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A new species of *Paraonis* and an annotated checklist of polychaetes from mangroves of the Brazilian Amazon Coast (Annelida, Paraonidae)

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Abstract

The polychaete fauna from the mangroves of the Amazon Coast in Maranhão state, Brazil, is reported in this study. Fourteen species are listed, namely *Alitta succinea* (Leuckart, 1847); *Arabella* (*Arabella*) *iricolor* Montagu, 1804; *Capitella capitata* (Fabricius, 1780) complex; *Exogone* (*Exogone*) *breviantennata* Hartmann-Schröder, 1959; *Heteromastus filiformis* (Claparède, 1864); *Isolda pulchella* Müller, 1858; *Mediomastus californiensis* Hartman, 1944; *Namalycastis fauveli* Nageswara Rao, 1981; *Namalycastis geayi* (Gravier, 1901); *Namalycastis senegalensis* (Saint-Joseph, 1901); *Nephtys simoni* Perkins, 1980; *Paraonis amazonica* **sp. n.**; *Sigambra bassi* (Hartman, 1945); and *Sigambra grubii* Müller, 1858. Among them, *Namalycastis fauveli* and *Namalycastis geayi* are recorded for the first time in Brazil. *Paraonis amazonica* **sp. n.** is a new species for science, characterized by a rounded prostomium, 4–8 pairs of foliaceous branchiae, absent eyes, and two types of modified neurochaetae, acicular and hook-shaped.

Keywords

annelid, mangrove, Maranhão, new records, *Paraonis*, taxonomy

Introduction

The two largest rivers that drain South America, the Amazon and the Orinoco, are respectively, the first and third largest rivers in the world in terms of water volume (Degens et al. 1991). The Orinoco and Amazon Rivers are responsible for the discharge of an enormous amount of freshwater and sediment into the ocean, representing nearly 20 % of the total global annual freshwater (Hu et al. 2004; Miloslavich et al. 2011). These rivers have been recognized as zoogeographic barriers to the dispersal of marine fauna between the Caribbean and southwestern Atlantic (Gilbert 1972; Floeter and Gasparini 2000). Accordingly, they influence the Brazilian Northern Coast, also known as the Brazilian Amazon Coast, which extends from the north of the Amapá State to the Gulf of Maranhão and represents 35 % of the entire Brazilian Coast (Silveira 1964; Sousa et al. 2008). This region is characterized by a variety of poorly known estuarine and marine ecosystems with very diverse habitats (Couto et al. 2003).

Most of what is known about the marine biodiversity of the Brazilian Amazon Coast is related to fishing and mangrove habitats Nevertheless, the REVIZEE Program – Living Resources in the Exclusive Economic Zone provided important information regarding the continental shelf and offshore area (Miloslavich et al. 2011). In general, macrobenthos assemblages are one of the least known of Brazil (Amaral and Jablonski 2005; Miloslavich et al. 2011). The lack of studies in this region represents one of the major gaps in the knowledge of the biodiversity of Brazilian polychaetes (see Lana et al. 2009). The main studies concerning polychaetes in this region include ecological research with records in the coast of the states of Maranhão (see Ribeiro and Almeida 2014) and Pará (Rosa-Filho et al. 2006; Morais and Lee 2014) recording a total of 27 species and 24 families.

In this study, polychaetes collected in the mangrove of São Marcos Bay in the Gulf of Maranhão were examined. The current study contributes to increasing the knowledge of polychaetes in the South Atlantic, particularly in the Amazon coastal zone. This is the first taxonomic study with a focus on the polychaete fauna from Maranhão and includes new records and the description of a new species.

Materials and methods

Mangrove specimens from the Gulf of Maranhão were collected between April of 2010 and June of 2012 from two creeks in São Marcos Bay: Buenos Aires at the São Luís (02°35'56"S, 44°21'11.8"W) and Tronco at the Caranguejos Island (02°49'33.6"S, 44°28'51.1"W) (Fig. 1). Along of a 100 m transect, nine sediment samples were taken using a corer (20 cm long and 10 cm diameter) at the intertidal region of each creek. Samples were washed through a 0.5 mm mesh sieve with filtered freshwater in the

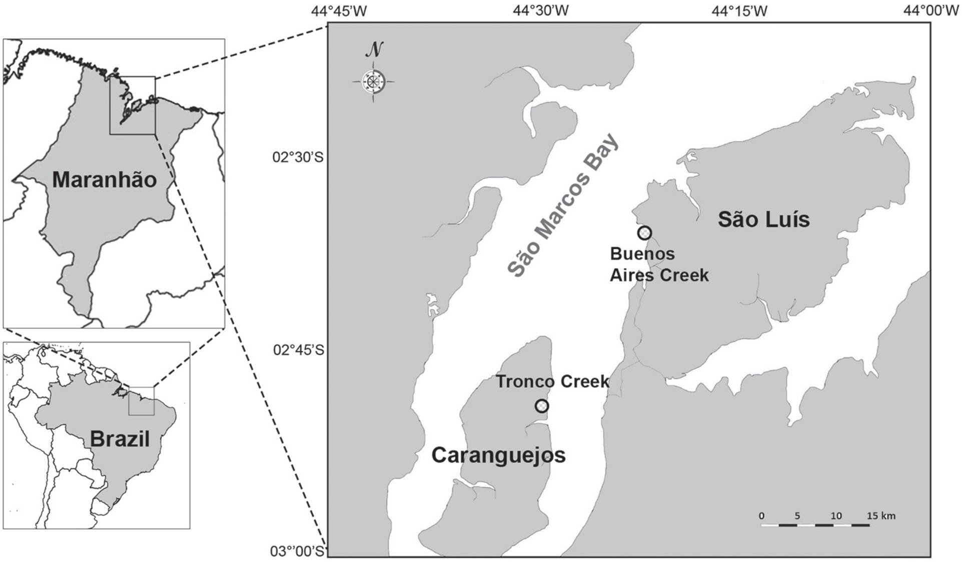

Figure 1. Study area. Buenos Aires and Tronco creeks in Maranhão, Brazilian Amazon Coast.

laboratory; specimens were fixed in 4 % formaldehyde and then transferred to 70 % ethanol for long-term storage.

Polychaetes were identified at the species level using stereo (Olympus SZX-16) and light microscope (Olympus CX31). Specimens were prepared for scanning electron microscopy (SEM) by critical point drying, prior to being mounted on stubs and coated with gold (200 A thick). These specimens were observed and analyzed in the Jeol JSM-6390LV scanning electron microscope of the Museu Nacional/Universidade Federal do Rio de Janeiro (MNRJ). Light microscopy images were taken with a camera attached to a Leica M205A stereo microscope and a Zeiss Axio Scope microscope. Drawings and pictures were processed using Adobe (San Jose, CA, USA) Photoshop CS6.

The specimens and type material referent to the new species were deposited in the research collection Coleção Científica de Invertebrados Marinhos e Costeiros (NPM) of the Núcleo em Ecologia e Desenvolvimento Sócio-Ambiental de Macaé (NUPEM), Macaé, Brazil, and in the Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain. Additionally, we elaborated a list of some Brazilian records of the species identified here, taking into account those reported by studies formally published (Suppl. material 1). We designated up to one previous record for each Brazilian state indicated in the species distribution section, plus original description, when applicable. Our criteria to select the studies were, preferably: taxonomic approach, ecological approach providing voucher-specimens, ecological approach without voucher-specimens.

Other abbreviations cited in this study:

BMHN	British Museum (Natural History), London.
IBUFRJ	Coleção de Polychaeta do Museu Nacional, Rio de Janeiro.
MCEM-BPO	Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná.
MZUSP	Museu de Zoologia da USP, São Paulo.
MPEG.ANL	Museu Paraense Emílio Goeldi, Belém.
POLY-UFPB	Coleção de Invertebrados Marinhos Paulo Young, Universidade Federal da Paraíba, Paraíba.
UK	United Kingdom.
USA	United States of America.
USNM	United States National Museum, Smithsonian Institution, Washington.
ZMH	Zoologisches Staatsinstitut und Zoologisches Museum Hamburg, Hamburg.
ZUEC	Coleção de Polychaeta do Museu de Zoologia "Prof. Adão José Cardoso", Universidade Estadual de Campinas, Campinas.

Taxonomy

A total of eight families, eleven genera, and 14 species were identified; new records of *Namalycastis geayi* and *Namalycastis senegalensis* (Nereididae) and a new species of *Paraonis* (Paraonidae) are reported from Brazil.

Phylum Annelida
Subclass Errantia
Order Eunicida
Family Oenonidae Kinberg, 1865
Genus *Arabella* Grube, 1850

Arabella (*Arabella*) *iricolor* (Montagu, 1804)

Fig. 2

Type locality. Devonshire, England, United Kingdom (50°34'N, 3°34'W; estimated geolocation).

Material examined. São Luís, 02°35'56"S, 44°211'1.8"W: two specimens, 18 March 2012 (NPM-Pol 115); one specimen, 1 June 2012 (NPM-Pol 090); one specimen, 18 November 2011 (NPM-Pol 886); complete and incomplete specimens.

Distribution. Pacific Ocean: New Zealand, Philippines, USA, Peru. Indian Ocean: Red Sea. Atlantic Ocean: Ireland, UK, France, Mediterranean Sea, Marmara

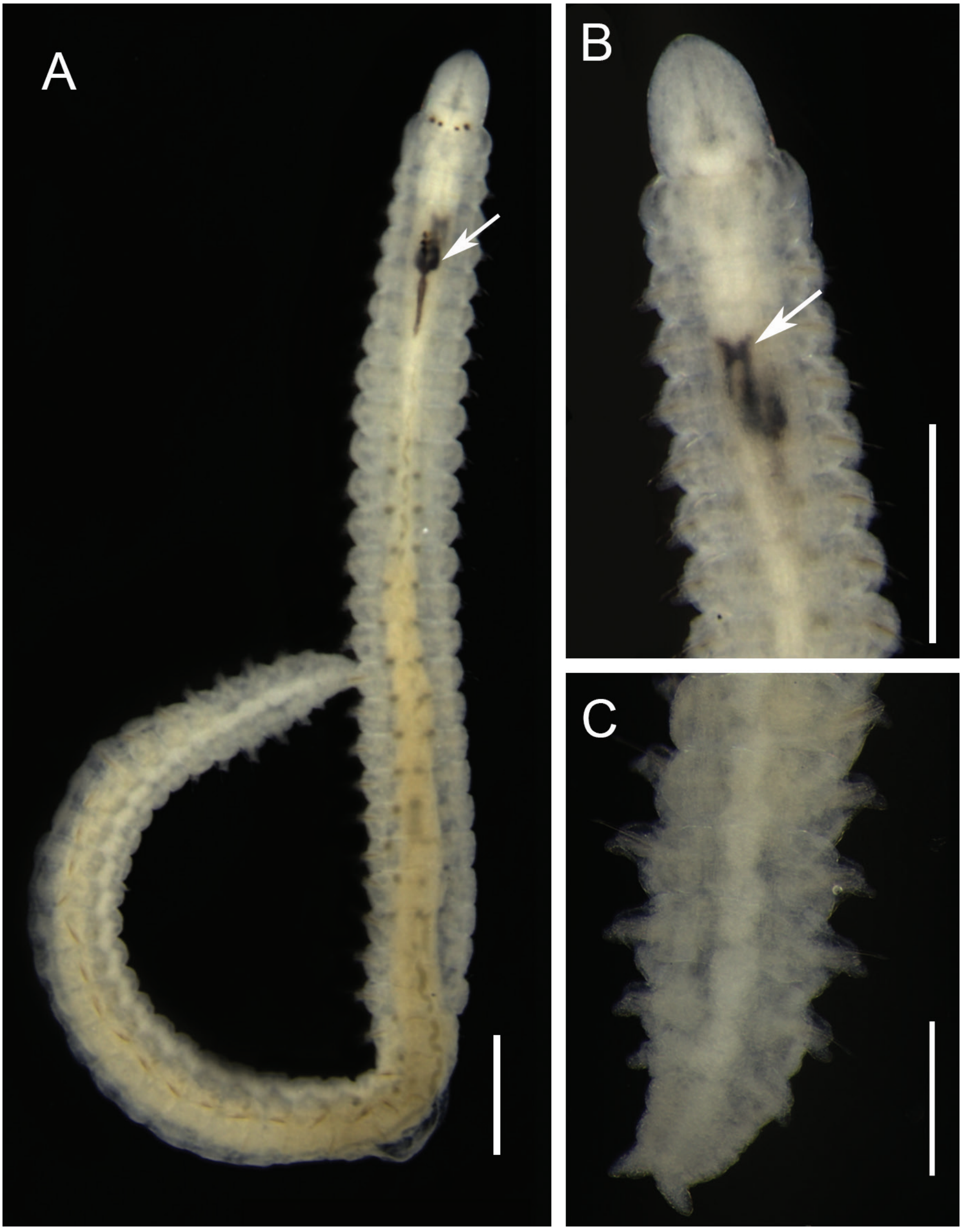

Figure 2. *Arabella* (*Arabella*) *iricolor*, fixed specimen. **A** Whole body, dorsal view, arrow point to maxillae and carriers **B** Anterior end, ventral view, arrow point to mandibles **C** Posterior end, dorsal view. Scale bars: 0.5 mm (**A, B**), 0.3 mm (**C**).

Sea (Turkey), Mauritania, South Africa, USA, Mexico, Caribbean Sea, Brazil (states of Maranhão, Bahia, São Paulo and Paraná, see Suppl. material 1).

Remarks. *Arabella* (*Arabella*) *iricolor* was described to the south coast of Devonshire (UK) as *Nereis iricolor* (Montagu, 1804). The description of specimens from the

Caribbean Sea (Augener 1927) closely resembles specimens in this study, which were identified as this species due to the characteristics: ventralmost chaeta tapering gradually to guards in median and posterior chaetigers, the absence of hooded acicular chaetae, maxilla MxI unidentate and posterior post-chaetal lobe shorter than chaetae. Body surface whitish was observed in small fixed individuals, probably juveniles (Fig. 2A–C). (Montagu 1804). The species was recorded in ecological studies of the continental shelf, intertidal zone, coral reefs, estuaries, and mangroves (Paiva 1993, Santa-Isabel et al. 2000), but apparently, the material was not deposited in any collection and was not available for comparison. Previous record from Maranhão reports specimens found in mangroves (Oliveira and Mochel 1999). This species has been described with worldwide distribution and is probably a complex of species (Colbath 1989; Zanol and Ruta 2015). Studies on the variation of the symmetry in maxillae and modified ventral chaetae should be conducted to know the polymorphism in species of the genus *Arabella* (Steiner and Amaral 2009). That would be a challenge to species identification and new descriptions, once Oenonidae species are usually collected in low densities (Zanol 2010, Zanol and Ruta 2015).

Order Phyllodocida
Family Nephtyidae Grube, 1850
Genus *Nephtys* Cuvier, 1817

Nephtys simoni Perkins, 1980
Fig. 3

Type locality. Hutchinson Island, Florida, USA (27°21.6'N, 80°13.2'W; original geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, 23 April 2010 (NPM-Pol 868); four specimens, 21 October 2010 (NPM-Pol 869); one specimen, 27 January 2011 (NPM-Pol 870); four specimens, 27 January 2011 (NPM-Pol 871); one specimen, 6 September 2011 (NPM-Pol 872); one specimen, 18 December 2011 (NPM-Pol 873); complete and incomplete specimens. Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: 31 specimens, 20 October 2010 (NPM-Pol 874); 12 specimens, 17 March 2012 (NPM-Pol 455); six specimens, 5 September 2011 (NPM-Pol 875); complete and incomplete specimens.

Distribution. Atlantic Ocean: Mediterranean Sea, USA, Mexico, Brazil (states of Pará, Maranhão, São Paulo, see Suppl. material 1).

