of *A. arborella* (De Filippi, 1844), *A. albidus* (Costa, 1838), *A. belvica* Karaman, 1924, and *A. scoranza* in their analysis of mostly Turkish species and found the same pattern with *A. scoranza* as a closest sister clade to the three former species plus two from western Turkey.

While *A. arborella* occurs in northern Adriatic basin, the distribution of *A. belvica* is restricted to Prespa Lake with its tributaries (Kottelat and Freyhof 2007). *Alburnus neretvae* Buj, Šanda et Perea, 2010 is an endemic species of the Neretva River drainage (Buj et al. 2010) and the distribution area of *A. scoranza* comprises the basins of lakes Prespa, Ohrid, and Skadar (Kottelat and Freyhof 2007). Economou et al. (2007b) and later Geiger et al. (2014) listed this species for the Greek part of the Vjosa/Aoos River drainage. Shumka et al. (2018a) mentioned *A. scoranza* in a checklist for the Albanian section of the Vjosa but no exact locality data were given. Therefore, the specimens presented in this study from Selenica are the first voucher-confirmed record of *A. scoranza* for the Vjosa River system in Albania.

We could only morphologically compare our sample with the limited published data of *A. scoranza* (Buj et al. 2010; material from the Zeta, Skadar basin; Black Drin, Ohrid basin; and the Mat River, which is the geographically closest drainage south of the Drin). The Vojsa specimens have more numerous anal-fin branched rays, $14\frac{1}{2}-15\frac{1}{2}$ (vs. $13\frac{1}{2}-14\frac{1}{2}$); similar number of total lateral-line scales, 45-51 (vs. 46-53); and, the most striking difference, gill rakers 22-25 (vs. 15-20). Interestingly, the Vojsa sample does not differ by the diagnostic counts from two specimens that had been considered syntypes of *A. scoranza* Heckel & Kner, 1857 from Skadar Lake (NMW 55700: 1 and 2) until it was supposed that the species' name was made available earlier by Bonaparte (1845) (see below). These two specimens have a sharp scaleless keel; total lateral line scales 48, 47; anal-fin branched rays $14\frac{1}{2}$; gill rakers 21, 24; vertebrae 22+19 and 22+20 with predorsal abdominal vertebrae 15 and 16; for measurements see Table 2.

So far, clarification of the taxonomic status of *A. scoranza* from the Vjosa still needs additional morphological and genetic data, especially from the southern river basins in Albania.

Nomenclatural note on *Alburnus scoranza*. The most recent publications (e.g., Buj et al. 2010; Barbieri et al. 2015) follow Kottelat and Freyhof (2007: 598) in attributing the authorship to Bonaparte (1845). Bonaparte (1845: 12) lists *A. scoranza* (species No 122) with a reference to Heckel (no date) and the only morphological trait given in the description is the number of pharyngeal teeth (2.5–5.2). According to Art. 12.1 of the International Code of Zoological Nomenclature (the Code; International Commission on Zoological Nomenclature 1999) this indeed constitutes an available name as it is "accompanied by a description … of the taxon that it denotes". Heckel's publication is most probably dated 1843 where *Alburnus scoranza* is listed (on page 1036) as a name only (authorship attributed to Heckel) with the locality as Montenegro, among other species names under the description of the genus *Alburnus*. The pharyngeal teeth 2.5–5.2 are given as a characteristic feature of the genus. This may indicate that Bonaparte only referred to these data from Heckel (1843) and did not examine any *A. scoranza* specimens himself, so, Heckel's specimens may represent the type series of the species by bibliographic reference according to Art. 72.4.1 of the Code (International Commission on Zoological Nomenclature 1999).

Heckel had apparently examined specimens of *A. scoranza* as two specimens (as *Aspius scoranza* Heckel, acquisition number 1843.II.18b) were registered at the NMW from "Cettinje in Montenegro" collected by himself in his 1840 travels. Unfortunately, these specimens have not been found in NMW during recent searches. Cetinje is a city (the historic old capital of Montenegro) located in the Cetinje karst field 12 km from Skadar Lake and even closer to the Rijeka Cernojevića River, an inflow of Skadar Lake. Heckel received two more specimens (acquisition number 1856.VII.26) described by Heckel and Kner in 1857 (page 139 footnote) much later than 1843 from Belotti (sample NMW 55700). In case a designation of neotype to fix the species name *A. scoranza* is needed in the future, the information presented above on the Heckel's specimens from Cetinje should be taken into consideration to meet the conditions of Art. 75.3 of the Code (International Commission on Zoological Nomenclature 1999).

Recent studies provide evidence that species of *Alburnoides* and *Alburnus* Rafinesque were introduced into other river systems (e.g., Simić et al. 2012, Stierandová et al. 2016, Pofuk et al. 2017, Vukić et al. 2019). As intentional and unintentional introductions of non-native fish species are common in Adriatic lake and river systems (e.g., Shumka et al. 2008, Simić et al. 2012, Piria et al. 2017, Pofuk et al. 2017, Vukić et al. 2019), historic museum collections provide important information of natural fish distributions (e.g., Palandačić et al. 2017). If several phylogenetic lineages occur in one and the same river drainage, historic museum collections may be of a crucial importance to determine native populations and apply the nomenclaturally correct name.

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RESEARCH ARTICLE



Three new species of the planthopper genus Sinonissus Wang, Shi & Bourgoin, 2018 from southwest China (Hemiptera, Fulgoromorpha, Issidae)

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Abstract

The diagnostic characters of the Chinese planthopper genus *Sinonissus* Wang, Shi & Bourgoin, 2018 are redefined. Three new species of this genus, *S. daozhenensis* Chang & Chen, **sp. nov.** (Guizhou), *S. ha-mulatus* Chang & Chen, **sp. nov.** (Guizhou) and *S. longicaudus* Chang & Chen, **sp. nov.** (Sichuan) are described and illustrated, and their female genitalia compared. A checklist and key to the Chinese species of *Sinonissus* are given.

Keywords

Female genitalia, issid, Issini, morphology, Oriental region, taxonomy

Introduction

The family Issidae Spinola, 1839 is one of the largest planthopper families (Hemiptera, Fulgoromorpha), distributed in worldwide. Wang et al. (2016) proposed that the family Issidae was divided into Issinae Spinola, 1839 (including two tribes), Thioniinae Melichar, 1906 (including one tribe), and Hemisphaerinae, Melichar, 1906 (including

four tribes), based on molecular data of 18S, 28S, COXI, and Cytb. The tribe Issini Spinola, 1839 was placed in the subfamily Issinae with Hysteropterini Melichar, 1906, but it differs from Hysteropterini by a number of characters: forewings with veins running in parallel; ScP+R, MP, and CuA bifurcated, the veins nearly reaching to the apical margin of the forewing; hind wings well developed or rudimentary; phallobase with one paired digitate processes on the inner side of the dorsolateral lobe (Gnezdilov 2003, 2016). Currently, the tribe Issini consists of four genera: *Issus* Brullé, 1832, *Latissus* Dlabola, 1974, *Issites* Haupt, 1956, and *Sinonissus* Wang, Shi & Bourgoin, 2018 (Gnezdilov and Bourgoin 2016; Wang et al. 2016; Wang et al. 2018). Wang et al. (2018) established the genus *Sinonissus* with one species from China (Sichuan, Chongqing).

The aim of this paper is to describe three new species of *Sinonissus* from China bringing the total number of species to four. Generic characteristics are redefined and a checklist and key to Chinese species of *Sinonissus* is provided.

Materials and methods

The morphological terminology of the head and body follows Chan and Yang (1994) and Bourgoin et al. (2015), and the terminology of male and female genitalia follows Bourgoin (1993) and Gnezdilov (2002, 2003). Dry specimens were used for descriptions and illustrations. External morphology was observed under a stereoscopic microscope. All measurements are in millimeters (mm). The body measurements are from the apex of vertex to the tip of the forewings. The genital segments of the examined specimens were macerated in 10% NaOH, washed in water, and transferred to glycerin. Illustrations of the specimens were made with a Leica M125 and Olympus CX41 stereomicroscope. Photographs were taken with a Keyence VHX-1000C.

The type specimens and other examined specimens of the newly described species are all deposited in the Institute of Entomology, Guizhou University, Guiyang, China (**IEGU**).

Taxonomy

Genus Sinonissus Wang, Shi & Bourgoin, 2018

Sinonissus Wang, Shi & Bourgoin, 2018: 53, figs 1-18.

Type species. Sinonissus brunetus Wang, Shi & Bourgoin, 2018.