Remarks. First record for Maranhão. The specimens present the characters that define *Nephtys simoni* Perkis, 1980, such as interramal branchiae from the third chaetiger; proboscis with long middorsal and midventral subdistal papilla and 23 conical papilla distal, dorsal cirrus linked to pre-chaetal cirrus, short and finger-like lobes. Individuals that have one pair of eyespots and median reddish pigmentation in the prostomium

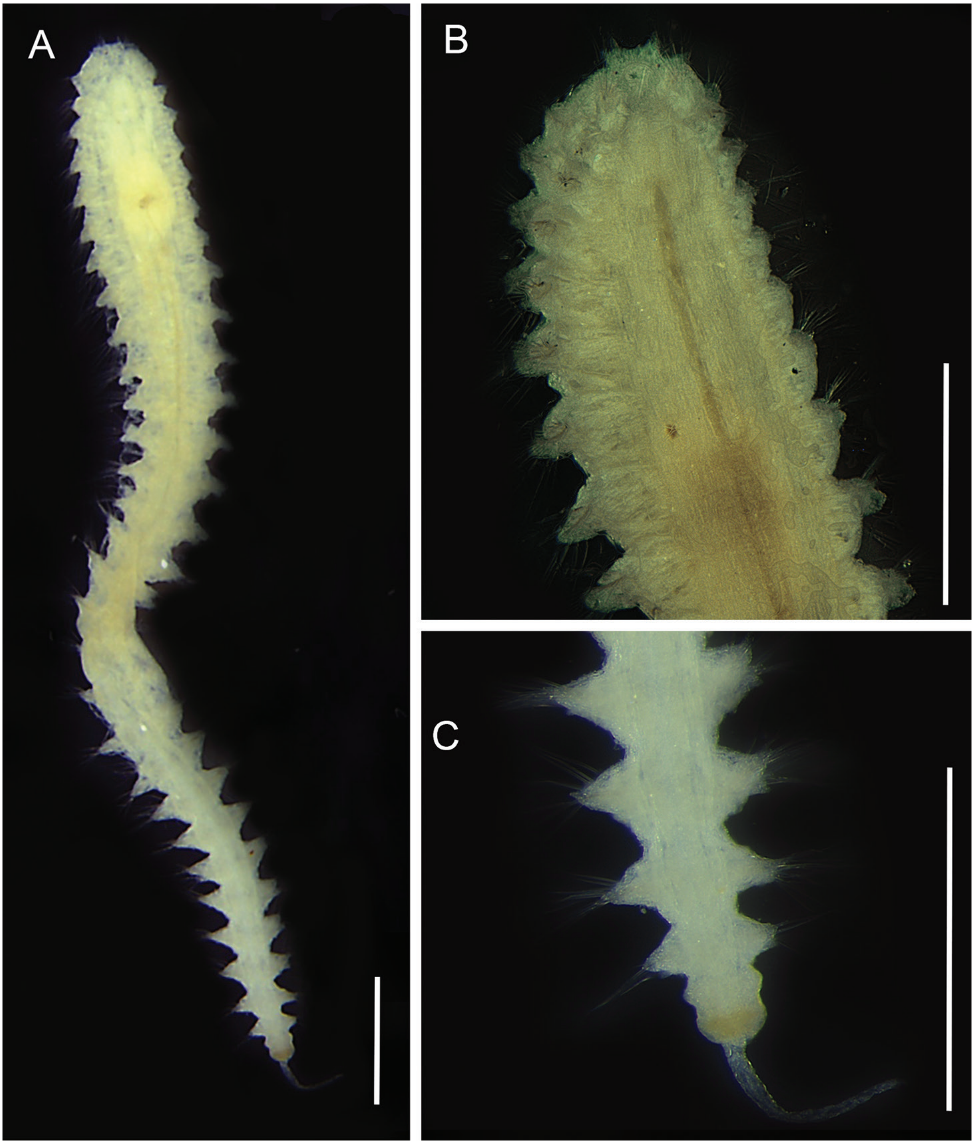

Figure 3. *Nephtys simoni*, fixed specimen. **A** Whole body, dorsal view **B** Anterior end, dorsal view **C** Posterior end, dorsal view. Scale bars: 0.5 mm.

were reported for juveniles by Perkins (1980). In this study, some specimens presented eyespots, but not the reddish pigmentation pattern. Specimens of *N. simoni* have been reported in estuarine areas as in the type locality (Perkins 1980) and in Amazon mangroves (Silva et al. 2011). In Brazil, the specimens recorded as *Nephtys simoni* in Paranaguá Bay, Paraná (Lana 1986) are in fact *Nephtys californiensis* Hartman, 1938 (Rizzo and Amaral 2007).

Family Nereididae Blainville, 1818
Genus *Alitta* Kinberg, 1865

Alitta succinea (Leuckart, 1847)
Fig. 4

Type locality. Helgoland and Cuxhaven, Germany (53°53'N, 8°37'E; estimated geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, 6 September 2011 (NPM-Pol 083); two specimens, 27 January 2011 (NPM-Pol 876); complete and incomplete specimens. Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one specimen, 20 October 2010 (NPM-Pol 877); complete and incomplete specimens.

Distribution. Pacific Ocean: Australia, New Zealand, USA, Mexico. Indian Ocean: Red Sea. Atlantic Ocean: North Sea, Mediterranean Sea, South Africa, Canada, USA, Caribbean Sea, Brazil (state of Pará, Maranhão, Pernambuco, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul, see Suppl. material 1).

Remarks. This species was described as *Nereis succinea* (Leuckart 1847), transferred to genus *Neanthes* (Imajima 1972), and later to *Alitta* (Bakken and Wilson 2005). The specimens examined in this study share the features of the specimens re-described by Villalobos-Guerrero and Carrera-Parra (2015), such as paragnaths present in all areas of the pharynx, homogomph spinigerous notochaetae, neurochaetae with heterogomph spinigers and homogomph and heterogomph falcigers and the widely expanded notopodial ligule in posterior parapodia. However they are smaller (major individual measuring 3.5 mm of length from the prostomium to the 25th chaetiger) than those described from the Caribbean Sea (Espinosa et al. 2007) and southern-southeastern Brazil (Amaral et al. 2005). On the other hand, specimens from northeastern Brazil measuring less than 5 mm length from the prostomium to the 25th chaetiger are considered recruits (Sette et al. 2013). Therefore, we suggest all the individuals collected in this study are juveniles. *Alitta succinea* is widely distributed in the world with records in different environments. This species was recorded in mangroves from the Caribbean Sea (Londoño-Mesa et al. 2002) and Brazil, including a record in Maranhão state (Mochel 1997). This species is reported in environments with different salinity levels and has been considered as a euryhaline species (Sato 2013).

Genus *Namalycastis* Hartman, 1959

Namalycastis fauveli Nageswara Rao, 1981
Fig. 5

Type locality. Estuary of Tachin River, Thailand (13°44'N, 100°30'E; original geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, 6 September 2011 (NPM-Pol 883). Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one

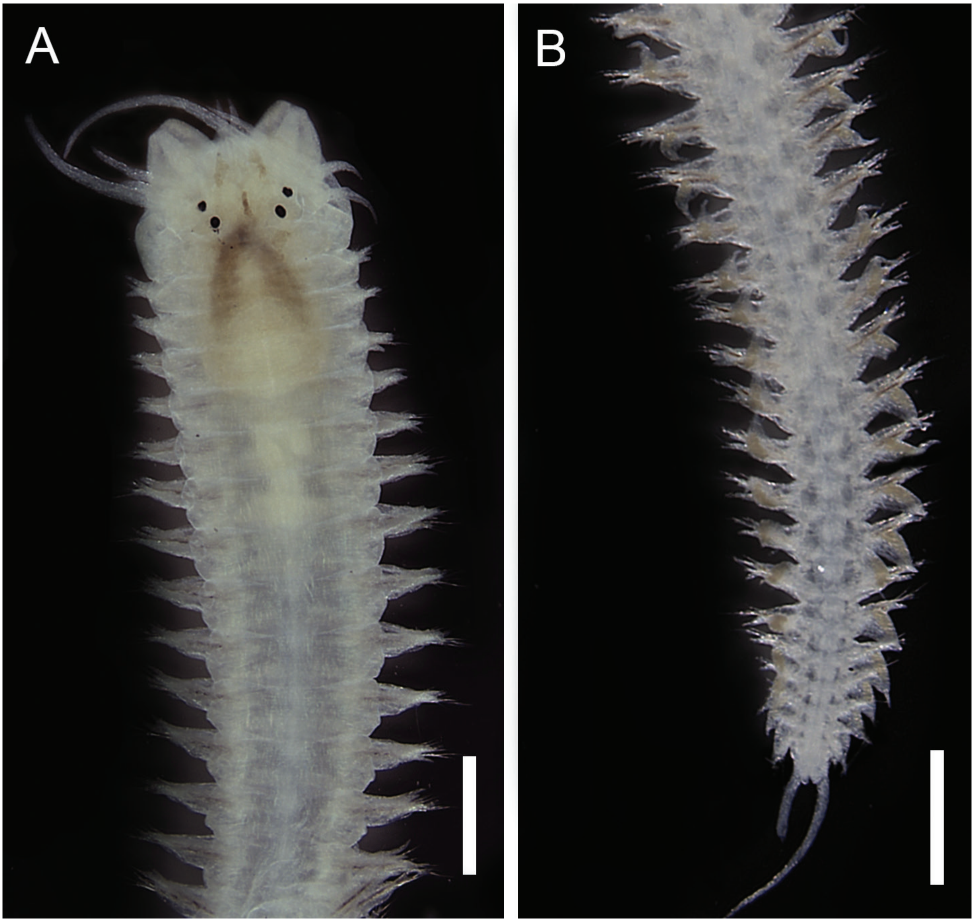

Figure 4. *Alitta succinea*, fixed specimen. **A** Anterior end, dorsal view **B** Posterior end, dorsal view. Scale bars: 0.5 mm.

specimen, 26 January 2011 (NPM-Pol 086); three specimens, 28 March 2011 (NPM-Pol 109); one specimen, 22 April 2010 (NPM-Pol 878); three specimens, 17 August 2010 (NPM-Pol 879); two specimens, 2 June 2012 (NPM-Pol 880); four specimens, 5 September 2011 (NPM-Pol 881). Complete and incomplete specimens.

Distribution. Indian Ocean: Thailand, India. Atlantic Ocean: Brazil (Maranhão state).

Diagnosis. Body widest mid-anteriorly. Prostomium anteriorly shallowly cleft or cleft absent. Antennae minute. Notochaeta present. Heterogomph setae with boss extremely prolonged. Supra-neuroacicular falcigers in chaetiger 10 with blades slightly curved (Glasby 1999).

Description. Based on specimens NPM-Pol 878 and 883. Complete specimen with 17.3 mm long, 0.72 mm wide (chaetiger 10), and 79 chaetigers (Fig. 5A). Body widest mid-anteriorly, gradually tapering anteriorly and posteriorly. Dorsum convex. Epidermal pigment absent. Prostomium trapezoidal, some individuals with lateral indentation on pros-

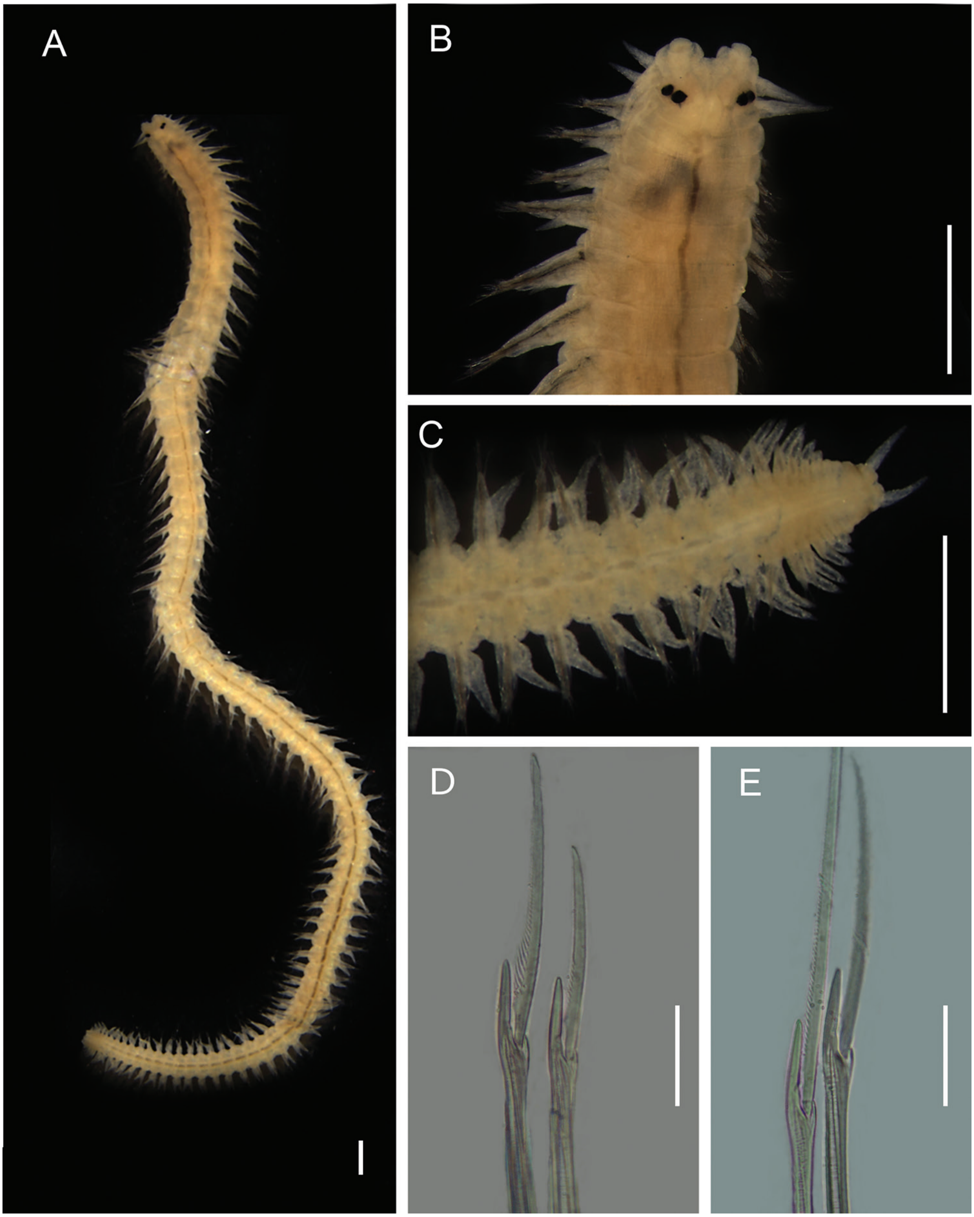

Figure 5. *Namalycastis fauveli*, fixed specimen, NPM-Pol 883. **A** Whole body, dorsal view **B** Anterior end, dorsal view **C** Posterior end, ventral view **D** Neurochaetae supra-acicular, 10th chaetiger **E** Neurochaeta spiniger supra-acicular, 10th chaetiger. Scale bars: 0.5 mm (**A–C**), 0.01 mm (**D, E**).

tomium. Prostomium anterior end smooth or with a shalow cleft (Fig. 5B). Narrow longitudinal groove extending form tip to mid-posterior prostomium. Antennae short, extending short of palpophore anterior end, laterally inserted. Two pair of eyes transversally arranged on prostomium. Four pairs of tentacular cirri with indistinct cirrophores and smooth cirrostyles. Posterodorsal pair extending posteriorly to third chaetiger. Pharynx smooth, lacking paragnaths or papillae. Parapodia sesquirramous (sub-birramous). Dorsal cirri increasing in length posteriorly. Neuropodial acicular ligulae bilobed. Notochaeta as sesquigomph spinigers present from third chaetiger. Supra-acicular neurochaeta as sesquigomph spinigers on postacicular fascicle and heterogomph falcigers on preacicular fascicle (Fig. 5D, E). Sub-acicular neurochaetae as heterogomph spinigers on postacicular fascicle and heterogomph falcigers in preacicular fascicle. Supra-acicular sesquigomph spinigers shaft with boss 1.2×–1.5× length of collar. Shaft of heterogomph chaeta with boss prolonged. Supra-acicular falcigers in chaetiger 10 with blades slightly curved, blades length 8.0×–9.5× width of shaft head. Sub-acicular falcigers blades in chaetiger 10 length, 8.2×–11.4× (dorsal-most) and 6.0×–7.3× (ventral most) width of shaft head. Sub-acicular spinigers in anterior region of body with blades finely serrated. Chaeta pale. Aciculae dark brown. Pigidium buttom-shaped (Fig. 5C). Anus terminal. Anal cirri smooth and subconical, arising ventro-laterally.

Colour. Specimens in alcohol yellow. No pigment visible throughout the body.

Remarks. First species record for the America. These specimens present some differences from the original description (Nageswara Rao 1981), such as a dorsal surface convex, body less arched mid-anteriorly, longer antennae and tentacular cirri (Fig. 2A). However, the projection of heterogomph chaetae with an extremely long boss supports this identification for this species (Fig. 2B, C). The differences found are probably because the specimens in this study are juveniles by the smaller size (around 15 mm long, and 80 chaetigers), compared to type material, 21–45 mm long, 134–282 chaetigers, after Glasby (1999). Some Namanereidinae species, as *Namalycastis abiuma*, can have juveniles with blades longer and up to 80 chaetigers. *Namalycastis fauveli* is recorded in estuarine beaches and coastal lagoons in the type locality (Nageswara Rao 1981) and in mangroves of this study.

Namalycastis geayi (Gravier, 1901)

Fig. 6

Type locality. Ouanary, French Guiana (4°12'N, 51°39'W; estimated geolocation).

Material examined. Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one specimen, 17 December 2011 (NPM-Pol 082); one specimen, 27 March 2011 (NPM-Pol 882); one specimen, 20 October 2010 (NPM-Pol 884); all incomplete specimens.

Distribution. Atlantic Ocean: French Guiana, Brazil (state of Maranhão).

Diagnosis. Prostomium anterior end smooth or with a shallow cleft. Antennae extending short of the palpophore tip or of the prostomium tip. Two pairs of eyes nearly longitudinally arranged. Dorsal cirri short, similar in length throughout the body. Notochaetae present (Glasby 1999).