Diagnostic characters. Body small, slightly flat in vertical view. Width of head (Figs 1, 3, 5, 7) including eyes narrower than pronotum. Vertex (Figs 13, 32, 51) with width at base longer than length in middle ca. three times, disc of vertex depressed distinct, without median carina, anterior margin slightly convex or nearly straight, posterior margin obviously arched concave. Gena (Figs 14, 33, 52) with one obvious ocellus between compound eye and antenna in lateral view. Frons (Figs 15, 34,

53) rectangular, with median carina explicit, without lateral carina, the apical margin straight or not obviously forked, nearly reaching to frontoclypeal suture, with weeny tubercles near lateral margin, lateral margin nearly paralleled, the base slightly narrow, broader toward to apical margin, the widest below level of compound eyes. Clypeus (Figs 15, 34, 53) triangular, with median carina distinct or obscure. Rostrum surpassing mesotrochanters. Pronotum (Figs 13, 32, 51) without median carina or degraded, with lateral carina, without sub-lateral carina, pit each other between median carina and lateral carina, apical margin obtuse-angle concaved, posterior margin straight. Mesonotum (Figs 13, 32, 51) triangular, with median carina obvious or obscure or not, without sub-lateral carina. Forewings (Figs 9, 16, 35, 54) ovate, with length ca. 1.8 times longer than maximum width, anterior margin slightly cambered, anterior margin and posterior margin subparallel, apical margin obtusely rounded, longitudinal veins obvious and elevate, short transverse veins pale, with wide "hypocostal plate", ScP and RP convergent near base, ScP vein long, no forked, nearly reaching the apical margin forewing, MP bifurcating two branches in basal 1/3, CuA forked into two branches near middle, behind the joint of Pcu and A₁; CuP present, Pcu and A₁ uniting in middle of clavus. Hindwings (Figs 17, 55) absent or reduced, small, vein simple. Hind tibiae each with two lateral spines, spinal formula of hind leg (7-9)-(8-9)-2.

Male genitalia. Anal tube (Figs 11, 19, 37, 57) moderately long, irregularly pentagonal in dorsal view, the basal part narrow, the apical part more broad, maximum width in apical 1/3 of anal tube. Anal style (Figs 11, 19, 37, 57) moderately long, not surpassing anal tube. Pygofer (Figs 10, 18, 36, 56) symmetrical, irregularly rectangular; anterior margin and posterior margin nearly paralleled in lateral view, dorsal margin and ventral margin nearly paralleled in lateral view. Genital styles (Figs 10, 18, 38, 56) relatively rectangular, dorsal margin and ventral margin slightly arched, without triangular prominence near dorsal margin before capitulum. Capitulum of genital styles irregularly triangular, the basal part with half-elliptical process, the apical part with thin triangular process, neck obvious. Phallobase (Figs 12, 21, 40, 59) symmetrical, "U"-shaped tube in lateral view, dorsal lobe with apical part membranous, splitting into one sclerous branch in apical 1/3, with lateral lobe splitting into two branches, with ventral lobe shorter than dorsal lobe. Aedeagus (Figs 12, 21, 40, 59) with various long processes in lateral view.

Female genitalia (Figs 23–25, 42–44, 61–63). Anal tube (Figs 26, 45, 64) ovate, long in middle than the width, apical margin with unobvious or obvious membranous triangular protuberance. Anal style (Figs 26, 45, 64) long, located near base of anal tube. Hind margin of gonocoxa VIII with endogonocoxal lobe not obvious (Figs 27, 46, 65), endogonocoxal process membranous, narrowing gradually. Anterior connective lamina of gonapophysis VIII irregularly rectangular, with sclerous triangular process in basal dorsal margin, with two or three lateral teeth bearing two or three keels in lateral group and three teeth in apical group (Figs 27, 46, 65). Posterior connective lamina of gonapophysis IX (Figs 28, 29, 47, 48, 66, 67) triangular, with lateral field and sublateral field without obvious process (Figs 28, 47, 66); median field with prominence (median dorsal process) (Figs 28, 47, 66); ventroposterior lobes bent angle

obtuse or acute (posterior ventral lobes) (Figs 29, 48, 67). Gonoplacs (Figs 30, 49, 68) without keels. Hind margin of sternum VII (Figs 31, 50, 69) median sunken, without any process in ventral view.

Checklist of Chinese species of Sinonissus Wang, Shi & Bourgoin, 2018

Sinonissus brunetus Wang, Shi & Bourgoin, 2018; Chongqing, Guizhou, Sichuan. Sinonissus daozhenensis Chang & Chen, sp. nov.; Guizhou. Sinonissus hamulatus Chang & Chen, sp. nov.; Guizhou. Sinonissus longicaudus Chang & Chen, sp. nov.; Sichuan.

Key to species of *Sinonissus* (based on males)

1	Vertex with the width ca. 2.5 times as long as the middle line (Fig. 13)			
	S. daozhenensis sp. nov.			
_	Vertex with the width ca. 3.0 times as long as the middle line (Figs 32, 51)2			
2	Aedeagus with flagellate process in the middle in lateral view (Fig. 59); p			
	lobase with ventral lobe triangular in ventral view (Fig. 60)			
_	Aedeagus with short hooked process in the middle in lateral view; phallobase			
	with ventral lobe sub-rectangular in ventral view			
3	Anal tube with spoon-like protrusion in lateral view (Fig. 36); aedeagus with			
	short hooked process, tip of process directed to dorso-posterior (Fig. 40)			
_	Anal tube without spoon-like protrusion in lateral view (Figs 10, 11); aedea-			
	gus with short hooked process, tip of process directed to dorso-anterior (Fig.			
	12) <i>S. brunetus</i>			

Key to species of Sinonissus (based on females)

1	Posterior connective lamina with median field with two ear-shaped promi-
	nences (Fig. 28) S. daozhenensis sp. nov.
_	Posterior connective lamina without the above characters
2	Posterior connective lamina with median field with near circular prominences
	(Fig. 47) S. hamulatus sp. nov
_	Posterior connective lamina with median field with tubercle-like prominenc-
	es (Fig. 66) S. longicaudus sp. nov

Notes: The female of *S. brunetus* has not been examined, so this species cannot be included in the key.

Sinonissus brunetus Wang, Shi & Bourgoin, 2018

Figs 1, 2, 9–12

Sinonissus brunetus Wang et al., 2018: 54: figs 1-18.

Material examined. 1∂, China: Guizhou, Chishui Alsophila National Nature Reserve (28°26'N, 106°01'E, 315 m), 28–29 May 2006, Y Tang leg..
Distribution. China (Chongqing, Guizhou, Sichuan).

Sinonissus daozhenensis Chang & Chen, sp. nov.

http://zoobank.org/1FF7BADC-7A3B-4665-B50F-91F090D2F252 Figs 3, 4, 13–31

Type material. Holotype: \Diamond , China: Guizhou, Daozhen County, Sanqiao Town (29°03'N, 107°30'E, 1300–1600 m), 22–24 May 2004, B Zhang and P Xu leg.; paratypes: $3 \heartsuit \heartsuit$, same data as holotype; $1 \circlearrowright$, Guizhou, Daozhen County, Sanqiao Town (29°03'N, 107°30'E, 1500 m), 23 May 2004, X-S Chen leg.; $2 \heartsuit \heartsuit$, Guizhou, Daozhen County, Dashahe National Nature Reserve (26°38'N, 108°03'E, 600–700 m), 25–27 May 2004, B Zhang and P Xu leg.; $1 \heartsuit$, Guizhou, Daozhen County, Sanqiao Town (29°03'N, 107°30'E, 600–900 m), 16 Sept. 2005, Q-Z Song leg..

Diagnosis. This species is similar to *S. brunetus*, but it differs from the latter by phallobase with ventral lobe with lobe-like process near middle in lateral view (Fig. 21: a); aedeagus with long flexuous process near middle in lateral view (Fig. 21: b); posterior connective lamina of gonapophysis IX with median field with symmetrical ear-shaped prominences (Fig. 28).

Description. Body length: male 3.85–4.04 mm, female 4.14–4.4 mm. Forewing: male 3.27–3.33 mm, female 3.38–3.54 mm.

Coloration. General color brown (Figs 3, 4). Vertex, pronotum and mesonotum (Fig. 13) yellow brown. Eyes brown to black (Fig. 14). Forewings (Fig. 3) pale brown, longitudinal veins pale brown, transverse veins pale white. Hindwings brownish black. Legs yellow brown, with tips of spines on hind tibiae and tarsi black.

Head and thorax. Head (Fig. 13) including eyes slightly narrower than pronotum (0.80: 1.00). Vertex (Fig. 13) shorter in middle than the wide at base (1.00: 2.52). Frons (Fig. 15) longer in midline than the widest breath (1.15: 1.00), median carina with the apical margin straight, nearly reaching to frontoclypeal suture. Clypeus (Fig. 15) triangular, with distinct median carina. Pronotum (Fig. 13) with median carina obscure, lateral carina reaching to the posterior margin. Mesonotum (Fig. 13) triangular, with median carina obscure. Forewings (Fig. 16) elongate, 1.67 times as long as maximum breadth. Hindwings (Fig. 17) reduced, small, with one vein. Hind tibiae each with two lateral spines, spinal formula of hind leg (8-9)–(8-9)–2.