Description. Based on specimen NPM-Pol 884. Incomplete specimen with 4.93 mm long, 1.1 mm wide and 18 chaetigers. Body widest mid-anteriorly, tapering gradually anteriorly and posteriorly (Fig. 6A). Dorsum and venter convex. Epidermal pigment absent. Prostomium trapezoidal, some individuals with lateral indentation on prostomium (Fig. 6A). Prostomium anterior end smooth. Antennae short and smooth,

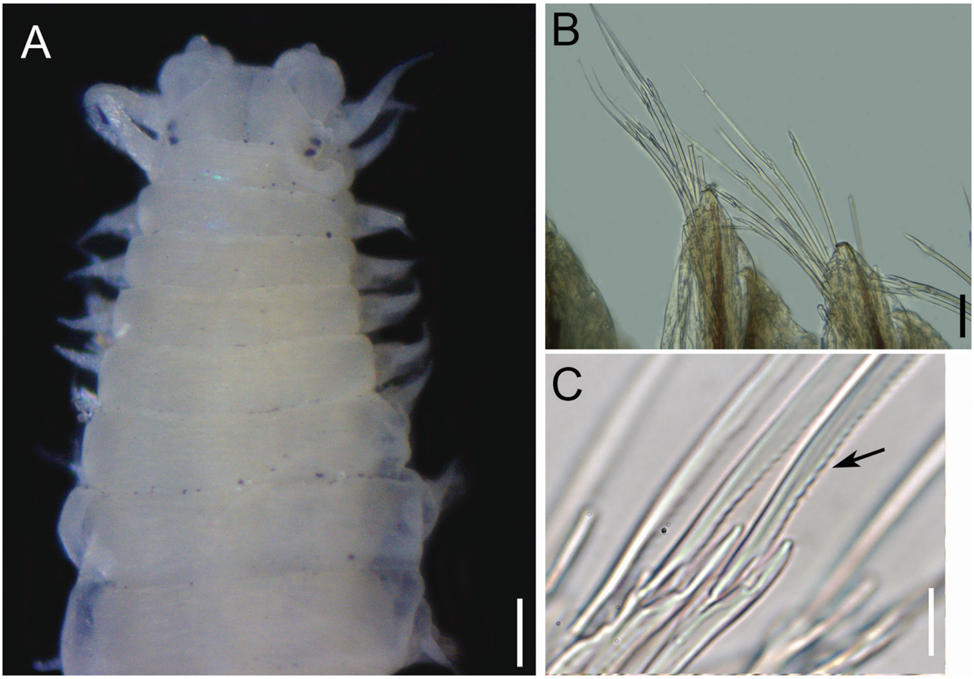

Figure 6. *Namalycastis geayi*, fixed specimen, NPM-Pol 882 and 884. **A** Anterior end, dorsal view **B** Parapodia sub-birramous, anterior region, dorsal view **C** Supra-acicular spiniger, arrow point to fine serrations proximally to the base of chaetae blades, parapodium 17, dorsal view of chaetae. Scale bars: 0.2 mm (**A**), 0.05 mm (**B**), 0.01 mm (**C**).

extending short of the anterior end of the prostomium, laterally inserted. Two pairs of eyes, arranged nearly longitudinally on prostomium. Four pairs of tentacular cirri with indistinct cirrophores and smooth cirrostyles. Posterodorsal pair extending posteriorly to third chaetiger. Pharynx smooth, lacking paragnaths or papillae. Parapodia sesquirramous (sub-birramous). Dorsal cirri short, similar in length throughout the body. Neuropodial acicular ligulae bilobed. Notochaeta as sesquigomph spinigers present from third chaetiger. Neurochaetae as heterogomph spinigers in all fascicles. Supra-acicular sesquigomph spinigers (postacicular) shaft with boss 1.9×–2.0× length of collar (Fig. 6B). Shaft of heterogomph chaeta with boss slightly prolonged. Sub-acicular spinigers in anterior region of body with blades moderately serrated (Fig. 6C). Chaeta pale. Aciculae dark brown.

Colour. Specimens in alcohol yellow. No pigment visible throughout the body.

Remarks. First species record for Brazil. The collected specimens of this study were not complete, but they present the same characters of *Namalycastis geayi* (Gravier, 1901) based on the anterior end (Fig. 6A). The identification of this species is supported by the presence of only heterogomph spinigers in sub- and supra-preacicular fascicle in the parapodia (Fig. 6B, C). In the original description, *N. geayi* has been recorded in freshwater environments, muddy river banks, and in coarse sediments (Gravier 1901). This study recorded *N. geayi* in mangroves and brackish water.

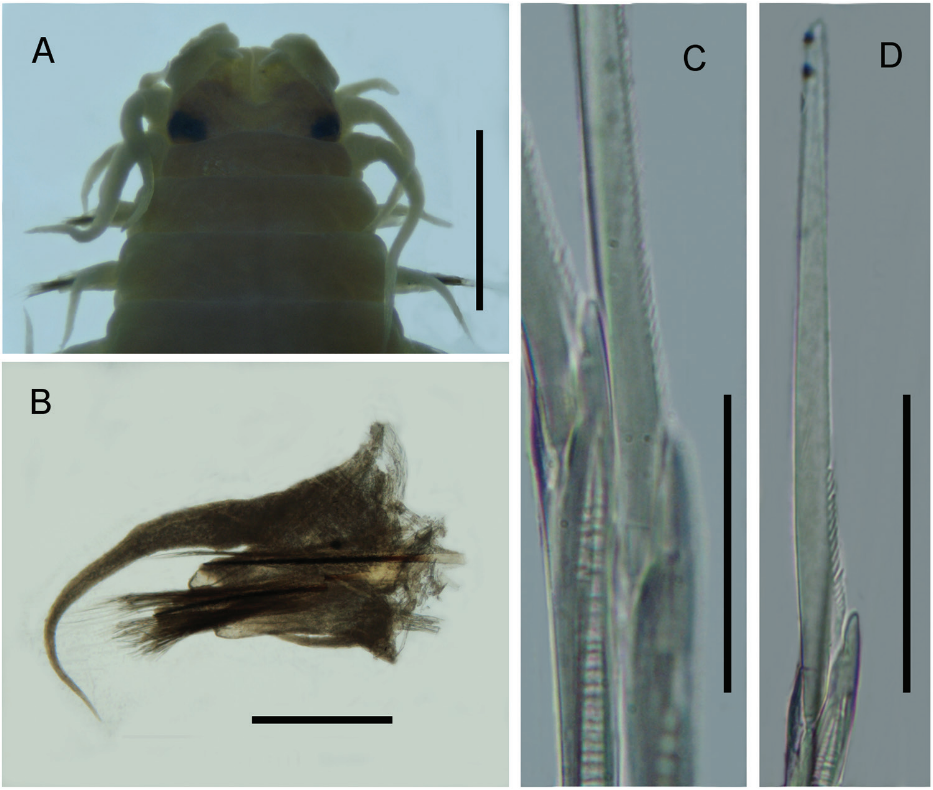

Figure 7. *Namalycastis senegalensis*, fixed specimen, NPM-Pol 105. **A** Anterior end, dorsal view **B** Parapodia of 10th chaetiger, anterior view **C** Sub-acicular neurochaetae spiniger of 10th chaetiger **D** Sub-acicular neurochaeta falciger of 10th chaetiger. Scale bars: 2.3 mm (**A**), 0.2 mm (**B**), 0.02 mm (**C, D**).

Namalycastis senegalensis (Saint-Joseph, 1901)

Fig. 7

Type locality. Marsassoun, Senegal (13°59'N, 16°43'W; estimated geolocation).

Material examined. Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one specimen, incomplete, 22 October 2010 (NPM-Pol 105).

Distribution. Atlantic Ocean: Senegal, Nigeria, Congo, Suriname, Brazil (states of Pará and Maranhão, see Suppl. material 1).

Remarks. First record for Maranhão. Complete specimens were not found in this study; however, the features of the anterior body are very similar to the re-description of Glasby (1999). The presence of thick cuticle covering the eyes, supra neuro acicular sesquigomph spinigers in the parapodia of chaetiger 10, with a 1.4 × length of collar or more boss, and distally smooth falciger blades supports the identification of the species. Previous Brazilian records include the Amazon coast, the estuarine beaches of Marajó Island in the mouth of the Amazon River (Glasby 1999), and the delta of the Amazon River (one specimen, ZHM PE405) (Glasby 1999). This species is known to live in brackish water and freshwater environments such as mangroves, creeks, and marshes (Glasby 1999).

Family Pilargidae Saint-Joseph, 1899
Genus *Sigambra* Müller, 1858

Sigambra bassi (Hartman, 1945)
Fig. 8A

Type locality. Lemon Bay, Florida, USA (26°54'N, 82°20'W, estimated geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, complete, 6 September 2011 (NPM-Pol 111).

Distribution. Pacific Ocean: USA, Mexico, Chile. Atlantic Ocean: USA, Caribbean Sea, Brazil (state of Maranhão and São Paulo, see Suppl. material 1).

Remarks. First record for Maranhão. The specimens examined in this study present a long medium antenna reaching up to setiger 5–12; a dorsal hook beginning in the posterior chaetigers supports the identification as *Sigambra bassi*. The records in the Caribbean and Brazil include estuaries and beaches (Gillet 1986, Amaral et al. 2003).

Sigambra grubii Müller in Grube, 1858
Fig. 8B

Type locality. Florianópolis, Santa Catarina, Brazil (27°36'30"S, 48°26'30"W; original geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, 18 August 2010 (NPM-Pol 110); one specimen, 27 January 2011 (NPM-Pol 887). Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one specimen, 22 April 2010 (NPM-Pol 888). Complete and incomplete specimens.

Distribution. Atlantic Ocean: USA, Caribbean Sea, Brazil (states of Pará, Maranhão, Sergipe, Rio de Janeiro, São Paulo, Santa Catarina and Rio Grande do Sul, see Suppl. material 1).

Remarks. First species record for Maranhão. The presence of notopodial hooks distally curved appearing in setiger 20 and a medium antenna reaching the second chaetiger are characteristics that support the identification of the species based on the original description by Müller (1858) and re-description by Salazar-Vallejo (1990). In this study, the hooks appeared among the segments 6–29, in specimens shorter and with reduced number of chaetigers, the hooks appeared before the chaetiger 20. This type of variability in the hooks position related with the body size and number of chaetigers was also reported by Salazar-Vallejo (1990). No other morphological variation was found. This species is widely recorded in the coast of Brazil, mainly in estuarine environments, including mangroves and coastal lagoons as the type locality (Müller 1858). In the Caribbean, the species was recorded in a coastal lagoon (Liñero-Arana and Díaz-Díaz 2005).

Figure 8. Pilargidae species. **A** *Sigambra bassi*, whole body, dorsal view **B** *Sigambra grubii*, whole body, dorsal view. Scale bars: 0.5 mm.

Family Syllidae Grube, 1850
Genus *Exogone* Örsted, 1845
Subgenus *Exogone* (*Exogone*) Örsted, 1845

Exogone (*Exogone*) *breviantennata* Hartmann-Schröder, 1959
Fig. 9

Type locality. Estero Jaltepeque, El Salvador (13°18'N, 88°52"W; estimated geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, 18 August 2010 (NPM-Pol 889); three specimens, 27 January 2011 (NPM-Pol 890); one specimen, 29 March 2011 (NPM-Pol 112); one specimen, 6 September 2011 (NPM-Pol 891); five specimens, 18 December 2011 (NPM-Pol 892); all complete specimens.

Distribution. Pacific Ocean: Australia, Panama, Ecuador. Indian Ocean: Seychelles, Red Sea, Australia. Atlantic Ocean: Spain (Canary Islands), South Africa, Caribbean Sea, Brazil (states of Maranhão, Paraíba, Pernambuco, Espírito Santo, and São Paulo, see Suppl. material 1).

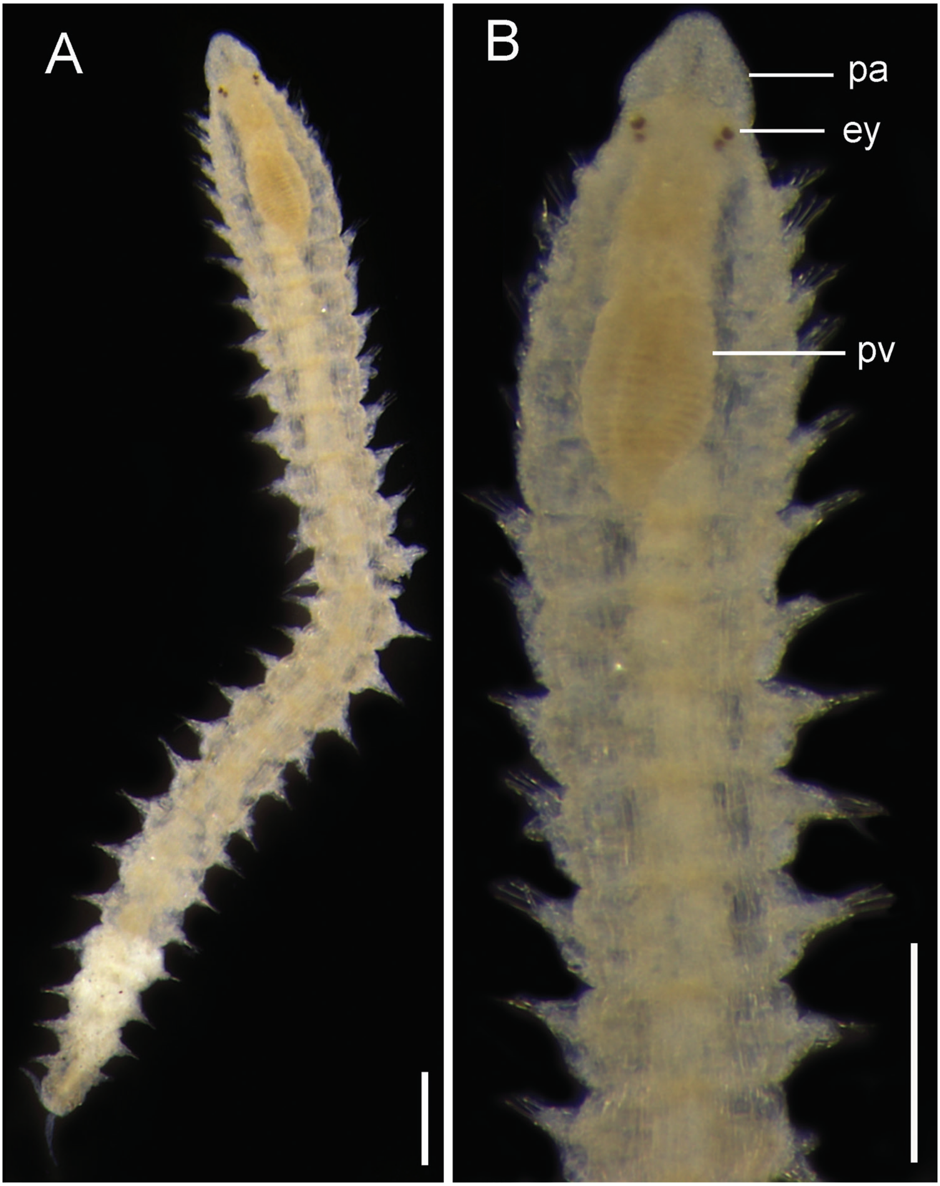

Figure 9. *Exogone* (*Exogone*) *breviantennata*. **A** Whole body, dorsal view **B** Anterior end, dorsal view. Abbreviations: pa, palps; ey, eye; pv, proventricle. Scale bars: 0.15 mm.

Remarks. First species record for the Brazilian Amazon Coast. The features that confirm these specimens as *Exogone* (*Exogone*) *breviantennata* Hartmann-Schröder, 1959 are median and lateral antennae of similar size, compound spinigers and falcigers with bidentate blades (subdistal tooth larger than distal tooth) and falcigers in the anterior body with 3–4 relatively thick spines. This species is found worldwide in several habitats such as in seagrass in the intertidal zone, rocky shores, algae assemblages, soft bottoms (San Martín and Bone 2001, Paresque et al. 2014), and others. The type material of *E.* (*E.*) *breviantennata* is from a mangrove (Hartmann-Schröder 1959) as in the present study. However, this species has been recorded in several environments and it presents a circumtropical distribution (Núñez et al. 1992).

Subclass Sedentaria
Order Terebellida
Family Ampharetidae Malmgren, 1866
Genus *Isolda* Müller, 1858

Isolda pulchella Müller, 1858
Fig. 10A–C

Type locality. Florianópolis, Santa Catarina, Brazil (27°36'S, 48°27'W; estimated geolocation).

Material examined. São Luís, 02°35'56" S, 44°21'11.8"W: seven specimens, 6 September 2011 (NPM-Pol 849); two specimens, 18 December 2012 (NPM-Pol 067); 14 specimens, 18 December 2012 (NPM-Pol 848). Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one specimen, 17 December 2012 (NPM-Pol 850). Complete and incomplete specimens.

Distribution. Pacific Ocean: Australia, USA. Indian Ocean: Red Sea, Australia. Atlantic Ocean: Portugal, Mediterranean Sea, South Africa, USA, Mexico, Caribbean Sea, Brazil (states of Pará, Maranhão, Sergipe, Rio de Janeiro, São Paulo, Paraná and Santa Catarina, see Suppl. material 1).

Remarks. The presence of two groups of four branchiae, post-branchial notopodium with sharply curved hooks; twelve or thirteen thoracic segments with pectinate uncini with four to seven teeth support the identification of these specimens as *Isolda pulchella* Müller, 1858. This species was described in south Brazil and is found along the coast inhabiting estuarine environments, including mangroves and coastal lagoons. The specimens described by Díaz-Díaz and Liñero-Arana (2012) for Caribbean Sea are also similar to the specimens in this study and are recorded in estuaries.

Infraclass Scolecida
Family Capitellidae Grube, 1862
Genus *Capitella* Blainville, 1828

Capitella capitata (Fabricius, 1780), complex
Fig. 11A, B

Type locality. Uummannaq, West Greenland (71°6.5'N, 51°17'W; original geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: six specimens, 29 March 2011 (NPM-Pol 069); one specimen, 23 September 2012 (NPM-Pol 102); 17 specimens, 18 December 2011 (NPM-Pol 851). Caranguejos Island, 02°49'33.6"S,

Figure 10. *Isolda pulchella*. **A** Whole body, dorsolateral view **B** Anterior end, dorsal view **C** Pygidium, ventral view. Scale bars: 0.5 mm.

44°28'51.1"W: five specimens, 17 October 2010 (NPM-Pol 852); two specimens, 26 January 2011 (NPM-Pol 853); two specimens, 17 December 2011 (NPM-Pol 854). Complete and incomplete specimens.

Distribution. Arctic Ocean: Greenland. Pacific Ocean: China, Japan, Australia, USA, Mexico, Costa Rica. Indian Ocean: Red Sea. Atlantic Ocean: North Sea, Ireland, UK, Germany, Netherlands, France, Spain, Mediterranean Sea, Ukraine, South Africa, USA, Mexico, Caribbean Sea, Brazil (states of Pará, Maranhão, Ceará, Paraíba, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul, see Suppl. material 1).

Remarks. First record for Maranhão. The specimens examined in this study are similar to the neotype description of *Capitella capitata* by Blake (2009). *C. capitata* was considered as a globally distributed species, but allozyme analyses have demonstrated that this species is composed of at least six sibling species (Grassle and Grassle 1976). Additionally, Blake (2009) indicates that *C. capitata* may be only distributed in Arctic regions, suggesting that the numerous records from lower latitudes are not this species. Nevertheless, the specimens from warmer waters such as in the Caribbean (Amoureux 1985) and Brazil (Pardo et al. 2010) are also similar to the neotype descriptions by Blake (2009). Recently, four new species of *Capitella* were described from the *Capitella capitata* complex (Silva et al. 2017). Studies including molecular data must to be conducted on these animals from Maranhão, and the specimens should be re-examined.

Genus *Heteromastus* Eisig, 1887

Heteromastus filiformis (Claparède, 1864)

Fig. 11C

Type locality. Port-Vendres, France (42°30'N, 3°07'E; estimated geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: one specimen, incomplete, 6 September 2011 (NPM-Pol 070); two specimens, 27 January 2011 (NPM-Pol 852); four specimens, 18 December 2011 (NPM-Pol 856); one specimen, 18 March 2012 (NPM-Pol 857); complete and incomplete specimens.

Distribution. Pacific Ocean: New Zealand, USA, Costa Rica. Indian Ocean: Red Sea, Mozambique. Atlantic Ocean: Ireland, UK, Belgium, France, Mediterranean Sea, South Africa, USA, Mexico, Caribbean Sea, Brazil (states of Pará, Maranhão, Bahia, Rio de Janeiro, São Paulo, see Suppl. material 1).

Remarks. *Heteromastus filiformis* from São Marcos Bay share the same characters of the specimens described by Day (1967) and Dean (2001) such as thoracic region with 12 segments, the first achaetous; thoracic hooks with long hood and about six denticles above the main tooth; abdominal hooks narrow and three to four denticles above the main tooth, gills in subsequent medial segments. The specimens of *H. filiformis* examined in this study are very similar to *H. similis* Southern, 1921. One of the main differences between those species is the presence of gills processes and the shape of neuropodial hooks in *H. filiformis*. According to Hartman (1947), *Heteromastus similis* is considered an inhabitant of freshwater areas and *H. filiformis* is typical of marine environments. Both species have distribution in estuarine environments such as mangroves from Brazil (Silva et al. 2011). In the Caribbean Sea, the records are also in estuarine areas and especially in the muddy intertidal areas of the Caribbean Sea (Gobin 1990). Both species seems to be distributed worldwide, independent of environmental salinity, but descriptions based on fewer characters can be related to several records around the world.

Figure 11. Capitellidae species. **A** *Capitella capitata* complex, whole body, lateral view and **B** anterior view, arrow point genital spines in 9th chaetiger **C** *Heteromastus filiformis*, thoracic region, lateral view **D** *Mediomastus californiensis*, thoracic region, lateral view. Scale bars: 0.5 mm.

Genus *Mediomastus* Hartman, 1944

Mediomastus californiensis Hartman, 1944

Fig. 11D

Type locality. Tomales Bay, California (38°18'N, 122°56'W; estimated geolocation).

Material examined. São Luís, 02°35'56"S, 44°21'11.8"W: two specimens, 21 October 2010 (NPM-Pol 73); three specimens, 18 August 2010 (NPM-Pol 858); one specimen, 18 March 2012 (NPM-Pol 859). Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W: one specimen, 22 April 2010 (NPM-Pol 860), three specimens, 26 January 2011 (NPM-Pol 861); three specimens, 28 March 2011 (NPM-Pol 862); eight specimens, 28 March 2011 (NPM-Pol 863); one specimen, 17 December 2011 (NPM-Pol 864); four specimens, 2 July 2012 (NPM-Pol 865). Complete and incomplete specimens.

Distribution. Pacific Ocean: Australia, USA, Mexico. Atlantic Ocean: Caribbean Sea, Brazil (states of Pará, Maranhão, Rio de Janeiro, São Paulo, Paraná and Santa Catarina, see Suppl. material 1).

Remarks. First record for Maranhão. The specimens examined in this study have triangular prostomium with cylindrical palpodium, in dorsal view; peristomium devoid of setae with a pair of ocelli; 10 chaetigers in thoracic region; only capillaries in chaetigers 1–4; abdominal chaetigers only with hooded hooks defining them as *Mediomastus californiensis* (Hartman, 1944). In the present study, we found specimens exceeding 100 segments as observed by Warren et al. (1994). Although *M. californiensis* has been recorded in the Pacific (USA) and Atlantic Ocean (Canada and the USA), Warren et al. (1994) examined specimens from both oceans and did not observe differences among them. This species has been recorded in muddy bottoms of estuarine environments in the Brazilian Amazon Coast (Rosa-Filho et al. 2006) and in the Caribbean Sea (Gobin 1990).

Family Paraonidae Cerruti, 1909

Genus *Paraonis* Cerruti, 1909

Paraonis amazonica sp. n.

http://zoobank.org/D7449E5D-1126-4135-A4B2-DB76AE4CFCCE
Figs 12, 13, 14

Type locality. Brazil, Maranhão: São Luís, 02°35'56"S, 44°21'11.8"W, mangrove, 21 October 2010, R.P. Ribeiro.

Material examined. Holotype: São Luís, 02°35'56"S, 44°21'11.8"W, one specimen, complete, 21 October 2010 (NPM-Pol 906). Paratypes: São Luís, 02°35'56"S, 44°21'11.8"W, one specimen, incomplete, 18 August 2010 (NPM-Pol 907); 80 specimens, all incomplete, 27 January 2011 (NPM-Pol 908); two specimens, both complete, 21 October 2010 (NPM-Pol 929); two specimens, both incomplete, 18 March 2012 (MNCN 16.01/17766). Caranguejos Island, 02°49'33.6"S, 44°28'51.1"W, three specimens, all incomplete, 26 January 2011 (NPM-Pol 930); 11 specimens, all incomplete, 28 March 2011 (MNCN 16.01/17765).

Distribution. Only known from the type locality.

Diagnosis. Rounded prostomium, clearly wider than longer. Dorsal brownish pigmentation reaching the beginning of the prostomium. Rounded to foliaceous branchiae (4–8 pairs), from the fourth segment. Neurochaetae of two types: acicular chaeta with lateral spine beginning in pre-branchial segments, and hook-shaped chaeta with terminal spines in post-branchial segments.

Description. Complete holotype, 2.68 mm long, 0.17 mm wide (chaetiger 8), and 46 chaetigers. Three complete paratypes with 2.43–2.94 mm long, 0.18–0.20 mm wide and 36–54 chaetigers. Incomplete paratypes up to 4.607 mm long, 0.283 mm wide, and 16–61 chaetigers. Fixed individuals with brown pigmentation that reaches the distal end of the prostomium and extends along the body. Anteriorly flattened body, wider than longer, cylindrical from the 8th chaetiger and in all middle body region (Fig. 12A, B). Branchial region dorsoventrally flattened. Rounded prostomium, wider than longer (Fig. 12B, D). Absence of antenna, palpode, ciliated bands and eyes in the prostomium (Fig. 12A, B). The anterior segments are short, wider than longer. Long and biannulate segments in the post-branchial region. One pair of nuchal organs located on the posterior edge of the prostomium (Fig. 13A). Notopodial post-chaetal lobes absent in the pre-branchial region, the first notopodial post-chaetal lobe appear in the fifth branchial chaetiger. Notopodial post-chaetal cirrifom lobes, longer

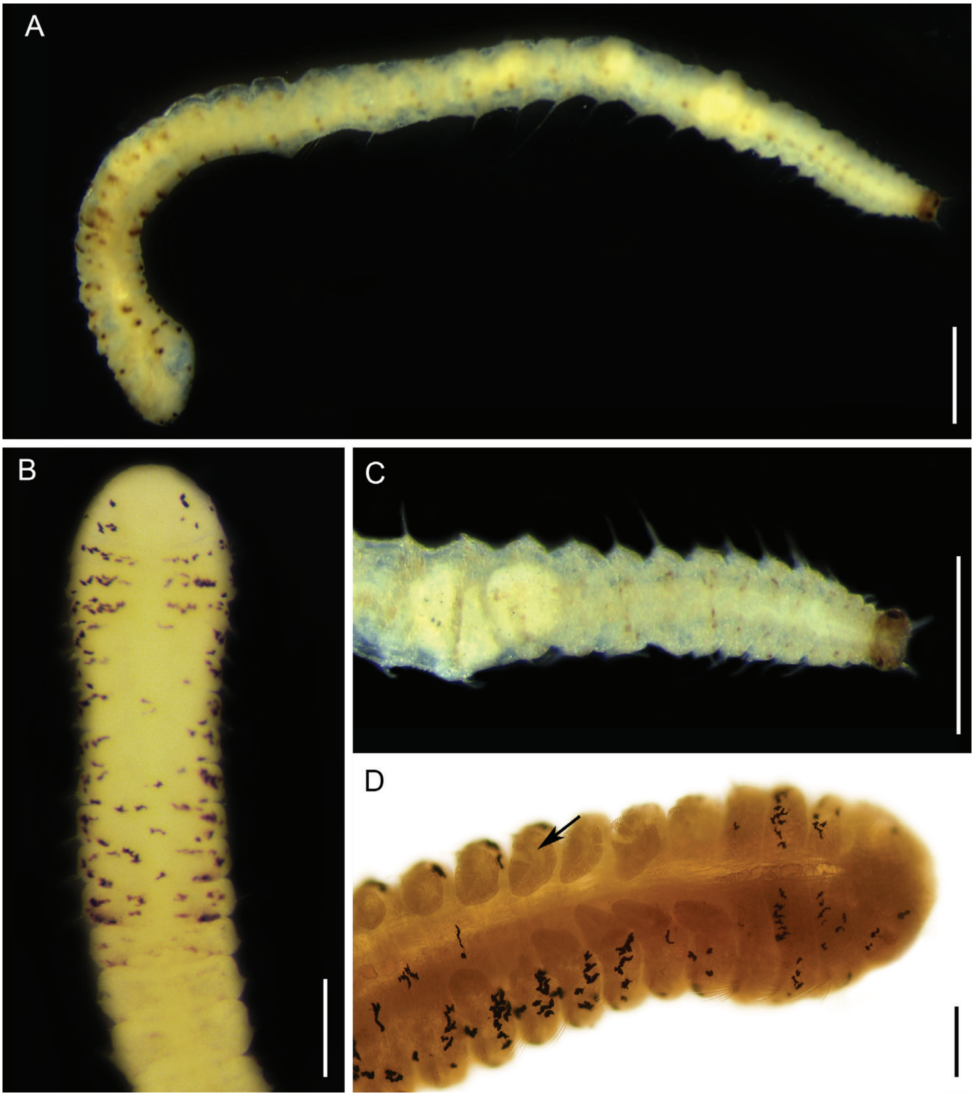

Figure 12. *Paraonis amazonica* sp. n., fixed specimen, NPM-Pol 906. **A** Whole body, lateral view **B** Anterior end, dorsal view **C** Posterior end, dorsal view **D** Anterior end, the arrow indicates foliaceous branchiae, dorsolateral view. Scale bars: 0.5 mm (**A**), 0.1 mm (**B**) 0.25 mm (**C, D**).

from the middle and posterior regions. Branchiae from chaetiger 4, rounded to foliaceous, flat, short, 4–8 pairs, first and last pairs are shorter (Fig. 12D). Notopodial capillary chaetae throughout the body. Curved capillary chaetae in the neuropodium and notopodium of the pre-branchial and branchial segments (Fig. 13B). Capillary neurochaetae progressively thinner, longer, and straight in the post-branchial segments. Capillary notochaetae of the posterior segments thicker than those anterior and median segments. Pre-branchial and branchial segments with 3–5 chaetae capil-

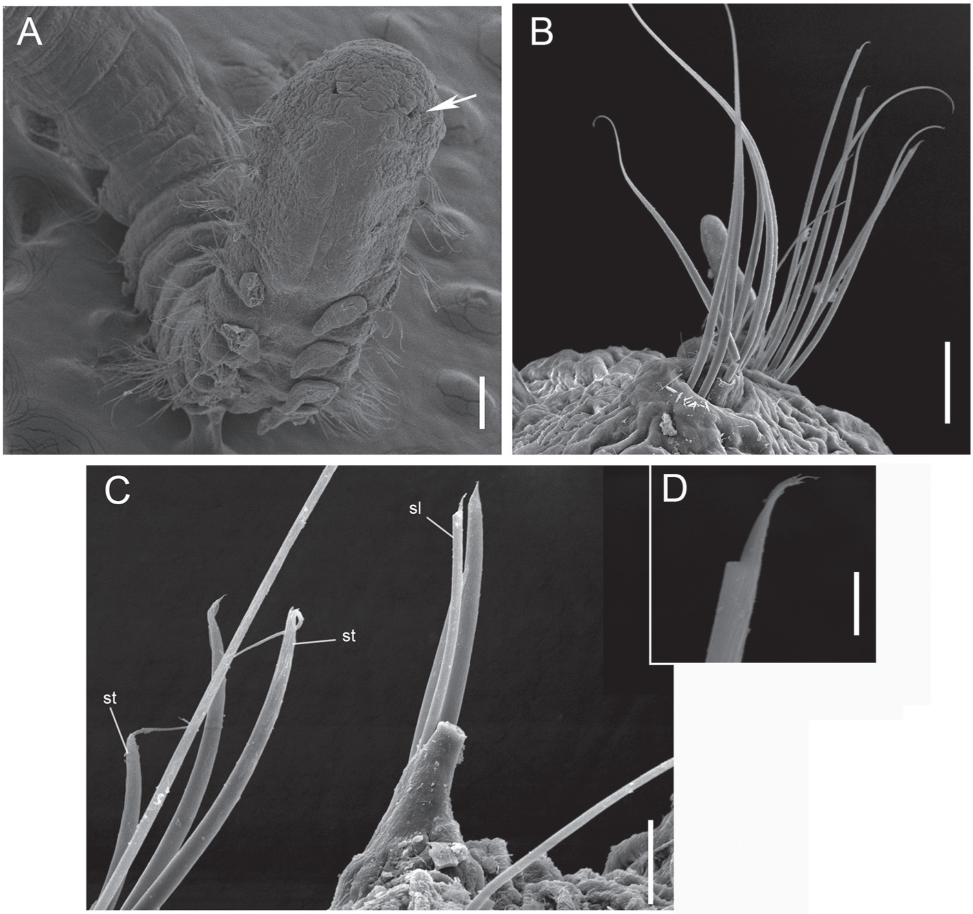

Figure 13. *Paraonis amazonica* sp. n., SEM. **A** Anterior end, arrow point to the nuchal organ, dorsal view **B** Anterior parapodium of chaetiger 3, arrow point to the acicular lateral spine, dorsal view **C** Parapodium of setiger 35, acicular chaeta with a lateral spine (**sl**) hook-shaped chaeta with a terminal spine (**st**) **D** Acicular chaeta with a lateral spine enlarged. Scale bars: 0.1 mm (**A**), 20 µm (**B**), 10 µm (**C**), 1 µm (**D**).

laries in the notopodium and 2–5 in the neuropodium. Post-branchial segments with 1–2 chaetae capillary in the notopodium, absent in the neuropodium. First acicular neuropodial chaetae with a lateral spine in chaetiger 2–8, and 2–3 chaetae in the branchial segments (Figs 13B, 14A). Neuropodium in the post-branchial middle segments and posterior end segments with one acicular chaeta with a lateral spine (Figs 13B, C, 14A–C). Hook-shaped neurochaetae with terminal spine beginning in post-branchial chaetigers, 1–2 chaetae. Neuropodium in the post-branchial middle chaetigers with 2–4 hook-shaped chaetae with a terminal spine. Neuropodium in posterior chaetigers with two hook-shaped chaetae with a terminal spine (Figs 13B, C, 14B, C). Pygidium rounded with two anal lobes and three anal cirri: two dorsolateral and one medium-ventral (Figs 12C, 14D).

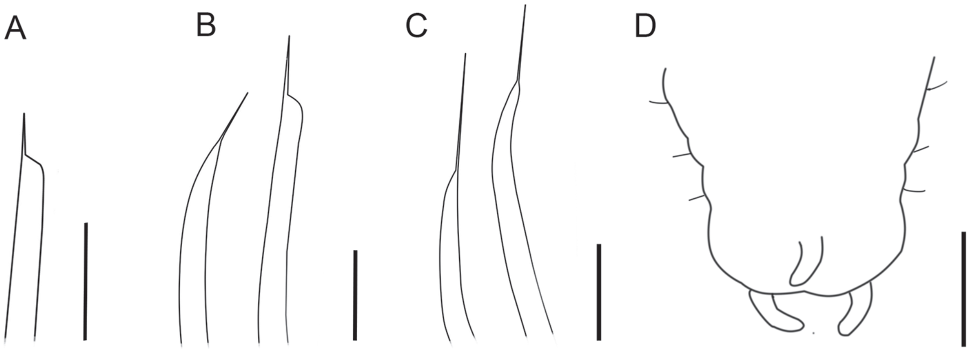

Figure 14. *Paraonis amazonica* sp. n., chaetae. **A** Acicular chaetae with a lateral spine of anterior setiger 3 **B** Posterior hook-shaped chaeta with terminal spine and acicular chaetae with a lateral spine (left) in setiger 30 **C** Hook-shaped chaeta with a terminal spine in the last setiger, 36 **D** Pygidium with three anal cirri, ventral view. Scale bars 50 µm (**A–C**), 0.25 mm (**D**).

Colour. Specimens in alcohol show brownish pigment spots all over the body, two pairs of reddish brown lateral spots in the pygidial lobes of some specimens.