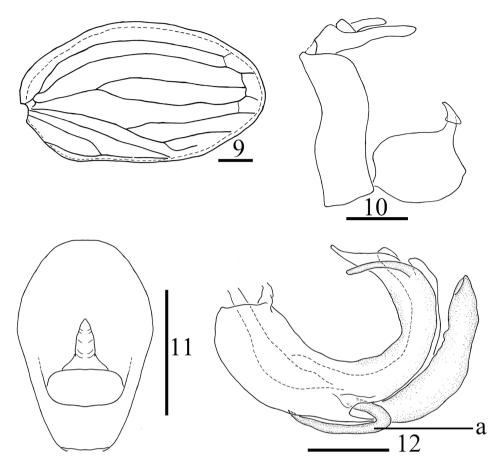
Male genitalia. Anal tube (Fig. 19) irregularly pentagonal in dorsal view, the widest in apical 1/3, longer in midline than the width (1.49: 1.00). Anal style (Fig. 19)



Figures 1–8. Habitus of *Sinonissus* species. 1, 2 *Sinonissus brunetus* Wang, Shi & Bourgoin, 2018 3, 4 *Sinonissus daozhenensis* Chang & Chen, sp. nov. 5, 6 *Sinonissus hamulatus* Chang & Chen, sp. nov. 7, 8 *Sinonissus longicaudus* Chang & Chen, sp. nov. Scale bars: 0.5 mm.

sturdy and long, located at the base 1/3 of anal tube. Pygofer (Fig. 18) with dorsal margin slightly narrow than ventral margin, posterior margin convex in middle. Genital styles (Fig. 18) relatively rectangular, dorsal margin and ventral margin nearly parallel. Capitulum of genital styles relative long, irregularly triangular, neck obvious (Fig. 20). Phallobase (Figs 21, 22) with dorsal lobe cystiform at apical part, with stout rod-like process in apical half in lateral view; lateral lobe splitting into two stout branches; ventral lobe with one lobe-like process near middle in lateral view (Fig. 21: a), in ventral view, looking like three obvious lobes (Fig. 22: a), short, the apical margin arced convexly, reaching to 2/3 of dorsal lobe. Aedeagus with long flexuous process at middle in lateral view (Figs 21: b, 22: b).

Female genitalia (Figs 23–31). Anal tube (Fig. 26) nearly oval, longer in middle than the widest breadth (1.61: 1.00), the apical margin arced, with unobvious membranous triangular protuberance, the widest at the basal 1/2. Anal style long, located at the basal 1/4 of anal tube (Fig. 26). Anterior connective lamina of gonapophysis VIII with obviously sclerous triangular process in basal dorsal margin, with three lateral teeth bearing three keels in lateral group and three apical teeth (Fig. 27). Posterior connective lamina of gonapophysis IX (Figs 28, 29) relative broad, median field symmetrical, with two ear-shaped prominences (medial dorsal process) (Fig. 28);



Figures 9–12. *Sinonissus brunetus* Wang, Shi & Bourgoin, 2018 **9** forewing **10** male genitalia, lateral view **11** anal segment, dorsal view **12** phallobase and aedeagus, lateral view. Scale bars: 0.5 mm. Abbreviations: a, short hooked process.

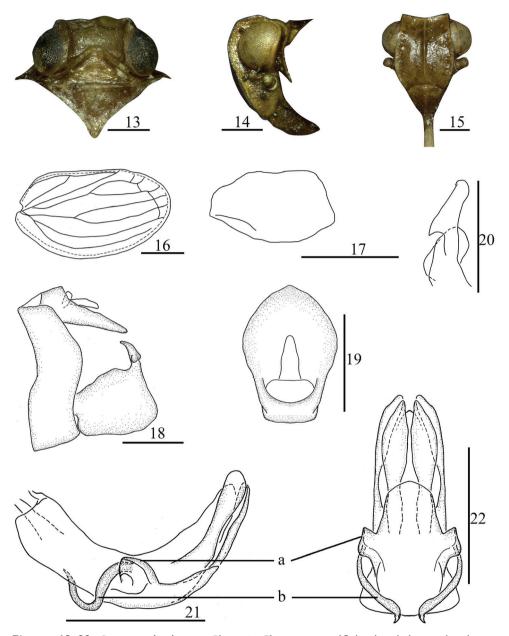
ventroposterior lobes bent at obtuse angle (posterior ventral lobes) (Fig. 29). Gonoplacs (Fig. 30) without keels. Hind margin of sternum VII median slightly concaved in ventral view (Fig. 31).

Etymology. The new species is named for its collecting location in the Daozhen County (Guizhou Province).

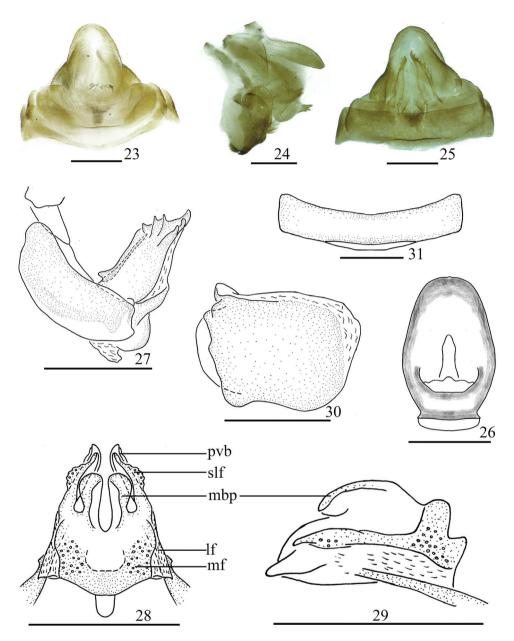
Host plant. Bamboo (Qiongzhuea communis Hsueh & Yi).

Distribution. China (Guizhou).

Remark. This species is similar to *S. brunetus*, but it differs from the latter by: 1) the width of vertex (Fig. 13) as long as 2.52 times in middle line; 2) phallobase with ventral lobe with lobe-like process near middle in lateral view, in ventral view ventral lobe tree lobes (Figs 21, 22); 3) aedeagus with long flexuous process near middle in lateral view (Fig. 21); 4) female genitalia with posterior connective lamina of gonapophysis IX with median field with symmetrical ear-shaped prominences (Fig. 28).



Figures 13–22. *Sinonissus daozhenensis* Chang & Chen, sp. nov. 13 head and thorax, dorsal view 14 head and thorax, lateral view 15 head, ventral view 16 forewing 17 hindwing 18 male genitalia, lateral view 19 anal segment, dorsal view 20 capitulum of genital styles, ventral view 21 phallobase and aedeagus, lateral view 22 phallobase and aedeagus, ventral view. Scale bars: 0.5 mm. Abbreviations: a, lobe-like process; b, long flexuous process.



Figures 23–31. Female genitalia. *Sinonissus daozhenensis* Chang & Chen, sp. nov. 23 dorsal view 24 lateral view 25 ventral view 26 anal segment, dorsal view 27 anterior connective lamina of gonapophysis VIII, lateral view 28 posterior connective lamina of gonapophysis IX, dorsal view 29 posterior connective lamina of gonapophysis IX, lateral view 30 gonoplacs, lateral view 31 sternum VII, ventral view. Scale bars: 0.5 mm. Abbreviations: lf, lateral field of posterior connective lamina of gonapophysis IX; mdp, medial dorsal process; mf, medial field of posterior connective lamina of gonapophysis IX; pvd, posterior ventral lobes; slf, sublateral field of posterior connective lamina of gonapophysis IX.

Sinonissus hamulatus Chang & Chen, sp. nov.

http://zoobank.org/57E722C1-CB99-42BD-B7A9-2BC8FA0084E9 Figs 5, 6, 32–50

Type material. Holotype: 3° , China: Guizhou, Jiangkou County, Fanjingshan National Nature Reserve (27°54'N, 108°38'E, 500–1800 m), 1–3 June 2002, X-S Chen leg.; paratypes: 1033 1099, same data as holotype.

Diagnosis. This species is similar to *S. brunetus*, but it differs from the latter by anal tube with spoon-like protrusion in lateral view (Fig. 36) (without spoon-like protrusion in *S. brunetus*); dorsal lobe of phallobase with rod-like cystiform processes at apical part (Fig. 40) (without rod-like process in *S. brunetus*); aedeagus with short hooked process, tip of process directed to dorso-posterior (Fig. 40) (tip of process directed to dorso-anterior in *S. brunetus*).

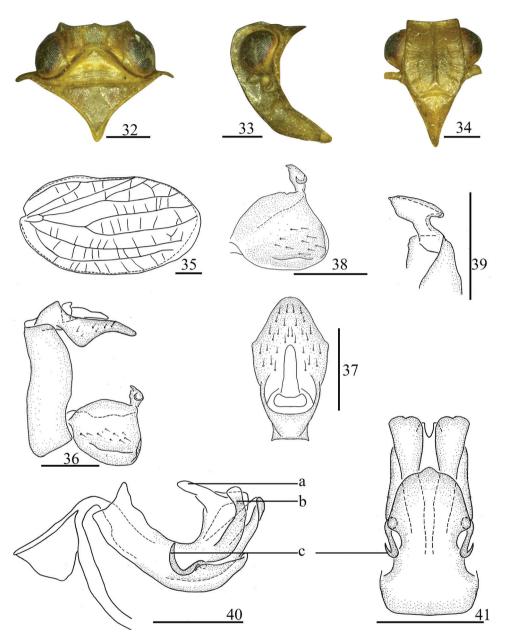
Description. Body length: male 3.61–3.98 mm, female 4.12–4.52 mm. Forewing: male 2.97–3.39 mm, female 3.46–3.80 mm.

Coloration. General color pale yellow to yellowish brown (Figs 5, 6). Vertex, pronotum and mesonotum (Fig. 32) pale yellow. Eyes brown to black (Fig. 33). Forewings (Fig. 5) pale yellow or yellowish brown, longitudinal veins pale brown, transverse veins pale white. Legs yellow brown, with tips of spines on hind tibiae and tarsi black.

Head and thorax. Head (Fig. 32) including eyes slightly narrower than pronotum (0.75: 1.00). Vertex (Fig. 32) shorter in middle than the wide at base (1.00: 3.00). Frons (Fig. 34) longer in middle than the widest breath (1.09: 1.00), median carina with the apical margin obscurely forked, nearly reaching to frontoclypeal suture. Clypeus triangular, with distinct median carina (Fig. 34). Pronotum (Fig. 32) with median carina obscure, lateral carina reaching to the posterior margin. Mesonotum (Fig. 32) triangular, without median carina. Forewings (Fig. 35) elongate, 1.82 times as long as maximum breadth. Hindwings absolutely reduced. Hind tibiae each with two lateral spines, spinal formula of hind leg 7–9–2.

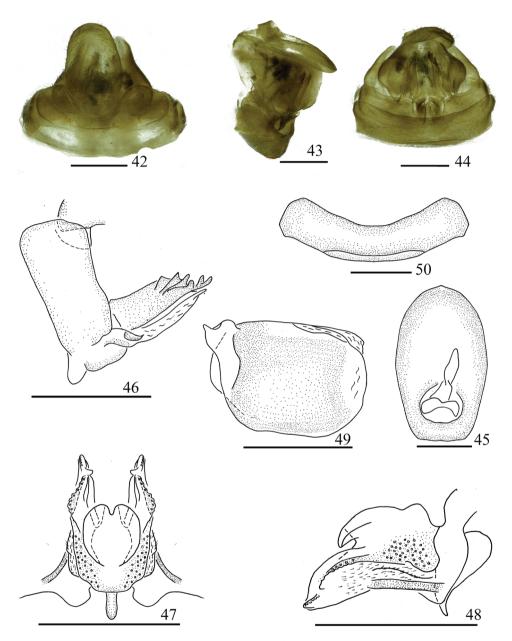
Male genitalia. Anal tube (Fig. 37) irregularly ligulate in dorsal view, the widest in apical 1/3, longer in midline than the width (1.85: 1.00), in lateral view anal tube with spoon-like protrusion (Fig. 36). Anal style (Fig. 37) sturdy and long, located at the base third of anal tube. Pygofer (Fig. 36) with dorsal margin slightly narrow than ventral margin. Genital styles (Fig. 38) relatively rectangular, dorsal margin slightly arched. Capitulum of genital styles relative long, irregularly triangular, neck obvious (Fig. 39). Phallobase (Figs 40, 41) with dorsal lobe finger-like cystiform process near apical part (Fig. 40: a), with relatively curved rod-like process in apical 1/3 (Fig. 40: b) in lateral view; lateral lobe splitting into two stout branches, the apical margin truncated in ventral view; ventral lobe short, unobvious lobe-like process near middle, reaching to 3/4 of dorsal lobe in lateral view, with three unobvious small lobes in ventral view. Aedeagus with short hooked process in the middle in lateral view, directed to dorso-posterior (Figs 40: c, 41: c).

Female genitalia (Figs 42–50). Anal tube (Fig. 45) nearly oval, longer in middle than the widest breadth (1.70: 1.00), the apical margin arched, with unobvious membranous triangular protuberance, the widest at the basal 1/2. Anal style long, located at the basal fifth of anal tube (Fig. 45). Anterior connective lamina of gonapophysis



Figures 32–41. *Sinonissus hamulatus* Chang & Chen, sp. nov. 32 head and thorax, dorsal view 33 head and thorax, lateral view 34 head, ventral view 35 forewing 35 male genitalia, lateral view 37 anal segment, dorsal view 38 genital styles, lateral view 39 capitulum of genital styles, ventral view 40 phallobase and aedeagus, lateral view 41 phallobase and aedeagus, ventral view. Scale bars: 0.5 mm. Abbreviations: a, finger-like cystiform process; b, curved rod-like process; c, short hooked process.

VIII with obviously sclerous triangular process in basal dorsal margin, with three lateral teeth bearing three keels in lateral group and three apical teeth (Fig. 46). Posterior connective lamina of gonapophysis IX (Figs 47, 48) relatively broad, median field



Figures 42–50. Female genitalia. *Sinonissus hamulatus* Chang & Chen, sp. nov. 42 dorsal view 43 lateral view 44 ventral view 45 anal segment, dorsal view 46 anterior connective lamina of gonapophysis VIII, lateral view 47 posterior connective lamina of gonapophysis IX, dorsal view 48 posterior connective lamina of gonapophysis IX, lateral view 49 gonoplacs, lateral view 50 sternum VII, ventral view. Scale bars: 0.5 mm.

symmetrical, with nearly circular prominences, apical margin deeply incised in middle (medial dorsal process) (Fig. 47); ventroposterior lobes bent at obtuse angle (posterior ventral lobes), with membranous triangular process at inner region near the apical part

(Fig. 48). Gonoplacs (Fig. 49) without keels. Hind margin of sternum VII median distinctly concave in ventral view (Fig. 50).

Etymology. This new species is derived from the Latin word *hamulatus*, referring to the short hamular process of aedeagus.

Host plant. Unknown.

Distribution. China (Guizhou).

Remarks. This new species is distinguished from other species of this genus by: 1) anal tube irregularly ligulate in dorsal view, with spoon-like protrusion in lateral view (Fig. 37); 2) phallobase with dorsal lobe rod-like cystiform processes at apical part, ventral lobes with three not obvious small lobes in ventral view (Fig. 40); 3) aedeagus with short hooked process in middle in lateral view (Fig. 40); 4) female genitalia with posterior connective lamina of gonapophysis IX in median field with nearly circular process (Fig. 47).

Sinonissus longicaudus Chang & Chen, sp. nov.

http://zoobank.org/730FE54F-DB72-4DC8-9A13-69C16ED1A8DD Figs 7, 8, 51–69

Type material. Holotype: ♂, China: Sichuan, Emeishan, Da'e Village (29°33'N, 103°24'E), 12–14 July 2010, Y-L Zheng leg.; paratypes: 1♂6♀♀, same data as holotype, Y-L Zheng and P Zhang leg.; 1♂1♀, Sichuan, Emeishan (29°30'N, 103°20'E), 3 Aug. 2012, H Li leg..

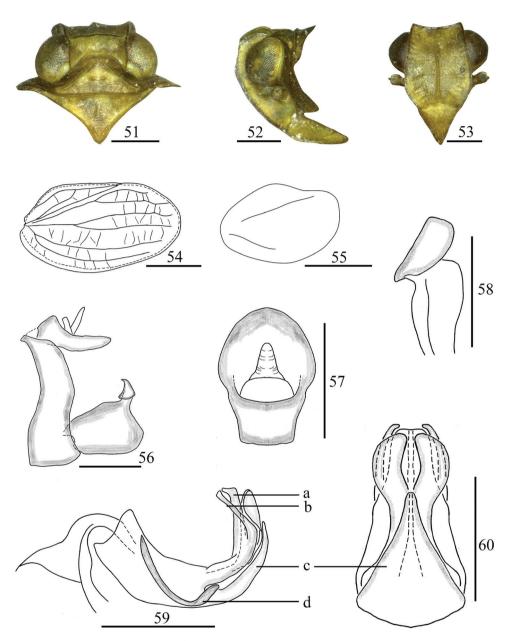
Diagnosis. This species is similar to *S. brunetus* but can be distinguished from the latter by aedeagus (Fig. 59) with long flagellate process in the middle in lateral view; phallobase (Fig. 60) with ventral lobe triangular, apical margin extremely narrow, the basal part broad in ventral view.

Description. Body length: male 3.38–3.63 mm, female 4.05–4.36 mm. Forewing: male 2.74–3.01 mm, female 3.27–3.62 mm.

Coloration. General color pale yellow to pale yellowish brown (Figs 7, 8). Vertex, pronotum and mesonotum (Fig. 51) pale yellow. Eyes brown (Fig. 52). Forewings (Fig. 7) pale yellow or yellowish brown, longitudinal veins pale brown, transverse veins pale white. Legs yellow brown, with tips of spines on hind tibiae and tarsi black.