Etymology. Named after the Amazon Coast, region where type locality is located.

Remarks. *Paraonis amazonica* sp. n. differs from all other species by the presence of acicular and hook-shaped modified neurochaetae. Currently, there are five valid species named in the genus *Paraonis*: *Paraonis fulgens* (Levinsen, 1884); *Paraonis paucibranchiata* Cerruti, 1909; *Paraonis pycnobranchiata* Fauchald, 1972; *Paraonis pygoenigmatica* Jones, 1968; and *Paraonis strelzovi* Hartmann-Schröder, 1980 (see Table 1). Several species first described as *Paraonis* were established as a synonymy of *Aricidea* (López 2008), *Levinsenia* (Gaston 1984), *Paradoneis* (Mackie 1991), and *Paraonides* (Parapar et al. 2012). *Paraonis tenera* Grube, 1873 is a species considered *nomen oblitum* by Strelzov (1973) because its description was inaccurate, being based on a single specimen and probably referring to a species of *Aricidea*.

Among the five valid species of *Paraonis*, *P. fulgens*, *P. paucibranchiata*, and *P. strelzovi* also have the first pair of branchiae in the fourth chaetiger as seen in *P. amazonica* sp. n. However, *P. fulgens* has more than 25 pairs of branchiae and the first post-chaetal lobe starts in the third chaetiger, whereas *P. amazonica* sp. n. has 4–8 pairs of branchiae and first post-chaetal lobe in the 9th chaetiger. In addition, *P. fulgens* (about 120 chaetigers in total) seems to be longer than *P. amazonica* sp. n. (up to 54 chaetigers in complete individuals). However, longer animals could be found, since incomplete individuals of *P. amazonica* sp. n. showed up to 61 chaetigers. Only four pairs of branchiae are described in *P. paucibranchiata* and *P. strelzovi* whereas P. a*mazonica* sp. n. has 4–8 pairs of branchiae. Moreover, *P. paucibranchiata* differs from *P. amazonica* sp. n. by the presence of eyes and longer and straighter branchiae. The other two species mainly differ on the first chaetiger with branchiae and post-chaetal lobe. *Paraonis pygoenigmatica* has approximately 20 pairs of branchiae that begin in the sixth chaetiger, joined to the first dorsal lobes. In *P. pycnobranchiata*, the branchiae (about 19) are present from chaetiger 6–25. *P. amazonica* sp. n. and *P. pycnobranchiata* have the same pigmentation pattern consisting in small pigment spots scattered along the body.

Table 1. Key features of *Paraonis* based on original descriptions and redescriptions. NI: no information.

Features	**Species**					
	***P. amazonica* sp. n.**	***P. fulgens* (Levinsen, 1884)**	***P. paucibranchiata* Cerruti, 1909**	***P. pycnobranchiata* Fauchald, 1972**	***P. pygoenigmatica* Jones, 1968**	***P. strelzovi* Hartmann-Schröder, 1980**
Eyes	absent	present	present	present	present	absent
Prostomial ciliated bands	absent	present	absent	absent	present	NI
First chaetiger with branchiae	4	4	4	6	6	4
Number of branchiae pairs	4–8	16–25	4	20	15–19	4
Branchiae shape	foliaceous to rounded	foliaceous to oval	cylindrical	thick and distally blunt	Lanceolate	large, smooth and ciliated
Prostomium	rounded	conical	ovoid	rounded pentagonal	Conical	conical
Number of chaetigers	36–54	110–120	at least 20	at least 48	62–81	> 27
Notochaetae	capillary	capillary	capillary	capillary	capillary or limbate	capillary and capillary fringed
Pre-branchial and branchial neurochaetae	capillary and acicular with lateral spine	capillary and hook-shaped with fringe	capillary and hook-shaped	capillary	capillary or limbate	capillary and capillary fringed and hooded spine
Post-branchial neurochaeta	acicular with lateral spine and hook-shaped with terminal spine	hook-shaped with fringe	hook-shaped	curved and pilose without aristae	capillary or limbate and modified	hooded spine
Number of anal cirri	3	3	3	NI	3 to 8	3
Habitat	estuarine, intertidal	marine, intertidal	marine	deep sea	marine, subtidal	estuarine, subtidal
Bottom	muddy	sand bottom	NI	NI	sand bottom	NI
Type locality	Amazon Coast, Brazil	Denmark	Mediterranean Sea	Gulf of California, USA	Cape Cod Bay, USA	Australia

Species of *Paraonis* are usually reported in marine, inshore and continental shelf environments (Glasby and Wilson 2003). There are some exceptions, such as *P. fulgens,* recorded in the intertidal zone from Caribbean Sea (Helguera et al. 2011), *P. strelzovi* in mangroves from Australia (Hartmann-Schröder 1980), and P. py*goenigmatica* recorded in estuarine areas from Brazil (Barros et al. 2001). *Paraonis amazonica* sp. n. is the first record of a *Paraonis* species found in muddy bottoms in mangrove vegetated areas.

Conclusion

In total, 14 species belonging to eight families and eleven genera were identified in São Marcos Bay, Maranhão, Brazilian Amazon Coast. Two of them were first recorded to Brazilian Coast (*N. fauveli*, *N. geayi*) and one new species was described (*P. amazonica* sp. n.). Two other species are new records for the Brazilian Amazon Coast (*E.* (*E.*) *breviantennata* and *S. bassi*), and five species are new records for the Maranhão Coast (*C. capitata* complex, *M. californiensis*, *N. senegalensis*, *N. simoni*, and *S. grubii*).

This study expands the occurrence of *N. geayi* to the Brazilian Amazon Coast (in estuarine muddy sediments) because the type specimens of *N. geayi* were collected in freshwater and muddy bottoms in the Ouanary Stream in French Guiana (Gravier 1901). In addition, a new species of *Paraonis* is described in Amazon mangroves, although Paraonidae is a family commonly found and highly diversified in deep-sea environments (Aguirrezabalaga and Gil 2009). We encourage further studies on this genus because many species need improved descriptions, given that some features lack information in the original descriptions.

In summary, this checklist increases the number of recorded species in the Brazilian Amazon Coast. Further studies targeting sampling beyond mangroves and soft bottoms, including deep sea, seagrasses, and algal mats, can lead to the discovery of higher diversity of annelids in the Brazilian Amazon Coast. We assume that other new species can be found in this region or described from the worldwide species reported here, since they probably correspond to species complexes.

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Supplementary material 1

Brazilian records of the species identified from Amazon coast, Maranhão

Authors: Rannyele Passos Ribeiro, Paulo Ricardo Alves, Zafira da Silva de Almeida, Christine Ruta

Data type: species data

Explanation note: Information on deposit number, record, state, coordinates, habitat, substrate and depth and references of the records are provided.

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A new species of *Cotesia* Cameron (Hymenoptera, Braconidae, Microgastrinae) reared from the hickory horned devil, *Citheronia regalis*, and luna moth, *Actias luna*, in east Texas

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Abstract

The braconid wasp parasitoid *Cotesia nuellorum* Whitfield, new species, is described from specimens reared from a caterpillar of the hickory horned devil, *Citheronia regalis* (F.), and from a caterpillar of the luna moth, *Actias luna* (L.), in eastern Texas. The species is diagnosed with respect to other species of *Cotesia* recorded from North American Saturniidae, and details of its biology are provided.

Keywords

Lepidoptera, parasitism, Saturniidae

Introduction

Cotesia Cameron is a common and diverse genus of microgastrine Braconidae that largely specializes in parasitizing exposed larvae of macrolepidopteran moths and butterflies (Whitfield et al. 2018). It is one of the larger genera of Microgastrinae in terms of currently described species worldwide; its highest species richness lies in temperate zones, and it is relatively ubiquitous in terrestrial habitats where caterpillars occur.

Currently, four species in this genus are recorded from saturniid caterpillars in North America (Marsh 1979; Tuskes et al. 1996) – *C. anisotae* (Muesebeck), *C. electrae* (Viereck), *C. hemileucae* (Riley) and *C. teleae* (Muesebeck). Tuskes et al. (1996) provide a table of these associations along with records of other Nearctic saturniid parasitoids.

Recently, two of the authors (RJNJr and RJNIII) collected a batch of larvae of the hickory horned devil, *Citheronia regalis* (F.), in eastern Texas, and one of these larvae yielded a brood of *Cotesia* wasps (see below). While *Cotesia teleae* has been previously recorded as a parasitoid of *C. regalis* especially in the northeastern U. S. where the moth is now relatively rare (in addition to its more usual host *Antheraea polyphemus* (Cramer)), the Texas material appears to belong to a new species, described below. It is possible that at least some previous records of *C. teleae* from *C. regalis* actually belong instead to the new species, but we have been unable to confirm this. The geographical location of the Texas record places it far from the northeastern U. S., near the southwestern limit of the range of *C. regalis*, so it is not surprising if the parasitoid community is different in this ecologically distinct area.

Subsequently, *Cotesia* specimens reared by Richard S. Peigler from larvae of the luna moth, *Actias luna,* from the same area were found to be apparently conspecific, and are also included in our definition of the new species.

Below, JBW describes the new species of *Cotesia*, diagnosing it versus other species of *Cotesia* known to attack North American saturniids, and RJNJr and RJNIII provide discussion concerning its discovery and field biology.

Materials and methods

During October of 2014, RJNJr and RJNIII collected three caterpillars of *Citheronia regalis* (Fig. 1) in larval form on small American sweetgum (*Liquidambar styraciflua* L.) trees in the Sam Houston National Forest near Stubblefield Lake Park, Walker County, Texas. One of the specimens was a 2nd or 3rd instar caterpillar which subsequently died after about 13 days during the emergence of the braconid parasitoids described below. The parasitoid emergence was not observed by the authors, but the cocoons were saved and some were allowed to produce adult wasps. The original host, some larval parasitoids, cocoons, and adult parasitoids were saved for further study.

It was later noted that Richard S. Peigler had collected larvae of the luna moth, *Actias luna* (Fig. 2), in the same area, same month, but two years earlier, and recovered parasitoids that appeared similar in adult and cocoon appearance to those from *C. regalis*.

We examined these as part of the material described below.

The three caterpillars of *C. regalis* were raised on leaves of American sweetgum, *Liquidambar styraciflua* L., which were changed daily. The caterpillars were housed separately in well-ventilated plastic containers. The food plant was harvested daily, cleaned and the stems were trimmed under water to ensure a well-hydrated food source. Enclosures were cleaned daily. The caterpillars varied in size, with two appearing to be nearly mature larvae and the third appearing to be much younger. After 13 days, the smallest

Figures 1, 2. 1 Larva of the hickory horned devil, *Citheronia regalis* **2** Larva of the luna moth, *Actias luna*. Photo in **1** by Clayton Bownds, used with permission, photo in **2** by Richard S. Peigler, used with permission.

of the 3 caterpillars stopped eating, as if it was preparing to molt. The following morning the caterpillar was found lying on the floor of its enclosure (Fig. 3), surrounded by clear, luteous liquid, a large number of white, parasitoid cocoons and a few emerged wasp larvae.

The caterpillar host and 18 cocoons were immediately preserved together in 100 % ethyl alcohol. The other 30 cocoons were placed in a sealed container at room temperature for 5 days. During this period many of the wasps eclosed, and the sealed container was placed in the freezer for 3 days to kill all specimens. These specimens were placed in 100 % Ethyl alcohol.

The authors believe that this larva had been parasitized prior to capture, as none of the other larvae captured and reared with this specimen were likewise parasitized. One other more mature caterpillar, captured in the same area on the same day, completed its development successfully. It pupated 7 to 10 days after this parasitic incident occurred. A third specimen, captured in a different location, two weeks later, also completed its larval development and pupated successfully.

The reared *Cotesia* specimens from both *C. regalis* and from *A. luna* were compared to specimens of the described species of *Cotesia* known to attack Nearctic saturniid caterpillars (*C. anisotae* (Muesebeck), *C. electrae* (Viereck), *C. hemileucae* (Riley), *C. teleae* (Muesebeck)). All of these species were treated by Muesebeck in his (1920) revision of *Apanteles* (as then circumscribed), except *C. teleae*, which he described later (Muesebeck 1926). *C. teleae* in particular has been recorded to attack *Citheronia regal* is in the northeastern U.S., (Tuskes et al. 1996, see also Table 1), although it is most commonly recovered from the Polyphemus moth caterpillar, *A. polyphemus*. In both cases the parasitoids attack the earlier instars, and not the last instar larvae. The two species of *Cotesia* resemble each other in general appearance, but differ in the various features outlined below in the description. It remains to be seen whether *Cotesia* reared in other parts of North America from *C. regalis* are indeed *C. teleae* or sometimes belong to the new species described here. A molecular study of the complex of *Cotesia* species attacking Neartic saturniids is likely to reveal additional new species. The genus as a whole has proven taxonomically challenging except when ecological and/or molecular data are available to aid in species separation. A small table of described differences among the species attacking saturniids in North America is provided (Table 1), but there are no guarantees that the color characters listed will prove to be stable especially across broad geographic areas.

It is interesting that *Actias luna* is a commonly reared and widespread species that has not been officially recorded to yield *Cotesia* parasitoids before at any locality, although Peigler (1994) suggests that *C. teleae* might have been the species Fiske and Thompson (1909) found to attack earlier instar larvae of *A. luna* in experiments. The *Cotesia* from Peigler's rearing described here were tentatively previously identified as *C. schizurae* (Ashmead) (Peigler 2013), but that species has light buff-colored cocoons spun together in parallel rows, and attacks notodontids of the genus *Schizura*.

Possibly in nature this is an unusual association, and only occurred because *Actias* larvae co-occurred with *C. regalis* on sweetgum in this habitat. It remains to be seen if further rearings of the two host caterpillar species in east Texas continue to both yield *C. nuellorum*.

Table 1. Recorded hosts, cocoon types, and several color traits putatively varying between described species of *Cotesia* known to attack saturniid larvae in North America, including the new species described here. All of the species in this list are similar in having relatively smoother sculpturing on the propodeum and anterior metasomal tergites than is typical. *host are from Tuskes et al. (1996).

Cotesia species	Recorded hosts*	Cocoons	Tegulae	Fore and mid coxae	Hind femur
anisotae	*Anisota senatoria*	deep buff	blackish	black	black
	A. stigma	spun singly			
	A virginiensis				
	Dryocampa rubicunda				
electrae	*Agapema anona*	white	dark brown	variable	black
	A. galbina	spun singly			
	A. homogena				
	Automeris io				
	Coloradia doris				
	C. pandora				
	Hemileuca burnsi				
	H. chinatiensis				
	H. eglanterina				
	H. electra				
	H. grotei				
	H. hera				
	H. nevadensis				
	H. oliviae				
	H. tricolor				
hemileucae	*Automeris io*	white	yellowish	mostly yellowish	mostly yellowish
	Hemileuca maia	spun singly			
	H. slosseri				
nuellorum	*Citheronia regalis*	white	dark brown	mostly yellowish	mostly yellowish
	Actias luna	spun singly			
teleae	*Antheraea polyphemus*	white	yellowish	mostly black	variable
	Citheronia regalis	spun singly			

The description of the new *Cotesia* species presented below generally follows the terminology and format used in Fernandez-Triana et al. (2014) and uses primarily terms adopted by the Hymenoptera Anatomy Ontology (Yoder et al. 2010).

Taxonomy

Cotesia nuellorum Whitfield, sp. n.

http://zoobank.org/1DEC4342-CBC6-444E-A0AF-6057B804C131
Figs 3–7

Type locality. The original habitat is located within the Sam Houston National Forest, Walker County, Texas, near Stubblefield Lake Recreational area 338 feet AMSL

Figure 3. Larva of *C. regalis* with emerged larvae and cocoons of *C. nuellorum*, in rearing container. Photo by R. J. Nuelle, Jr.

(Lat: 30.524930 Lon: -95.622750 Accuracy: 10 m). This area is described as Pineywoods: Pine Forest or Plantation, according to the Texas Parks and Wildlife; Texas Ecosystem Analytical Mapper (TPWD T.E.A.M.) application. It is in a managed National Forest and is subject to occasional fire events. This successional area contains sweetgum, hickory, oak and various conifers as dominant trees. Many of the deciduous trees are relatively short (less than 6 feet tall) near the borders of roads and trails, and the generally open forest floor is thus highly convenient for sampling caterpillars.