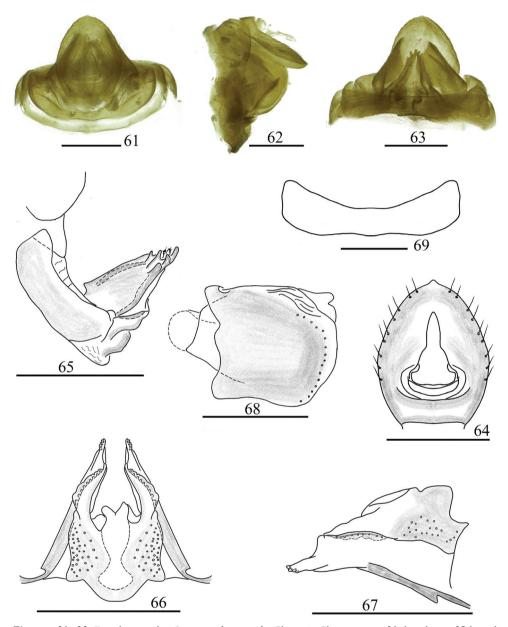
Head and thorax. Head (Fig. 51) including eyes slightly narrower than pronotum (0.73: 1.00). Vertex (Fig. 51) shorter in middle than the wide at base (1.00: 3.33). Frons (Fig. 53) longer in middle than the widest breath (1.14: 1.00), median carina with the apical margin straight, nearly reaching to frontoclypeal suture. Clypeus triangular, with obscure median carina (Fig. 53). Pronotum (Fig. 51) with median carina obscure, lateral carina reaching to the posterior margin. Mesonotum (Fig. 51) triangular, with median carina obvious. Forewings (Fig. 54) elongate, 1.78 times as long as maximum breadth. Hindwings (Fig. 55) reduced, small, with two veins. Hind tibiae each with two lateral spines, spinal formula of hind leg 8–8–2.

Male genitalia. Anal tube (Fig. 57) irregularly pentagonal in dorsal view, widest in the middle, longer in midline than the width (1.41: 1.00), ventral margin nearly straight. Anal style sturdy and short, located at the base half of anal tube (Fig. 57).



Figures 51–60. *Sinonissus longicaudus* Chang & Chen, sp. nov. 51 head and thorax, dorsal view 52 head and thorax, lateral view 53 head, ventral view 54 forewing 55 hindwing 56 male genitalia, lateral view 57 anal segment, dorsal view 58 capitulum of genital styles, ventral view 59 phallobase and aedeagus, lateral view 60 phallobase and aedeagus, ventral view. Scale bars: 0.5 mm. Abbreviations: a, horned cystiform process; b, thin rod-like process; c, ventral lobe process; d, long flagellate process.

Pygofer (Fig. 56) with dorsal margin narrower than ventral margin. Genital styles (Fig. 56) rectangular, dorsal margin and ventral margin nearly parallel. Capitulum of genital styles relatively short, irregularly triangular, neck obvious (Fig. 58). Phallobase



Figures 61–69. Female genitalia. *Sinonissus longicaudus* Chang & Chen, sp. nov. 61 dorsal view 62 lateral view 63 ventral view 64 anal segment, dorsal view 65 anterior connective lamina of gonapophysis VIII, lateral view 66 Posterior connective lamina of gonapophysis IX, dorsal view 67 Posterior connective lamina of gonapophysis IX, lateral view 68 Gonoplacs, lateral view 69 Sternum VII, ventral view. Scale bars: 0.5 mm.

(Figs 59, 60) with dorsal lobe small horned cystiform process at apical part (Fig. 59: a), with relatively straight thin rod-like process in apical 1/4 (Fig. 59: b) in lateral view; lateral lobe splitting into two stout branches, the apical margin arced in ventral view; ventral lobe short, reaching to 5/6 of dorsal lobe in lateral view, in ventral view the

apical part triangular, apical margin extremely narrow, the basal part broad (Figs 59: c, 60: c). Aedeagus with long flagellate process in the middle in lateral view, directed to dorso-anterior (Fig. 59: d).

Female genitalia (Figs 61–69). Anal tube (Fig. 64) nearly oval, longer in middle than the widest breadth (1.29: 1.00), the apical margin arced, with obvious membranous triangular protuberance, the widest near the basal 1/3. Anal style long, located at the basal third of anal tube (Fig. 64). Anterior connective lamina of gonapophysis VIII with obviously sclerous triangular process in basal dorsal margin, with two lateral teeth bearing two or three keels in lateral group and two or three apical teeth (Fig. 65). Posterior connective lamina of gonapophysis IX (Figs 66, 67) relatively narrow, median field asymmetrical, with tubercle-like prominences (medial dorsal process) (Fig. 66); ventroposterior lobes bent at acute angle (posterior ventral lobes) (Fig. 67). Gonoplacs (Fig. 68) without keels. Hind margin of sternum VII median distinctly concave in ventral view (Fig. 69).

Etymology. This new species is named for the presence of one long flagellate process of aedeagus.

Host plant. Unknown.

Distribution. China (Sichuan).

Remarks. This new species is distinguished from other species of this genus by: 1) aedeagus with long flagellate process in the middle in lateral view, directed to dorso-anterior (Fig. 59: d); 2) phallobase with dorsolateral lobe relatively straight, thin, rod-like process in lateral view (Fig. 59: b), ventral lobes triangular, apical margin extremely narrow, basal part broad in ventral view (Fig. 60: c); 3) female genitalia with posterior connective lamina of gonapophysis IX median field asymmetrical, with tubercle-like prominences (Fig. 66).

Discussion

According to the geographic distribution of the four species of *Sinonissus*, all species are distributed in the Oriental region and appear to be found only in China (Fig. 70). Following the taxonomic system of Gnezdilov (2002, 2003, 2009, 2013), the family Issidae consists of three tribes: Issini Spinola, 1839, Hemisphaeriini Melichar, 1906, and Parahiraciini Cheng & Yang, 1991, all in the subfamily Issinae, and the genera *Sinonissus* and *Celyphoma* Emeljanov, 1971 may also be placed in Issini Spinola, 1839, due to the genera having the following characters in common: the small body size, the vertex with its width longer along the midline, the forewing with veins running in parallel, the hind wing reduced or absent, and the phallobase without paired digitate processes on the inner side of the dorsolateral lobe.

Wang et al. (2016, 2018) placed *Sinonissus* in the Issini and *Celyphoma* in Hysteropterini in a new taxonomic system, based on limited molecular data. According to Bourgoin (2018), the subfamily Issinae contains the tribe Issini (including 61 genera) and Hysteropterini (including four genera) in the world. The subfamily Issinae is characteristically distributed in Wallace's Palaearctic region. In China, there are two genera recorded in the tribe Issini, *Issus* Brullé, 1832, and *Sinonissus* Wang, Shi & Bourgoin, 2018, and two genera in Hysteropterini: *Celyphoma* Emeljanov, 1971, *Potaninum* Gn-

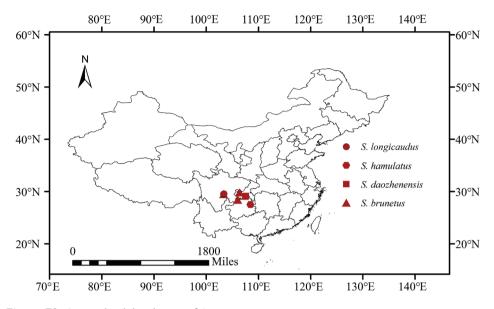
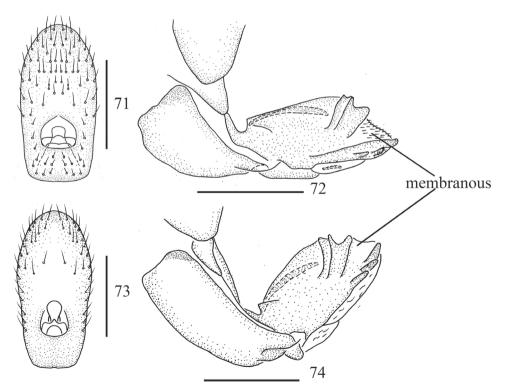


Figure 70. Geographical distribution of Sinonissus.



Figures 71–74. Female genitalia. 71, 72 *Celyphoma gansua* Chen, Zhang & Chang, 2014 73, 74 *Celyphoma yangi* Chen, Zhang & Chang, 2014 71, 73 anal segment, dorsal view 72, 74 anterior connective lamina of gonapophysis VIII, lateral view. Scale bars: 0.5 mm.

ezdilov, 2017. Fewer species were recorded in the subfamily Issinae: *Issus coleoptratus* (Fabricius, 1781) distributed in Hong Kong and four species of *Sinonissus* in Sichuan, Chongqing, and Guizhou (see Fig. 70). Gnezdilov (2017) recorded *Potaninum boreale* (Melichar, 1902) in Sichuan; four species of *Celyphoma* Emeljanov, 1971 have been recorded in Gansu, Inner Mongolia, Ningxia, Qinghai, and Xingjiang (Meng and Wang 2012, Chen et al. 2014). Except *Celyphoma*, other species and genera of Issinae in China are distributed in the Oriental region. Thus, the phylogeny based on the geographical distribution of Issinae is unstable and paradoxical.

For the female genitalia of Issinae, only female genitalia of *Sinonissus* and *Celypho-ma* were examined in this work. *Sinonissus* is obviously different from *Celyphoma* in the anal tube having an apical margin and an obvious membranous triangular protuberance, widest near the basal half; the anal style is long (Figs 26, 45, 64) [anal tube with apical margin without triangular protuberance, lateral margin parallel, anal style short in *Celyphoma* (Figs 71, 73)]; and the anterior connective lamina of gonapophysis VIII has the apical part sclerous (Figs 27, 46, 65) [membranous in *Celyphoma* (Figs 72, 74)].

The phylogeny based on a combination of the geographical distribution, male and female characters, and molecular data may be more convincing. Unfortunately, there is no further morphological information and molecular data is unavailable.

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RESEARCH ARTICLE



Redescription of Borboropactus jiangyong Yin, Peng, Yan & Kim, 2004 (Araneae, Thomisidae), with the first description of the male

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Abstract

The male of *Borboropactus jiangyong* Yin, Peng, Yan & Kim, 2004 is described for the first time from Jinggang Mountain, Ji'an City, Jiangxi Province, China. Based on male and female specimens, the species is redescribed, comprehensively illustrated, and its geographic distribution in China is delimited and discussed.

Keywords

China, digging spiders, distribution, Jiangxi Province, Jinggang Mountain, taxonomy

Introduction

Species in the genus *Borboropactus* Simon, 1884 are digging spiders, usually living in leaf litter, woody debris, tree bark, or on the forest ground, in a wide range of habitats, including tropical forests, subtropical forests, temperate forests, and early Tertiary Baltic amber (Wunderlich 2004a, b; Benjamin et al. 2008; Tang and Li 2010; Benjamin 2011; Yin et al. 2012; Ramírez 2014; World Spider Catalog 2019). Species can be easily recognised by a combination of somatic characters (Wunderlich 2004a, b; Benjamin et al. 2008; Benjamin et al. 2008; Benjamin 2011; Ramírez 2014), namely their body with adhered soil particles, numerous club-shaped hairs and powerful and long leg I.

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The genus was established based on the female specimens of *B. squalidus* Simon, 1884 collected from West Africa (Simon 1884). Subsequently, it was transferred in the genus Regillus O. Pickard-Cambridge, 1884 by Simon in 1895, along with another two species, namely B. bituberculatus Simon, 1884 and Thomisus vulcanicus Doleschall, 1859. Wunderlich (2004a, b) elevated Borboropactus to family rank, presumably due to its presence in Baltic amber and its unique? digging behavior. The new family Borboropactidae was subsequently rejected by Benjamin et al. (2008) based on the results of molecular phylogenetic analysis of three concatenated gene sequences (mtDNA 16S rRNA and cytochrome c oxidase subunit I and nuc DNA histone 3) of 25 genera of crab spiders and eleven out-groups. The molecular results were confirmed by a cladistic analysis of morphological data (Benjamin 2011). Based on molecular, morphological and additional ultrastructural characters, the genus Borboropactus is currently considered a specific lineage within Thomisidae (Benjamin et al. 2008; Benjamin 2011; Ramírez 2014). However, an enormous amount of work recently also shows that Borboropactus species are weakly supported among 44 terminals based on mitochondrial (12S, 16S, COI) and nuclear (histone H3, 18S, 28S) genomes, a result compatible with the family level recognition proposal of Wunderlich (2004b) (Wheeler et al. 2017).

Currently, there are 17 nominal species within *Borboropactus* (World Spider Catalog 2019), inhabiting tropical Africa and Asia. Taxonomic species identification is challenging because most species are described based either on single females or males, including *B. asper* (O. Pickard-Cambridge, 1884) (female), *B. australis* (Lawrence, 1937) (female), *B. biprocessus* Tang, Yin & Peng, 2012 (male), *B. cinerascens sumatrae* (Strand, 1907) (female), *B. elephantus* (Tikader, 1966) (female), *B. javanicola* (Strand, 1913) (female), *B. silvicola* (Lawrence, 1938) (female), *B. squalidus* Simon, 1884 (female), and *B. vulcanicus* (Doleschall, 1859) (female). The genus is represented by six species in China (World Spider Catalog 2019), half of which are also only known from either the male or female.

After examining spider specimens collected using the sieving method from the Jinggang Mountain National Nature Reserve in the past six years, the presumed male of *B. jiangyong* was found, and is here described for the first time. Additionally, female specimens belonging to this species have been identified among material collected from Yunnan, Guangdong and Hunan. The newly studied material allows for a more precise delimitation of the distribution of *B. jiangyong*. This study further includes photographs, SEM illustrations, and line drawings to provided more complete and detailed information of the somatic and genital morphology of this interesting species.

Materials and methods

Specimens were examined using a Zeiss Stereo Discovery V12 stereomicroscope with Zoom Microscope System. Further details were studied using a Zeiss Axio Scope A1 compound microscope with a KUY NICE CCD. Both the male palps and female genitalia were detached from the spider body and observed in 80–85% ethanol. For SEM photographs, the specimens were kept under natural dry conditions and photo-

stored in 80% ethanol after SEM. All morphological measurements were taken using a stereomicroscope (AxioVision SE64 Rel. 4.8.3) and given in millimetres. The body length of each specimen does not include the spinnerets. Leg measurements are given as total length (femur, patella, tibia, metatarsus, tarsus).

Terminology of the male and female genitalia follows Wunderlich (2004a, b), Benjamin et al. (2008), Benjamin (2011), and Ramírez (2014). Leg spines were documented by dividing each leg segment into two aspects, dorsal and ventral, the latter being divided into prolateral and retrolateral, e.g., I femur 0 (dorsal) 2 (prolateral ventral) 2 (retrolateral ventral); I tibia 1 (dorsal) 4 (prolateral ventral) 4 (retrolateral ventral). The abbreviations used in the text and figures are as follows:

Eyes

AME	anterior lateral eye; anterior median eye; median ocular area	posterior lateral eye; posterior median eye;
4		

Male palp

C E RTA	conductor; embolus; retrolateral tibial apophysis;	MA CD CO	median apophysis; copulatory duct; copulatory opening;			
Epygine						
ET LL	epigynal teeth; epigynal lateral lobe;	MF S	median field; spermathecae;			
Legs						
fe	femur;	ta	tarsus;			
me pa	metatarsus; patella;	ti	tibia			

Taxonomy

Family Thomisidae Sundevall, 1833

Genus Borboropactus Simon, 1884

Diagnosis. This genus can be easily distinguished from other genera in thomisid spiders by the body covered with numerous club-shaped hairs; posterior eye row recurved in

dorsal view; chelicerae toothed on both margins and with small teeth within its furrow; leg I powerful and distinctly the longest with the femur thickened prolaterally, bearing tubercles/spines, and with a depression; legs I and II with paired ventral tibial and metatarsal spines; legs III and IV without spines; metatarsal trichobothria with expansion, tarsal on sensory field with bumps in a long unexpanded area; presence of the tarsal pit organ (a special large leg sense organ); proclaw with a special patch of teeth; female epigynum teeth well developed; male palpal tibia with a retrodistal apophysis, bulbus simple and prominent, median apophysis present, conductor present or absent. See also Wunderlich (2004b) for a diagnosis of the genus and Wunderlich (2004a), Benjamin et al. (2008), Benjamin (2011), Ramírez (2014) and this paper for species descriptions.

Borboropactus jiangyong Yin, Peng, Yan & Kim, 2004

Figs 1-6

Borboropactus jiangyong Yin et al., 2004b: 27, figs 1–5; Yin et al., 2012: 1259, fig. 676a–e. Holotype not examined (see below in Remarks)

Material examined. 1 \bigcirc , 1 \bigcirc (JGSU), China: *Jiangxi Province*, Ji'an City, Jinggangshan County Level City, Luofu Town, Xiangzhou Village, Jinggang Mountain National Nature Reserve, 26°36'10.31"N, 114°15'15.52"E, 360 m, leaf litter, 5.X.2018, Ke-ke Liu and Hui-pu Luo leg.; as previous, 1 \bigcirc (JGSU), 26°36'10.8"N, 114°15'28.8"E, 375 m, leaf litter, 5 July 2017, Ke-ke Liu, Zhi-wu Chen, Ze-yuan Meng and Wen-jun Xie leg.; as previous, 1 \bigcirc (JGSU), 26°37'19.20"N, 114°15'54"E, 460 m, leaf litter, 6 August 2015, Ke-ke Liu, Sha Wu, Ze-yuan Meng, Ce Xu and Shi-cong He leg.; 1 \bigcirc (HNU), *Yunnan Province*, Baoshan City, Tengchong Town, Shangying Village, Chuanlong, 25°0'8.65"N, 098°25'24.85"E, 2000 m, 4 June 2006, Chang-min Yin, Jia-fang Hu and Xiao-hua Yang leg.; 1 \bigcirc (HNU), *Guangdong Province*, Shaoguan City, Ruyuan Town, Nanling National Nature Reserve, Qinshuigu, 24°55'07.89"N, 113°02'30.58"E, 830 m, 25 July 2016, Hai-qiang Yin, Tie-yang Zhou, Gu-chun Zhou, Chao-min Li, Ai-lan He, Wang Liu, Jin-xin Liu, Zhuo-er Chen and Chen Zeng leg.