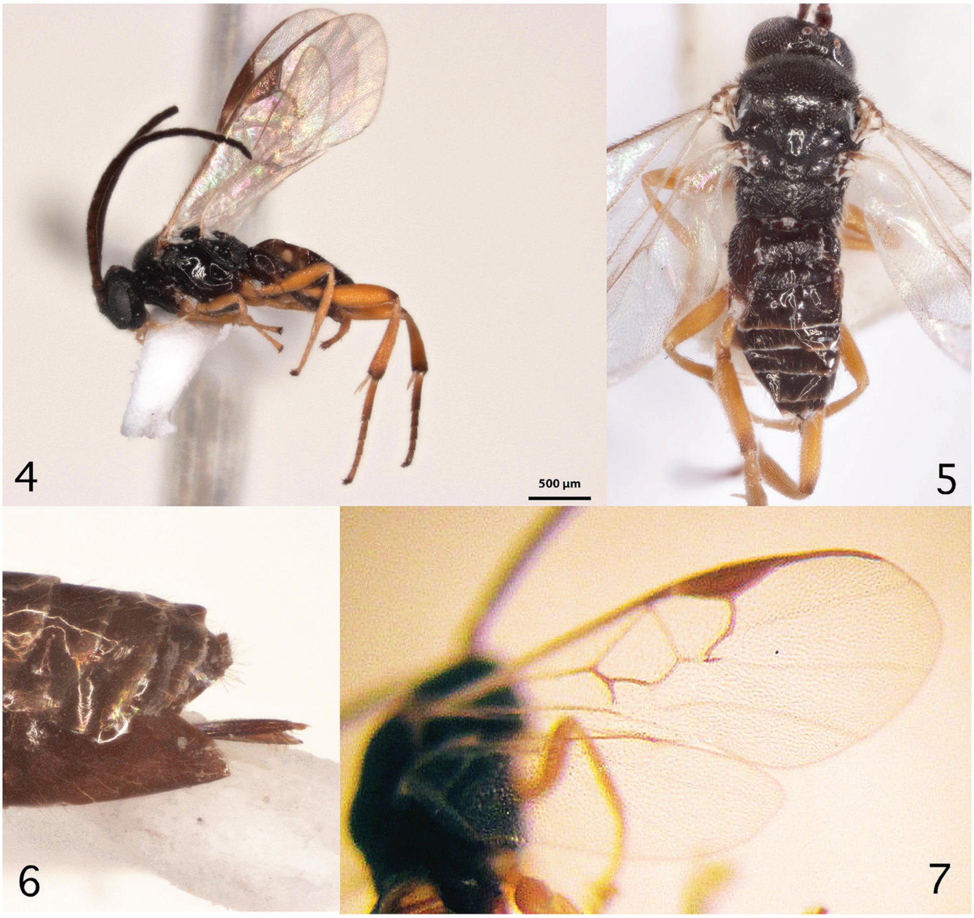
Holotype. Female deposited in USNM. TEXAS: Walker Co., Sam Houston National Forest, nr. Stubblefield Lake, 30.524930, -95.622750, October 2014, 100 m. elev., coll. R. J. Nuelle, Jr. and R. J. Nuelle, III, ex larva *Citheronia regalis* on sweetgum.

Paratypes. 4 females, 1 male with same data as holotype, plus 26 females, 7 males (deposited in CNC, INHS, SHSU, TAMUIC, UWIM (Laramie)) from: TEXAS: Walker Co., Sam Houston National Forest, Stubblefield Lake, ex. larva *Actias luna* on sweetgum, em. 21-22-X-2012, coll. R. S. Peigler.

Description. Female. Body color: body mostly dark except palps, portions of legs (see below) and ventral portions of anterior laterotergites. Antenna color: scape black, pedicel dark brown, flagellum dark brown/black. Coxae color (pro- , meso, metacoxa): honey yellow; honey-yellow; black proximally, shading to medium brown distally. Femora color (pro-, meso-, metafemur): honey-yellow; honey-yellow; honey-yellow with smoky spot dorsally near distal end. Tibiae color (pro-, meso-, metatibia): honey-yellow; honey-yellow; honey-yellow with darkened extreme distal end. Tegula and humeral complex color: tegula dark brown translucent, humeral complex dark brown translucent (both slightly more translucent and paler in males). Pterostigma color: dark greyish brown, with indistinct paler junction with C+SC. Fore wing veins color: partially pigmented (a few veins may be dark but most are pale – see figure for pattern). Antenna length/body length: antenna approximately as long as body (head to apex of metasoma). Body in lateral view: not distinctly flattened dorso–ventrally. Body length (head to apex of metasoma): 2.0–2.2 mm. Fore wing length: 2.2–2.4 mm. Ocular–ocellar line/posterior ocellus diameter: 2.3–2.5. Interocellar distance/posterior ocellus diameter: 2.0–2.2. Antennal flagellomerus 2 length/width: 2.9–3.1. Antennal flagellomerus 14 length/width: 1.9–2.1. Length of flagellomerus 2/length of flagellomerus 14: 2.1–2.3. Metafemur length/width: 3.2–3.3. Metatibia inner spur length/metabasitarsus length: 0.4–0.5, about 10% longer than outer spur. Anteromesoscutum: mostly with shallow, dense punctures (separated by less than 2.0 × maximum diameter), but with polished and virtually punctureless strip near scutoscutellar sulcus. Mesoscutellar disc: mostly punctured but sometimes indistinctly so. Number of pits in scutoscutellar sulcus: 9 or 10. Propodeal carinae: strong medial longitudinal carina, vague hints of a transverse carina both otherwise rugose, especially medially and anteriorly. Mediotergite 1 length/width at posterior margin: 0.9–1.1. Mediotergite 1 shape: barrel-shaped, broadest in posterior 0.2. Mediotergite 1 sculpture: mostly sculptured, albeit shallowly, otherwise shiny, especially anteriorly. Mediotergite 2 width at posterior margin/length: 2.0–2.2. Mediotergite 2 sculpture: punctate/rugose, but shinier and smoother laterally. Outer margin of hypopygium: evenly sclerotized, posterior margin reaching tip of metasoma and forming a shallow even convex curve. Ovipositor thickness: evenly narrowing towards tip. Ovipositor sheaths exerted but visible portion shorter than hypopygium length. Length of fore wing veins r/2RS: 1.1–1.2. Length of fore wing veins 2RS/2M: 1.1–1.3. Length of fore wing veins 2M/(RS+M)b: 0.9–1.0. Pterostigma length/width: 3.1–3.5. Point of insertion of vein r in pterostigma: at roughly half way point length of pterostigma. Angle of vein r with fore wing anterior margin: nearly perpendicular, slightly inclined towards fore wing apex. Shape of junction of veins r and 2RS in fore wing: distinctly but not strongly angled.

Male. As female but with slightly darker legs, more polished tergites and sometimes more translucent and paler tegulae. Body size usually about 10 % smaller than female.

Molecular data. None yet recorded. A broad sample of *Cotesia* reared from various larger Nearctic saturniids would be useful to clarify how distinct the parasitoid species are both in terms of host specificity and in terms of geographic distribution. In Costa Rica, where the diversity of Saturniidae is higher, the host specificity, at least to host genus, appears high (Smith et al. 2008; Janzen and Hallwachs 2017).



Figures 4–7. 4 Lateral habitus photo of *Cotesia nuellorum* female **5** Dorsal habitus photo of *Cotesia nuellorum* female **6** lateral view of posterior end of metasoma of *C. nuellorum*, showing hypopygium and ovipositor sheaths **7** Wings of *C. nuellorum* female.

Biology/ecology. Gregarious (Fig. 3) on early instar larvae of host. Host: Saturniidae: Ceratocampinae: *Citheronia regalis* (F.) and Saturniinae: *Actias luna* (L.). 4th and 5th instar larvae do not appear to serve as hosts, as with some other *Cotesia* parasitizing large *Sphingidae* and *Saturniidae*.

Distribution. Known so far only from Texas but likely to be much more widely distributed.

Ecologically and/or morphologically similar species. Table 1 provides a comparison of the species so far known from saturniids in North America.

Etymology. This species is named by JBW for the original discoverers, Robert J. Nuelle, Jr. and Robert J. Nuelle, III.

Acknowledgments

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RESEARCH ARTICLE

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Flanged Bombardier beetles from Shanghai, China, with description of a new species in the genus *Eustra* Schmidt-Goebel (Coleoptera, Carabidae, Paussinae)

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Abstract

Four paussine species belonging to three different genera are discovered in Shanghai. A new species, *Eustra shanghaiensis* Song, **sp. n.**, is described, illustrated, and distinguished from the treated congeners. New distributional data or biological notes on *Eustra chinensis* Bänninger, 1949, *Itamus castaneus* Schmidt-Goebel, 1846, and *Platyrhopalus davidis* Fairmaire, 1886 are provided.

Keywords

China, *Ectomomyrmes*, *Eustra*, *Itamus*, Paussinae, myrmecophilous, new species, *Pheidole*, *Platyrhopalus*, Shanghai

Introduction

The ground beetle subfamily Paussinae Latreille, 1807 currently contains more than 30 species from China (Nagel 2003; Wrase and Schmidt 2007; Guéorguiev 2014; Maruyama 2014, 2016; Song et al. 2017; Wang 2017), among which only one is known to occur in Shanghai: *Eustra chinensis* Bänninger, 1949.

During several recent collecting trips conducted in Shanghai, the senior author and his colleagues collected a large series of paussine specimens. The examination of the specimens revealed a new species of ozaenine genus *Eustra* and three known species.

According to the latest revision of *Eustra* (Deuve, 2001), the genus contains two species from China: *E. chinensis* (Shanghai, Taiwan; Type locality: Shanghai, China), *E. taiwanica* Deuve, 2001 (Taiwan; Type locality: Taiwan, China). In 2014, Guéorguiev described the first Chinese troglobitic *Eustra* species, *E. petrovi* from Xianrendong, Yunnan. In this paper, a new *Eustra* species is described from Shanghai, illustrations provideded of all Shanghainese paussines, and biological information about the habitats and behaviors of *Eustra shanghaiensis* sp. n., *Eustra chinensis*, *Platyrhopalus davidis,* and *Itamus castaneus* observed in nature and captivity are provided.

Materials and methods

Material used in this study is deposited in the following public and private collections:

SNUC	Insect Collection of Shanghai Normal University, Shanghai, China;
SNHM	Shanghai Natural History Museum;
KUM	The Kyushu University Museum, Fukuoka;
MNHN	The French National Museum of Natural History;
cBWX	private collection of Wen-Xuan Bi, Shanghai, China;
cLW	private collection of Wei Liu, Zhejiang, China;
cJRX	private collection of Ri-Xing Jiang, Shandong, China;
cSXB	private collection of Xiao-Bin Song, Shanghai, China;
cWYX	private collection of Yong-Xiang Wu, Shanghai, China;
cYZZ	private collection of Zhi-Zhou Yu, Shanghai, China.

The following abbreviations are applied in the text:

BL	body length, from the anterior margin of the head to the apices of elytra;
HW	head width, maximum width of the head;
AL	length of antenna;
ACL	maximum length of antennal club;
ACW	maximum width of antennal club;
PL	length of the pronotum along the midline;
PW	maximum width of pronotum;
EL	length of the elytra along the suture.

All measurements are in millimeters.

Taxonomy

Subfamily Paussinae Latreille, 1807
棒角甲亚科

Tribe Ozaenini Hope, 1838
折缘粗角步甲族

Subtribe Eustrina Jeannel, 1946
双斑粗角步甲亚族

Genus *Eustra* Schmidt-Gobel, 1846
双斑粗角步甲属

Eustra shanghaiensis Song, sp. n.
http://zoobank.org/26391AC8-3D78-41C6-BA55-F3322740E088
Figs 1A, 2, 3, 6A
上海双斑粗角步甲

Type material. Holotype. ♂, (SNUC), labeled 'CHINA: Shanghai, Pudong New District, Shanghai Binjiang Forest Park (上海滨江森林公园), 31°23'25"N, 121°22'10"E, alt. 5 m, 7.v.2017, Song, Peng, Hu, Wang & Liu leg. / HOLOTYPE [red], *Eustra shanghaiensis* sp. nov., Song det.2017'.

Paratypes. 3♂♂, 3♀♀, (SNHM), same data as holotype; 2♂♂, 2♀♀, (KUM), ditto; 1♂, 1♀, (MNHN), ditto; 5♂♂, 5♀♀, 84 exs, (SNUC), ditto; 74 exs, (cSXB), same data as holotype, but 27.vii.2017, Song, Zhou, Wang, Wang & Zhang leg; 11 exs, (cSXB), same data as holotype, but 24.ix.2016, Zhong Peng leg; 1 ex (cSXB), labeled 'CHINA: Shanghai, Changning District, Tianshan Park (天山公园), 31°12'45"N, 121°24'10"E, alt. 14 m, 20.iv.2008, Xiao-Bin Song leg.; 1ex, (cSXB), ditto, but 12.iv.2008; 1 ex, (cSXB), ditto, but iv.2008; 1 ex, (cBWX), labeled 'CHINA: Shanghai, Pudong New District, nr. Zhangjianggaoke (张江高科), 31°11'84"N, 121°34'82"E, alt. 4 m, 28.iii.2006, Wen-Xuan Bi leg.; 8 exs, (cSXB), ditto, but 5.ii.2009, Song & Ding leg. / all paratypes, labeled 'Paratype [yellow], *Eustra shanghaiensis* sp. nov. Song det. 2017'.

Comparative notes. *Eustra shanghaiensis* sp. n. is closely allied to *E. hammondi* Deuve, 2001 from Mindanao, Philippines in sharing similar body size, general habitus and aedeagal structure (Figs 1A, 3A). The new species can be readily separated from latter by the pronotal front angles strongly produced, the wider aedeagus, the apex of aedeagal median lobe much shorter and wider and the relatively long apical portion of right paramere. It differs from its Shanghainese congener *E. chinensis* by the smaller body size and the different shape of aedeagus.

Description. Body (Fig. 1A) 3.06–3.17 mm; yellowish-brown, head and pronotum somewhat reddish; each elytron with a dark spot.

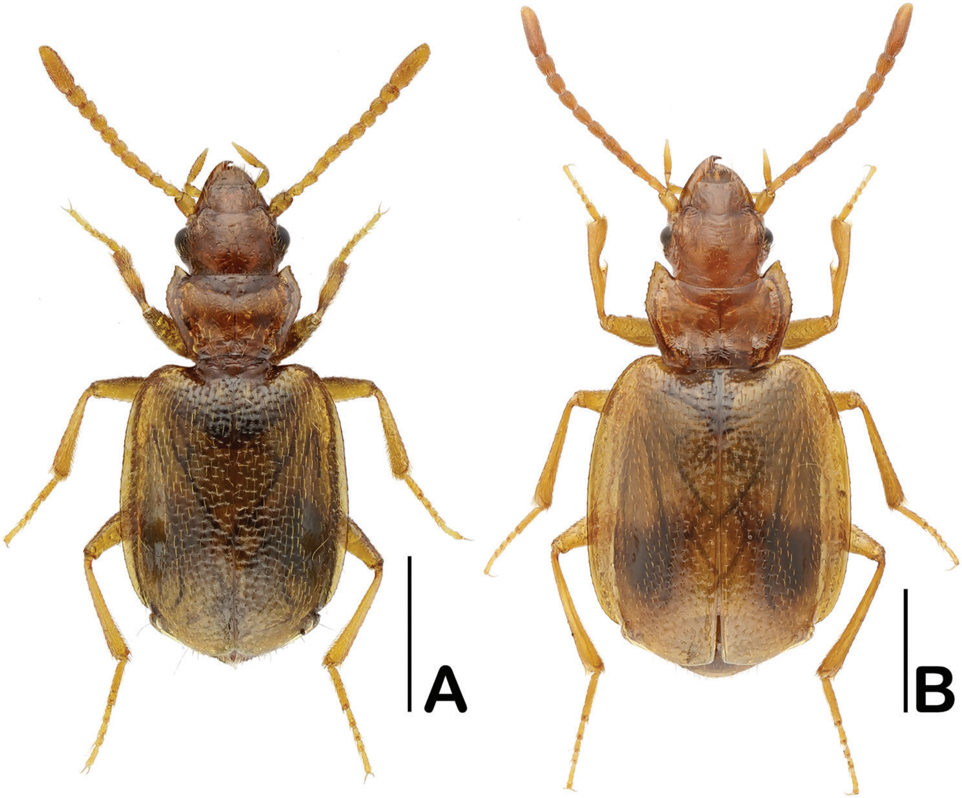

Figure 1. Dorsal habitus of *Eustra* species. **A** *E. shanghaiensis* sp. n., male (paratype) **B** *E. chinensis* Bänninger, 1949, female. Scale bars: 1 mm.

Head (Fig. 2A) convex, gently covered with yellow setae, microsculpture faint; fully carinate near eyes; clypeus anteriorly gently concave, with 2 pairs of long setae at anterior margin; labrum with anterior margin minutely denticulate, with 12–14 long setae; Eyes somewhat small; antennae (Fig. 2B) submoniliform, with antennomeres I and II clavate, increasing in diameter distally gradually; antennomere I somewhat shorter than 2nd and 3rd combined; antennomeres V–X almost as wide as long; antennomere XI evidently longer than the 1st.

Pronotum (Fig. 2C) sparsely covered with yellow setae; distinctly wider than long, widest at apical third; moderately contracted anteriorly and posteriorly; disc moderately convex medially and reflexed on lateral sides; front angles strongly produced; midline distinct, almost reaching both anterior and posterior borders.

Pterothorax shaped as in Fig. 2E, meso-coxae disjunct, meta-coxae separated in midline of body.

Elytra (Fig. 2F) densely punctulate and pubescent, distinctly wider than prothorax; shoulders rounded and not bordered; each side with an obscurely dark spot; surface moderately covered with short setae, but along the right side of dark spot glabrous.