Diagnosis. The male of this species resembles both *B. biprocessus* Tang, Yin & Peng, 2012 and *B. bituberculatus* by the ear-shaped median apophysis on the tegulum, but can be separated by cheliceral teeth number, 4 promarginal and 3 retromarginal, instead of 4 and 4 in species *B. biprocessus* and 4 and 5 in species *B. bituberculatus*; a strong RTA extending dorsally on palp cymbium, instead of relative thinner in species *B. biprocessus* and stouter in species *B. biprocessus* and the relatively narrowed membranous conductor, which is broad in species *B. biprocessus* and *B. bituberculatus*, and the relatively narrowed membranous conductor, which is broad in species *B. biprocessus* and *B. bituberculatus* (Figs 1C, D, F–H, 4C–G, 5) (see also Yin et al. 2012: 1258, fig. 675A–C; Tang and Li 2010: 18–20, figs 12A–D, 14A, B). Females are separated from similar species of *B. bituberculatus* Simon, 1884 and *B. brevidens* Tang & Li, 2010 by the shape of the broad, cruciform median field (tongue-shaped in *B. bituberculatus*; triangular in *B. brevidens*), chelicerae with four promarginal teeth and 4 or 3 retromarginal teeth

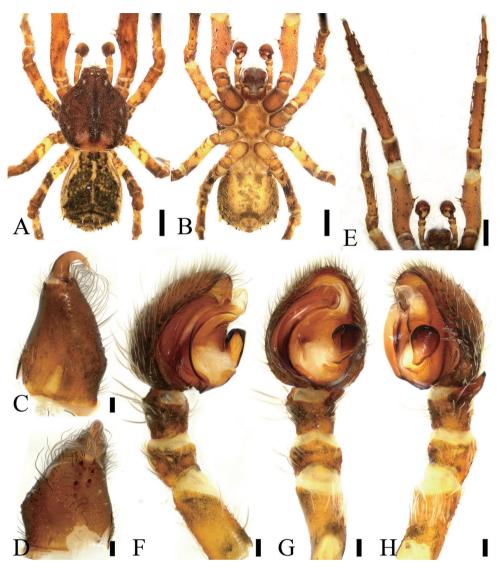


Figure I. *Borboropactus jiangyong* Yin, Peng, Yan & Kim, 2004, male. **A** Habitus, dorsal view **B** habitus, ventral view **C** left chelicera, dorsolateral view **D** same, ventral view **E** left leg I and II, ventral view **F** left palp, prolateral view **G** left palp, ventral view **H** left palp, retrolateral view. Scale bars: 1 mm (**A**, **B**, **E**), 0.1 mm (**C**, **D**, **F–H**).

(4 pro- and 5 retromarginal teeth in *B. bituberculatus*; 5 pro- and 4 retromarginal teeth in *B. brevidens*), longer epigynal teeth (relative shorter in *B. bituberculatus* and *B. brevidens*), and the enlarged, strongly twisted copulatory duct (Figs 2C, D, F, G, 3, 4A, B) (see also Tang and Li 2010: 8–20, figs 3A–C, 6C, D, 13A–D, 14C, D).

Description. *Male. Habitus* as in Fig. 1A, B. Total length 6.64. Prosoma (Fig. 1A) length 3.31, width 2.71. Eye (Fig. 1A) sizes and interdistances: AME 0.17; ALE 0.17; PME 0.17; PLE 0.20; AME–AME 0.08; AME–ALE 0.10; PME–PME 0.11; ALE–ALE

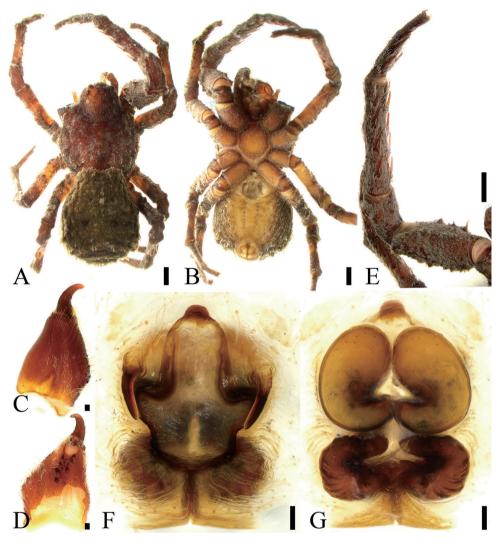


Figure 2. *Borboropactus jiangyong* Yin, Peng, Yan & Kim, 2004, female. **A** Habitus, dorsal view **B** habitus, ventral view **C** left chelicera, dorsolateral view **D** same, ventral view **E** left leg I, prolateral view **F** epigyne, ventral view **G** vulva, dorsal view. Scale bar: 1 mm (**A**, **B**, **E**), 0.1 mm (**C**, **D**, **F**, **G**).

0.54; PME–PLE 0.19; PLE–PLE 0.73; ALE–PLE 0.10, AME–PME 0.08; AME–PLE 0.33. MOA: 0.39 long; 0.41 front width, 0.46 back width, anterior and posterior eye row recurved, anteriorly located on prosoma. Chelicerae (Fig. 1C, D) with four promarginal teeth and four retromarginal teeth and including a vestige tooth, and two small denticles in-between teeth. Endites (Fig. 1B) nearly quadrilateral. Labium (Fig. 1B) rectangular, anteriorly with 6–10 strong setae. Sternum (Fig. 1B) shield-shaped, with abundant setae around margin. Leg (Fig. 1A, B, E) measurements: I 11.33 (3.50, 1.19, 3.61, 2.06, 0.97); II 7.88 (2.19, 0.93, 2.24, 1.59, 0.93); III 7.27 (2.18, 0.78, 1.90, 1.60,

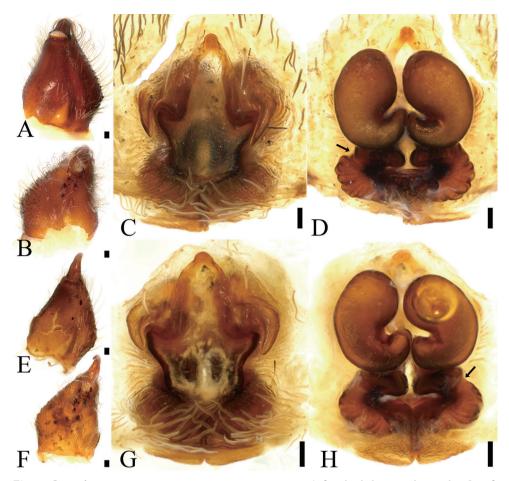


Figure 3. *Borboropactus jiangyong* Yin, Peng, Yan & Kim, 2004, female chelicera and genitalia. **A** Left chelicera, dorsolateral view **B** same, ventral view **C** epigyne, ventral view **D** vulva, dorsal view, black arrow shows anterior part of spermathecae with a constriction **E** left chelicera, dorsolateral view **F** same, ventral view **G** epigyne, ventral view **H** vulva, dorsal view; black arrow shows anterior part of spermathecae with a constriction. Scale bars: 0.1 mm (**A**–**H**).

0.81); IV 8.93 (2.86, 0.97, 2.14, 1.87, 1.09). Leg formula 1423. Spination: I fe 120, pa 001, ti 055, met 033, ta 000; II fe 000, pa 000, ti 044, met 033, ta 000. Fe I with six ventral cusps. Opisthosoma length 3.17, width 2.37, hardened, with abundant particles and two pairs of rugose sigillae, posteriorly with many clavate hairs on dorsal view.

Colouration and pattern. Prosoma pyriform, yellow brown, densely covered white feathery setae, with a longitudinal dark stripe, clustered short hairs at back of the PLE and near the posterior of the stripe, and four paired radial striae around fovea. Chelicerae, endites, and labium yellow brown. Sternum from yellow brown to orange. Legs from yellow to orange. Opisthosoma from orange to greyish black, with light longitudinal stripe and abundant dark and light spots.