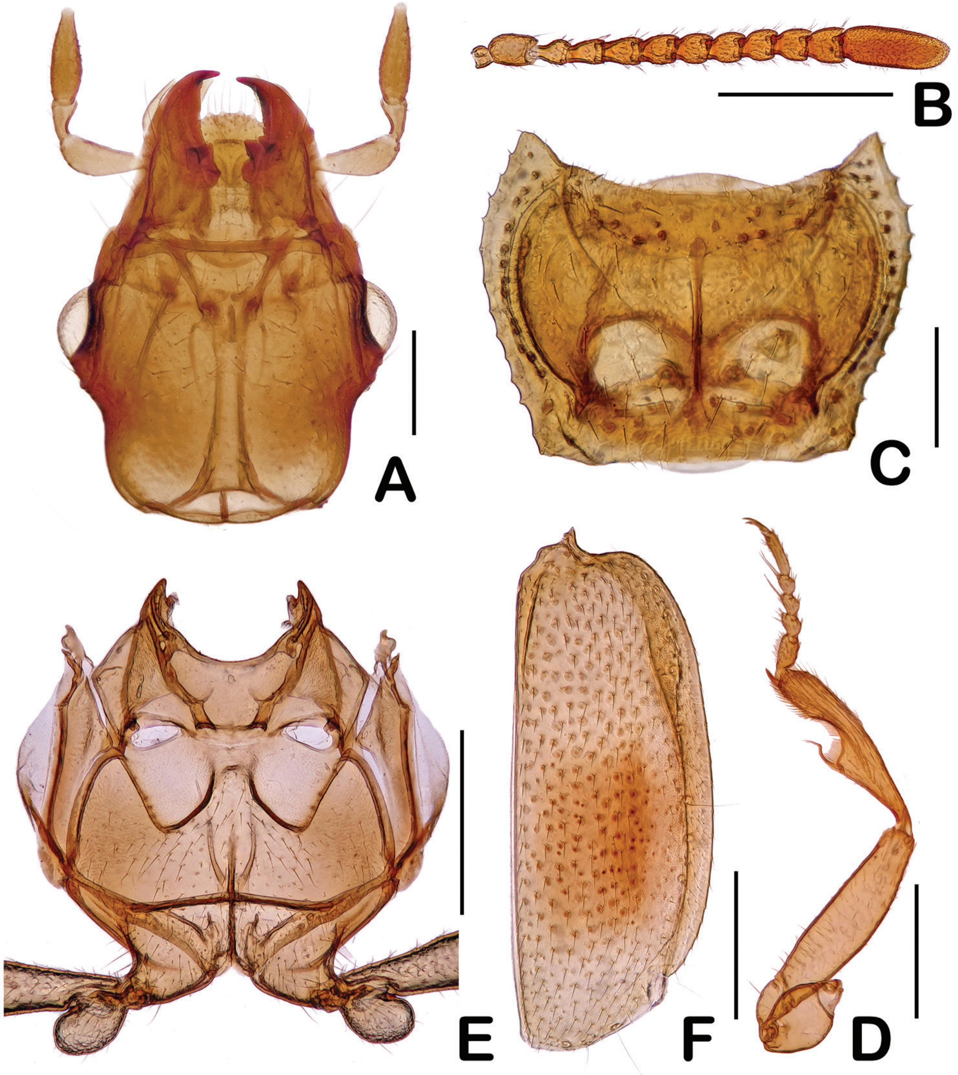

Figure 2. Diagnostic features of *Eustra shanghaiensis* sp. n. **A** Head **B** Antenna **C** Prothorax **D** Foreleg **E** Pterothorax **F** Elytron. Scale bars: 0.2 mm (**A, C**); 0.5 mm (**B, E, F**); 0.4 mm (**D**).

Hind wings well developed.

Legs (Fig. 1A) relatively long and slender; both spurs of pro-tibiae (Fig. 2D) are terminal, almost equal in length.

Male. Sternite VII (Fig. 3E) wide, widely truncate, slightly acute at middle, with 4 long setae near apex. Median lobe of aedeagus shaped as in Fig. 3A, ends in a blunt tip, with a spoon-shaped sclerite on endophallus; right paramere (Fig. 3B) arcuate, apical portion narrow and elongate; left paramere shaped as in Fig. 3C, large, almost glabrous, rounded at apex.

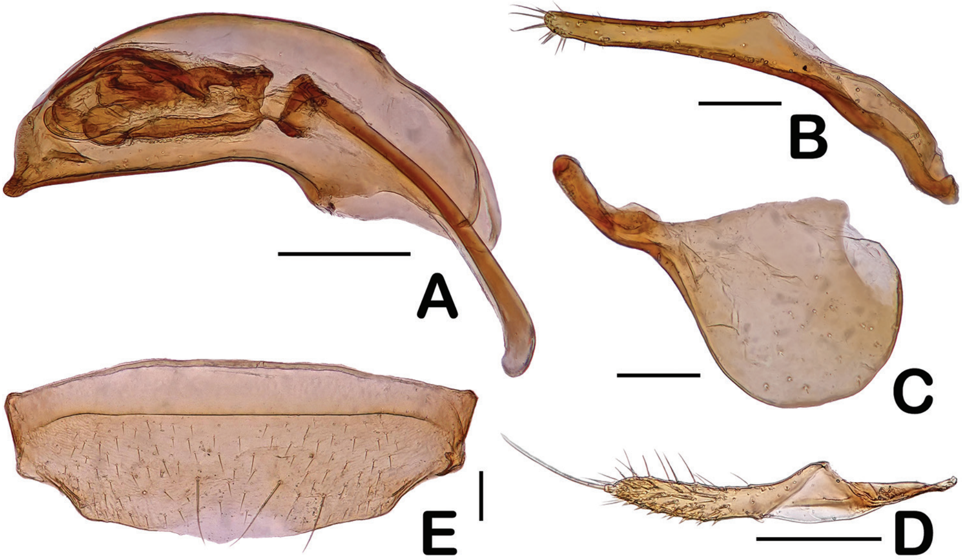

Figure 3. Diagnostic features of *Eustra shanghaiensis* sp. n. **A** Aedeagus, dorsal view **B** Right paramere **C** Left paramere **D** Gonopod IX **E** Male Sternite VII. Scale bars: 0.2 mm (**A–D, F**); 0.1 mm (**E**).

Female. Gonopod IX shaped as in Fig. 3D.

Comments. Moore et al. 2011 described and illustrated the larval structure of *Eustra chinensis* based on larval specimens collected together with some adults from Tianshan Park, Shanghai with no association ants (Fig. 6A). However, all these specimens are now reconsidered as larvae of the new species, *Eustra shanghaiensis* sp. n. described here.

Measurements. BL, 3.06–3.17; HW, 0.71–0.76; PL, 0.52–0.57; EL, 1.89–1.92.

Distribution. China: Shanghai.

Biological notes. Both adults and larvae are collected under rotten wood or bark during the whole year in Shanghai.

Symbiotic host. Free living, not associated with ant.

Etymology. Named after its type locality of Shanghai Latinized.

Eustra chinensis Bänninger, 1949

Figs 1B, 6B
中华双斑粗角步甲

Eustra chinensis Bänninger, 1949: 134 (original description, type locality: Shanghai, China); Deuve 2001: 570 (diagnosis, new record from Taiwan, China); Teradaet al. 2013: 31 (redescription); Maruyama et al. 2013: 2 (associated with *Ectomomyrmes javana*).

Material examined. 1♂, 1♀, (cSXB), labeled 'CHINA: Shanghai, Xuhui District, Shanghai Normal University (上海师范大学), 31°09'48"N, 121°24'45"E , alt. 4 m, 11.V.2017, Xiao-Bin Song leg., [from colony of *Ectomomyrmes javana*]'; 1♂, 1 ex, (cSXB), ditto, but 20.ix.2016, Zhong Peng leg.; 1 ex, (cJRX), ditto; 1 ex, (cSXB), labeled 'CHINA: Shanghai, Changning District, Zhongshan Park (中山公园), 31°13'25"N, 121°25'00"E, alt. 9 m, xi.2006, Xiao-Bin Song leg.'

Other material examined. Zhejiang: 1ex, (cSXB), labeled 'CHINA: Zhejiang, Hangzhou City, Lin'an District, West Tianmushan (西天目山), 30°19'28"N, 119°26'54"E , alt. 380 m, 16.vii–9.viii.2017, Xiao-Bin Song leg., [F. I. T.].'

Comments. *Eustra chinensis* is characterized by the large body size and the broad elytra. This is the only known myrmecophilous species of the genus *Eustra*. Adults are collected from *Ectomomyrmes javana* (Mayr, 1867) nests under the stone (Fig. 6B), and have been observed feeding on dead insects inside nest of *E. javana* (Maruyama et al., 2013). Wendy et al. (2011) described an unidentified *Eustra* larva which collected during the excavation of nest of *Ectomomyrmes javana* in Taiwan, based on its same special symbiotic host and the reasonable distribution, the larva should belongs to *Eustra chinensis*.

Measurements. BL, 4.03–4.30; HW, 0.94–0.96; PL, 0.65–0.68; PW, 1.21–1.25; EL, 2.32–2.61.

Distribution. China: Shanghai, Zhejiang (new provincial record), Taiwan; Japan: Yaeyama-shoto.

Symbiotic host. *Ectomomyrmes javana* (Mayr, 1867) (Figs 6B, 7A, B).

Subtribe Ozaenina Hope, 1838

折缘粗角步甲亚族

Genus *Itamus* Loew, 1849

伊塔粗角步甲

Itamus castaneus Schmidt-Goebel, 1846

Figs 4, 6C
栗伊塔粗角步甲

Itamus castaneus Schmidt-Goebel, 1846: 67 (original description, type locality: Myanmar); Zhao and Tian 2003: 57 (new record from Guangdong, China).

Material examined. 1♂, (cSXB), labeled 'CHINA: Shanghai, Changning District, nr. Zhongshan Park (中山公园), 31°12'59"N, 121°25'17"E, alt. 11m, 28.vii.2017, Xiao-Bin Song leg.'; 3♀♀, (cSXB), ditto, but 22.viii.2017; 4 exs, (cSXB), ditto, but 25.viii.2017; 1 ex, (cSXB), ditto, but 7.ix.2017; 2 exs, (cSXB), ditto, but 27.ix.2017; 1 ex, (cWYX), labeled 'CHINA: Shanghai, Jing'an District, nr. Jiang'an Temple (静安寺), 10.viii.2017, Yong-Xiang Wu leg.'; 1 ex, (cWYX), ditto, but vii.2017.

Other material examined. Yunnan: 1ex, (cSXB), labeled 'CHINA: Yunnan, Xishuangbanna, Xishuangbanna Tropical Botanical Garden (西双版纳植物园), iv-2009,

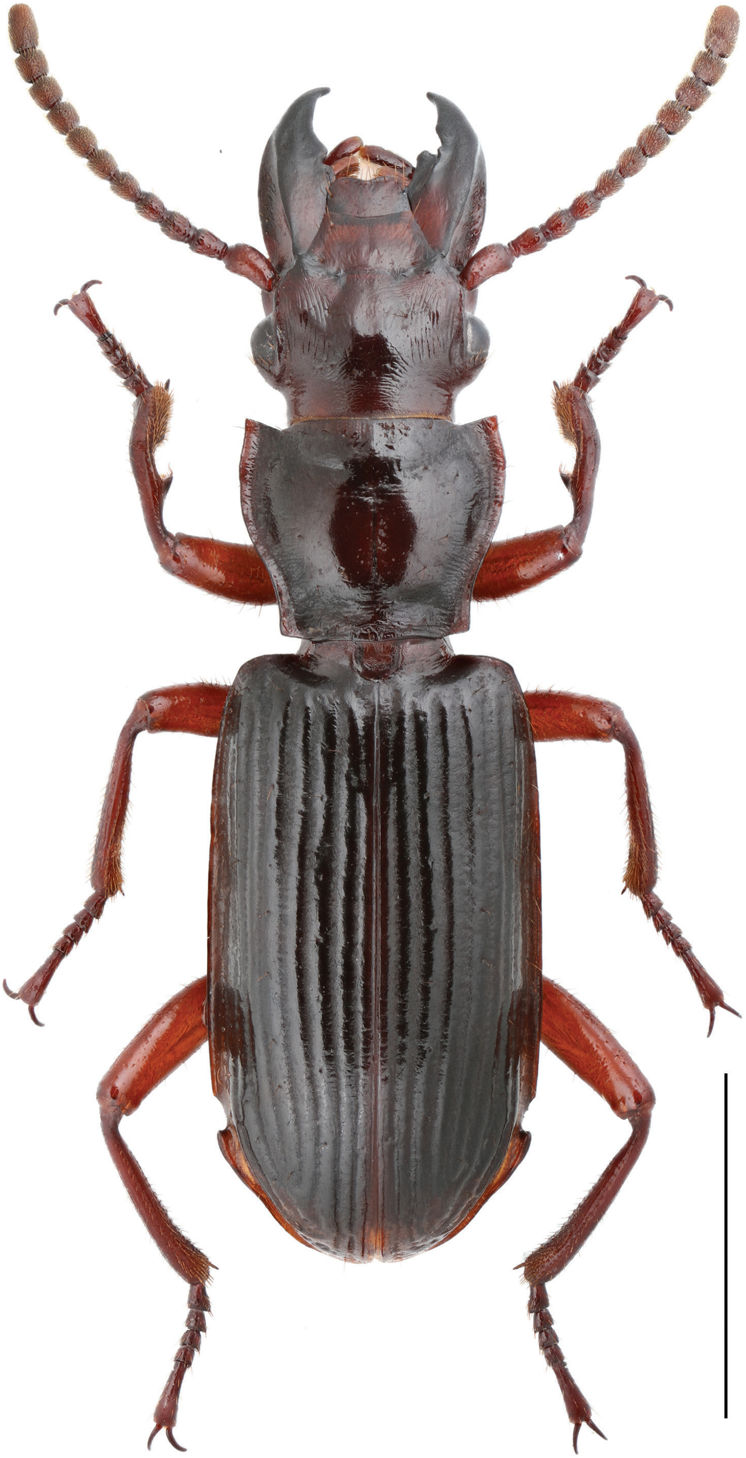

Figure 4. *Itamus castaneus* Schmidt-Goebel, 1846, Male. Scale bar 5 mm.

Xiao-Yu Zhu leg.'; Fujian: 1 ex, (cSXB), labeled 'CHINA: Fujian, Nanping City, Wuyishan (武夷山), Yunvfeng (玉女峰), Zu-Qi Mai leg., under rotten wood.'; Zhejiang: 1 ex, (cLW), labeled 'CHINA: Zhejiang, Hangzhou, Hangzhou Botanical Gardern, Taoyuanling (桃源岭), viii-2017, Wei Liu leg.'; 3 exs, (cLW), ditto, but Pujiaxincun (濮家新村), vi-2015, on *Broussonetia papyrifera* trees.

Comments. Zhao and Tian (2003) first recorded the ozaenine genus *Itamus* Loew, 1849 in China, with two known Asian species, i.e., *I. castaneus* from Guangdong and *I. dentatus* Andrews, 1919 from Guangxi. *Itamus castaneus* can be readily separated from its Chinese congener *I. dentatus* by the larger body size, shoulders of elytra almost without denticle and the fore-femur with an obvious projection. All specimens from Shanghai were founded walking on the ground or at light in July to October (Fig. 6C), individuals are observed to feed on amber snails (*Suecinea* sp. Draparnaud) and dead cave cricket (Rhaphidophoridae). One specimen from Fujian was collected under decaying wood (Mai per. comm.). Three individuals from Zhejiang are collected at night on the trunks of *Broussonetia papyrifera* (L.) L'Hér. ex Vent. trees (Liu per. comm.).

Measurements. BL, 15.62; HW, 3.61; PL, 3.22; PW, 4.28; EL, 8.90.

Distribution. China: Shanghai (new provincial record), Zhejiang (new provincial record), Fujian (new provincial record), Guangdong, Yunnan (new provincial record); Myanmar; Laos; Sri Lanka; Thailand.

Symbiotic host. Free living, not associated with ant.

Tribe Paussini Latreille, 1807

棒角甲族

Subtribe Paussina Latreille, 1807

棒角甲亚族

Genus *Platyrhopalus* Westwood, 1833

圆角棒角甲属

Platyrhopalus davidis Fairmaire, 1886

Figs 5A, 6D

大卫圆角棒角甲

Platyrhopalus davidis Fairmaire, 1886: 224 (original description, type locality: Kiang-si = Jiangxi, China); Luna de Carvalho 1987: 390 (diagnosis).

Material examined. 1♂, 1ex, (cSXB), labeled '上海植物园, 3-XI-2007, 毕文烜'; 1ex, ditto, but, 21-IV-2007, pinned with *Pheidole* ant (1 soldier, 3 workers); 1♀, (cSXB), labeled 'SH. Botanical Gardern Xuhui District, Shanghai City, 27-VII-2007'; 1 ex,

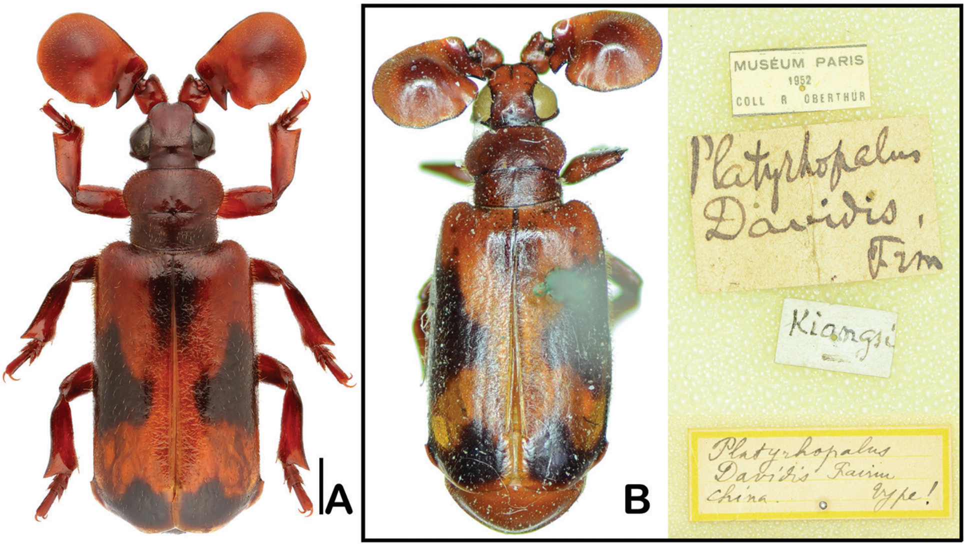

Figure 5. *Platyrhopalus davidis* Fairmaire, 1886. **A** Individual from Shanghai Botanical Gardern **B** Holotype. Scale bar 1 mm.