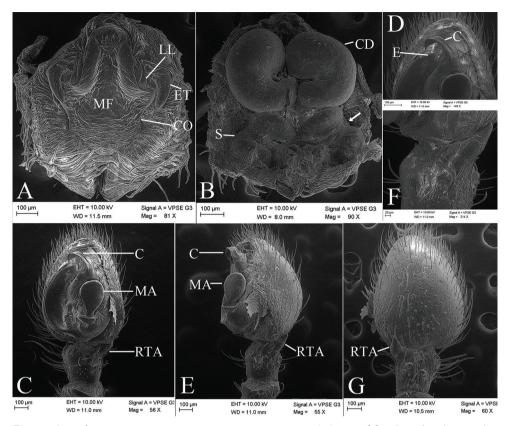


Figure 4. *Borboropactus jiangyong* Yin, Peng, Yan & Kim, 2004, SEMs of female and male genitalia. **A** Epigyne, ventral view **B** vulva, dorsal view, black arrow shows anterior part of spermathecae with a constriction **C** left palp, ventral view **D** detail of embolus and conductor **E** left palp, retrolateral view **F** detail of RTA, retrolateral view **G** left palp, dorsal view. Abbreviations: C – conductor, CD – copulatory duct, CO – copulatory opening, E – embolus, ET – epigynal teeth, LL – epigynal lateral lobe, MA – median apophysis, MF – median field, RTA – retrolateral tibial apophysis, S – spermathecae.

Palp (Figs 1F–H, 4C–G, 5). Palp with a relative long and strong RTA, extending dorsally; cymbium laterally protruded near the RTA; tegulum with an ear-shaped median apophysis; embolus twisted, apex slender; conductor translucent with wrinkled base.

Female. Habitus as in Fig. 2A, B. Total length 13.35. Prosoma (Fig. 2A) length 6.64, width 5.87. Eye (Fig. 2A) sizes and interdistances: AME 0.22; ALE 0.24; PME 0.24; PLE 0.26; AME–AME 0.25; AME–ALE 0.33; PME–PME 0.23; ALE–ALE 1.28; PME–PLE 0.60; PLE–PLE 1.79; ALE–PLE 0.26, AME–PME 0.29; AME–PLE 0.75. MOA: 0.67 long; 0.62 front width, 0.69 back width. Chelicerae (Fig. 2C, D) with four promarginal teeth and three retromarginal teeth and including a vestige tooth, and six small denticles in-between teeth. Endites (Fig. 2B) nearly quadrilateral. Labium (Fig. 2B) rectangular, anteriorly with 8 strong setae. Sternum (Fig. 2B) shield-shaped, with abundant setae around margin. Leg (Fig. 2A, B, E) measurements: I 16.68 (5.64, 2.51, 4.68, 2.58, 1.27); II 11.54 (3.77, 1.69, 3.02, 2.04, 1.02); III 11.40 (3.29, 1.66, 3.24,

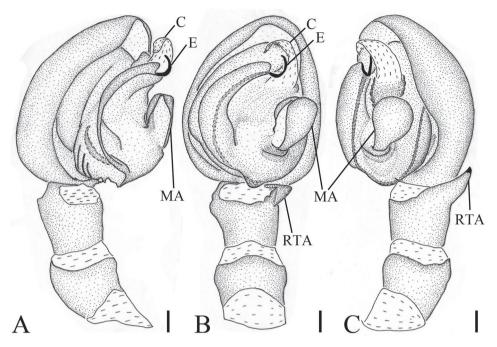


Figure 5. *Borboropactus jiangyong* Yin, Peng, Yan & Kim, 2004, male palp. **A** Left palp, prolateral view **B** left palp, ventral view **C** left palp, retrolateral view. Scale bars: 0.1 mm (**A–C**). Abbreviations: C – conductor, E – embolus, MA – median apophysis, RTA – retrolateral tibial apophysis.

2.30, 0.91); IV 12.26 (4.22, 1.53, 3.07, 2.45, 0.99). Leg formula 1423. Spination: I fe 220, pa 000, ti 055, met 033, ta 000; II fe 000, pa 000, ti 044, met 033, ta 000. Fe I with fourteen ventral cusps. Opisthosoma length 6.71, width 5.87.

Colouration and pattern. Prosoma orange or red-brown, without stripe. Opithosoma without clear stripe.

Epigynum (Fig. 2F, G). Median field cruciform, broad, delimited by furrows; epigynal lateral lobe long, arising from antero-lateral part of median field; epigynal teeth well advanced, situated anteriorly, arising bilaterally, sharp, slightly shorter than 1/2 median field length; copulatory ducts broad, wider than spermathecae, both ends swollen, C-shaped, located at anterior of vulva, anterior and posterior part are approaching each other; spermathecae curved laterally, tube-shaped, anterior part not have a constriction, median part C-shaped, both ends slightly swollen, a pair of wrinkled chitinous lamellae covered the posterior part of spermathecae.

Distribution. Known from Hunan, Yunnan, Jiangxi, and Guangdong provinces (Fig. 6). Specimens were collected from an area approaching 26°N in China (Fig. 6). It is possible that this species is also distributed in Guizhou, Fujian, and Sichuan provinces. This will have to be confirmed by future collecting and further research.

Variability. We conducted a survey of *Borboropactus jiangyong* female specimens from Hunan, Yunnan, Jiangxi, and Guangdong provinces in China available in muse-

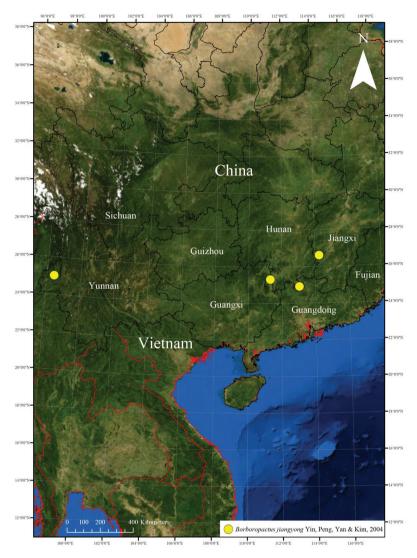


Figure 6. Collection localities of Borboropactus jiangyong Yin, Peng, Yan & Kim, 2004 in China.

ums. The detailed study of these specimens (Figs 2F, G, 3C, D, G, H, 4A, B) revealed that they all differ in the number of cheliceral denticles depending upon locality. Specimens from Yunnan bore four small denticles close to promarginal teeth and two close to retromarginal teeth; specimens from Jiangxi bore four small denticles close to promarginal teeth and four close to retromarginal teeth; or one small denticle close to promarginal teeth, three close to retromarginal teeth; or one small denticle close to promarginal teeth, four close to retromarginal teeth; from Guangdong one small denticle near promarginal teeth, one near retromarginal teeth. Similarly, specimens from different provinces also differed in the number of ventral cusps on their fe I: fourteen from Yunnan;

twelve from Jiangxi; twenty-three from Jiangxi; fourteen from Jiangxi; and ten from Guangdong. Meanwhile, their body sizes, eye sizes and eye interdistances are also in the range such as total length 9.48–14.37; prosoma length 5.50–6.65, width 4.74–5.87; opisthosoma length 3.98–8.04, width 3.48–5.87; AME 0.16–0.22; ALE 0.17–0.24; PME 0.17–0.24; PLE 0.17–0.26; AME–AME 0.24–0.33; AME–ALE 0.24–0.33; PME–PME 0.20–0.30; ALE–ALE 1.01–1.38; PME–PLE 0.46–0.60; PLE–PLE 1.56–1.83; ALE–PLE 0.22–0.39, AME–PME 0.22–0.45; AME–PLE 0.59–0.86; MOA 0.59–0.76 long, 0.53–0.65 front width, 0.64–0.71 back width; leg I 14.77–18.12; II 10.20–12.30; III 10.22–11.99; IV 11.23–13.28. Finally, variability was also observed in the epigynal teeth, which may either have a sharp tip or a blunt tip; and the anterior part of spermathecae, which may or may not have a constriction. The regional variability observed across the distribution of *Borboropactus jiangyong* may be the result of the influence of environmental factors, such as temperature, elevation or habitat.

Remarks. Unfortunately, the holotype of this species stored at the College of Life Sciences, Hunan Normal University (HNU), could not be studied because it was destroyed by slime moulds. However, the female holotype had been examined by Dr Guo Tang who contributed with many papers on crab spider taxonomy in China. Based on a comparative morphology analysis, he suggested that the female from Baoshan City in Yunnan Province was conspecific with the female holotype described in Tang's PhD dissertation in 2008.

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CORRIGENDA



Corrigendum: Recognising and defining a new crown clade within Stromboidea Rafinesque, 1815 (Mollusca, Gastropoda). ZooKeys 867: 1–7. https://doi.org/10.3897/ zookeys.867.34381

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The paper "Recognising and defining a new crown clade within Stromboidea Rafinesque, 1815 (Mollusca, Gastropoda)" contains a typographic error that occurred during copy editing: "Neostromboidea" should read "Neostromboidae". "-oidae" is the most correct epifamily rank declension in this case.

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