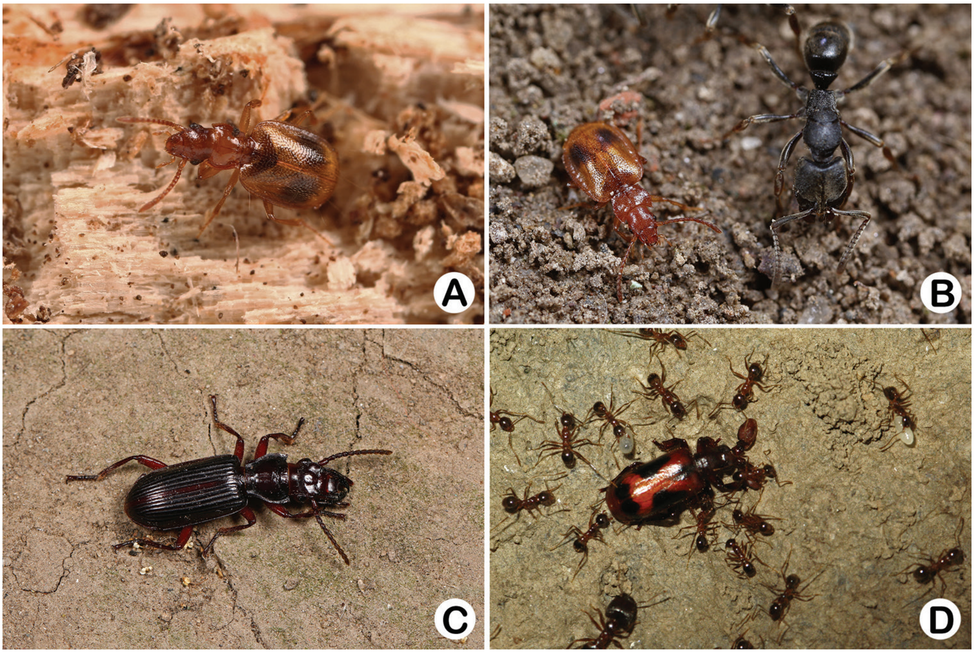

Figure 6. Habitus of Shanghainese paussines. **A** *Eustra shanghaiensis* sp. n. found in rotten wood **B** *Eustra chinensis*, with a work of *Ectomomyrmes javana* **C** *Itamus castaneus*, walking on the ground at night **D** *Platyrhopalus davidis*, associated with *Pheidole* ants. Photographs by Xiao-Bin Song (**A–C**) and Wen-Xuan Bi (**D**).

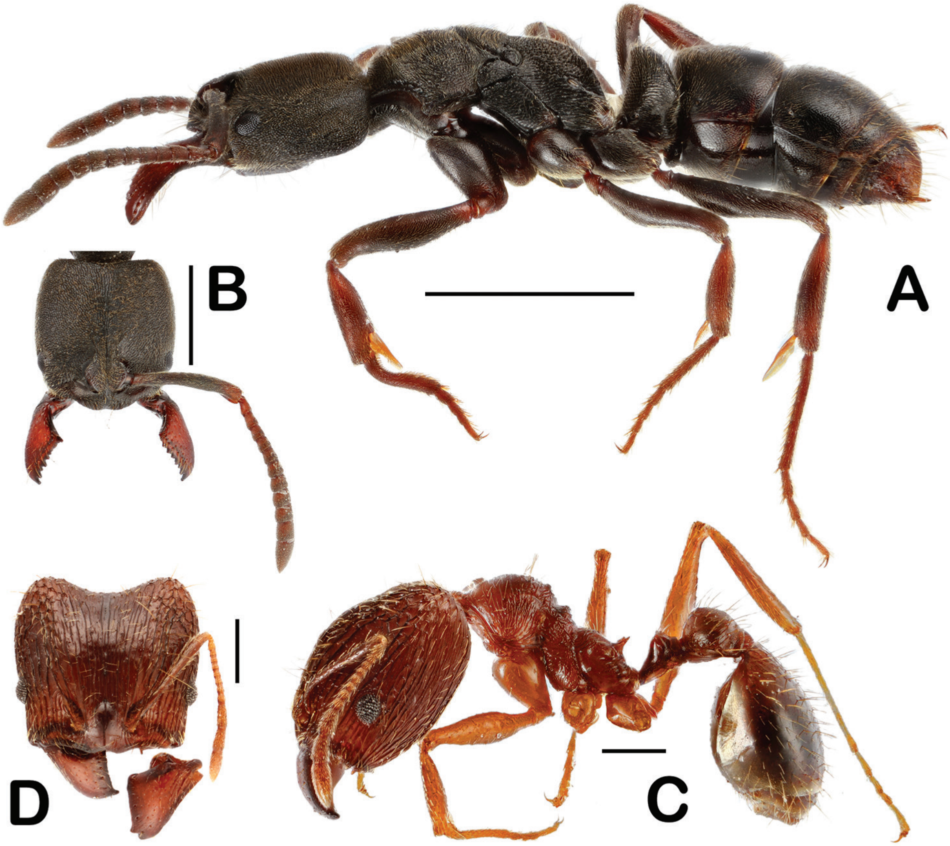

Figure 7. Host ants of *Eustra chinensis* and *Platyrhopalus davidis*. **A** *Ectomomyrmes javana* (Mayr, 1867), body, lateral view **B** ditto, but head, dorsal view **C** *Pheidole* sp., soldier, lateral view **D** ditto, but head, dorsal view. Scale bars: 2 mm (**A**); 1 mm (**B**); 0.5 mm (**C, D**).

(cSXB), ditto, but 25-VI-2008; 1 ex, (SNUC), labeled 'CHINA: Shanghai, Fengxian District, Shanghai Normal Univeristy (上海师范大学), 30°50'09"N, 121°31'09"E, alt. 6 m, 15.vi.2007, Xiao-Yu Zhu leg.'; 1 ex, (SNUC), ditto, but 20.v.2008, Yu-Di Wang leg.; 1 ex, (SNUC), ditto, but 1.2008; 1♀, (cSXB), labeled ' CHINA: Shanghai, Fengxian District, Shanghai Institute of Technology (上海应用技术大学), 30°50'15"N, 121°30'20"E, alt. 5 m, vii.2011, De-Yao Zhou leg.'; 2 ex, (SNUC), labeled 'CHINA: Shanghai, Chongming District, Dongtan N. R. (东滩), 7.v.2007, Jia-Yao Hu leg.'; 1♂, (SNUC), ditto, but 30.vi.2007; 1 ex, (SNUC), labeled 'CHINA: Shanghai, Chongming District, Beihu (北湖), 1.vii.2008, Jia-Yao Hu leg.', pinned with 6 *Tetramorium caespitum* workers; 1 ex (cYZZ), ditto, but Xitan (西滩), 15.vii.2007, Hong-Qiong Li leg.

Other material examined. Anhui: 1ex, (cSXB), labeled 'CHINA: Anhui, Fuyang City, Yingzhou District (颍州), Qiyuhedong Vill. (七渔河村), near dam, from ant nest, nr. 32°54'31"N, 115°46'29"E, 29-VI-2013, J-B Dong leg.'; Fujian: 1 ex, (SNUC), labeled ‘Mt. Wuyi, Fujian, Li-Zhen Li leg., 10~14-VII-2002’; Shandong: 1 ex, (cSXB), labeled ‘鲁, 莱阳, 旌旗山, 14.5.15., JRX.’; Hubei: 1 ex, (cSXB), labeled ‘湖北, 大店林场, 26.v.2016’ ; Hunan: 1 ex, (cSXB), labeled ‘湖南, 长沙, 1980.9, 灯下, 徐慧?’; Yunnan: 1 ex, (cSXB), labeled ‘CHINA: Hunan Province, Leiyang City (耒阳), vi-2011, Hao Xu leg.’; 1 ex, (cSXB), labeled ‘云南, 昭通, 黄华, 石水井—花椒地, 2007-8-13’; 1 ex, (cSXB), labeled ‘CHINA, Yunnan Prov., Yingjiang County (盈江县), Tongbiguan (铜壁关), alt. 1330 m, 23°36'N, 97°36'E , 23-V-2013, Chao Wu leg.’; Xizang: 1 ex, (cSXB), labeled ‘CHINA, Xizang, Linzhi, Motuo County, Beibeng Vill. (背崩乡), alt. 780 m, 10-viii-2010, Wen-Xuan Bi leg.’; 1 ex, (cSXB), labeled ‘CHINA, Xizang, Linzhi, Motuo County, Beibeng Vill. (背崩乡), 29.243469,95.169677,769.01, 26-vi-2017, Jing-Song Shi leg.’.

Comments. *Platyrhopalus davidis* is widely distributed in China, and specimens are often collected by light trap. Populations from Shanghai, Shandong, Hubei are recorded to be associated with *Pheidole* ants (Fig. 6D), but one individual from Beihu (北湖), Shanghai was founded with *Tetramorium* ants (Hu pers. comm.).

Measurements. BL, 6.84–7.55; HW, 1.41–1.56; PL, 1.37–1.46; PW, 1.59–1.80; EL, 4.45–5.00; ACL, 1.70–1.87; ACW, 1.50–1.57.

Distribution. China: Beijing, Shanxi, Shanghai (new provincial record), Jiangsu, Zhejiang (new provincial record), Anhui (new provincial record), Fujian, Jiangxi, Shandong (new provincial record), Henan, Hubei (new provincial record), Hunan, Guangdong (new provincial record), Sichuan, Guizhou, Yunnan (new provincial record), Xizang?, Shaanxi.

Symbiotic host. *Pheidole* sp. (Figs 6D, 7C, D).

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RESEARCH ARTICLE

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Taxonomic review of the deep water flathead genus *Parabembras* with description of the new species *Parabembras multisquamata* from the western Pacific Ocean (Teleostei, Parabembridae)

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Abstract

Three valid species of *Parabembras* are recognized: *P. curta*, *P. robinsoni*, and the new species *P. multisquamata*. *Parabembras robinsoni* from the southwestern Indian Ocean (South Africa to Mozambique) is easily distinguishable from the other species in having eleven spines in the first dorsal fin, a distinct symphyseal knob on the lower jaw, two preocular spines, and a single lachrymal spine. *Parabembras multisquamata* from the southwestern Pacific (Vanuatu, Papua New Guinea) and the Philippines, and *P. curta*, known from the northwestern Pacific (southern Japan to South China Sea), are similar in sharing the absence of a symphyseal knob on the lower jaw, the presence of two lachrymal spines, and a single preocular spine, but the former is clearly distinguished from the latter in usually having 10 spines in the first dorsal fin (vs. eight or nine spines in *P. curta*), 9–11 supraocular spines (vs. 6–8 in *P. curta*), 40–44 pored lateral line scales (vs. 34–39 in *P. curta*), and the pectoral fin extending beyond the level of the anus (vs. not reaching to the level of the anus in *P. curta*).

Keywords

New species, *Parabembras curta*, *Parabembras multisquamata*, *Parabembras robinsoni*, Papua New Guiana, Philippines, taxonomy, Vanuatu

Introduction

The family Parabembridae, or deep water flatheads, comprises only two species, *Parabembras curta* (Temminck & Schlegel, 1843) from the northwestern Pacific Ocean, and *P. robinsoni* Regan, 1921, from the western Indian Ocean (Eschmeyer et al. 2017). The former species was originally placed in the genus *Bembras* Cuvier, 1829, but assigned by Bleeker (1874) to the then monotypic genus *Parabembras*. Jordan and Hubbs (1925), established the family as Parabembradidae [currently Parabembradidae (van der Laan et al. 2014)], but several authors synonymized Parabembridae with Bembridae (e.g., Knapp 1986; Nelson et al. 2016).

Imamura (1996; 2004) recognized Parabembridae as a valid family on the basis of a phylogenetic analysis based on osteological and myological characters. According to Imamura (1996), the family is diagnosed by the presence of spines and absence of tubercles on the dorsal surface of the head; the lower jaw projecting beyond the tip of the upper jaw; the separation of the ascending process and the remaining part of the premaxilla; the absence of free fin rays from the pectoral fin; three spines in the anal fin; about 35–40 scales in the lateral line; and the absence of a swim bladder.

We examined four relatively recently collected (1980–2012) specimens of a species of *Parabembras* from the waters of Vanuatu, Papua New Guinea, and the Philippines. These specimens differ from the two currently known species of the family by the spines on the head, number of dorsal-fin spines and pored lateral line scales, and several proportional measurements, and are described herein as a new species of *Parabembras*. In addition, the two congeneric species *P. curtus* and *P. robinsoni* are redescribed, and a key to the species of *Parabembras* is presented.

Materials and methods

Counts and measurements follow Motomura (2004), except where otherwise noted. Body depths 1 and 2 are taken at the anterior insertions of the first and second dorsal fins, respectively; predorsal lengths 1 and 2 from tip the tip of the snout to the anterior insertion of the first and second dorsal fins, respectively; and the body width is measured between the uppermost part of the base of the right and left pectoral fins. Pored lateral line scales were counted from the first pored scale near the gill opening to the pored scale on the posterior margin of the hypural plate. The terminology of head spines follows Knapp et al. (2000). The standard length is abbreviated as SL. Characters given in the diagnosis of the genus were not repeated in the species descriptions. To provide an objectively defined score that summarizes the major components of variable measurements between specimens, a principal component analysis (PCA) was conducted on morphometric characters by using the function *prcomp* in the software package R 3.3.2. (R Core Team 2016). We removed the effect of changes in size by calculating the residuals from the linear regressions of changes in all variables on changes in SL (Revell et al. 2007). All variables were log-transformed prior to analysis.

The specimens examined in this study are deposited in the fish collections of the Natural History Museum, London (**BMNH**), Kyoto University, Kyoto and Maizuru (**FAKU**), Muséum national d'Histoire naturelle, Paris (**MNHN**), National Museum of Marine Biology and Aquarium, Taiwan (**NMMBA**), National Museum of Nature and Science, Tsukuba (**NSMT**), the National Taiwan University Museums, Taipei (**NTUM**), and the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (**MCZ**).

Taxonomy

Genus *Parabembras* Bleeker, 1874

Parabembras Bleeker, 1874: 370; Jordan and Richardson 1908: 644; Weber and de Beaufort 1911: 288; Jordan and Hubbs 1925: 281 (in family Parabembradidae); Barnard 1927: 936; Chu and Yin 1963: 478; Washington et al. 1984: 441; Knapp 1986: 481; Imamura 1996: 194 (in the monotypic family Parabembridae).

Type species. *Bembras curtus* Temminck & Schlegel, 1843 by monotypy.

Diagnosis. Body cylindrical, head somewhat depressed. Dorsal surface of head with spines only, tubercles absent. Ctenoid scales covering nape, postorbital, cheek, and opercular regions. Lower jaw projecting beyond upper jaw; dermal flap on posterior margin of maxillary. Two dorsal fins; first dorsal fin with 9 (rarely 8) to 11 spines; second dorsal fin with one spine and 8 or 9 soft rays. Anal fin with three robust spines and 5 soft rays. Pectoral fin without free rays. Pelvic fin with one spine and 5 soft rays, inserted below base of pectoral fin. Pored lateral line scales 34–44.

Remarks. Imamura (1996) diagnosed the then monotypic family Parabembridae on the basis of dissection of a single species, *Parabembras curtus*. Because of the rarity of the other species, we could not confirm the status of internal diagnostic characters given by Imamura (1996). Although Nelson et al. (2016) placed *Parabembras* under family Bembridae with *Bembradium* Gilbert, 1905: the former is clearly distinguishable from the latter in having three anal-fin spines (vs. anal-fin spines absent). In the phylogenetic analysis, Imamura (2004) recovered a sister relationship between *Bembradium* and *Plectrogenium* Gilbert, 1905, forming the family Plectrogeniidae.

Parabembras curta (Temminck & Schlegel, 1843)

Figs 1A, 2A

Bembras curtus Temminck & Schlegel, 1843: 42, pl. 16 (fig. 6–7), Nagasaki, Japan; Richardson 1846: 217, listed, Japan; Bleeker 1853: 11, listed, Japan; Bleeker 1855: 16, listed, Japan; Bleeker 1860: 49, listed, Japan; Günther 1860: 191, Sea of Japan; Boeseman 1947: 51, Nagasaki, Japan.

Parabembras curtus: Bleeker 1874: 370, new combination; Bleeker 1879: 12, listed, Japan; Jordan and Richardson 1908: 644, Kyushu, Japan (after Temminck and Schlegel, 1843); Weber and de Beaufort 1911: listed, 288; Jordan and Metz 1913: 54, listed, Busan, Korea; Jordan and Hubbs 1925: 281, Osaka, Japan; Reeves 1927: 12, listed, northeastern China and Korea; Liang 1951: 30, listed, Keelung, Taiwan; Kamohara 1952: 70, Tosa (= Kochi), Japan; Li 1955: 258, fig. 162, Yantai and Qingdao, Shandong, China; Nishibori 1959: 342, description of carotenoids; Chu and Jin 1963: 478, fig. 364, Zhejiang, East China Sea; Kamohara 1964: 77, listed, Tosa (=Kochi), Japan; Takegawa and Morino 1970: 386, listed, Wakasa Bay, Sea of Japan; Ochiai 1984: 321, pl. 288-A, in part, Pacific coast of Japan; Lindberg and Krasyukova 1987: 160, fig. 98 [after Temminck and Schlegel (1843)], Busan, Korea and East China Sea; Jean and Kuo 1988: 55, listed, northern Taiwan; Shen 1993: 260, pl. 66 (fig. 10), Taiwan; Suzuki and Kataoka 1997: 223, pl. 661, Owase, Mie, Japan; Randall and Lim 2000: 606, listed; Jin 2006: 490, fig. 233, Yellow Sea, Bohai Sea, northern Taiwan; Shao et al. 2008: 247, listed, Pintong, southern Taiwan; Shen and Wu 2011: 346, photo, Taiwan; Nakabo and Kai 2013: 718, 1950, key, Wakasa Bay and Kumano-nada, Japan southward to East China Sea; Shinohara et al. 2014: 247, listed, Sea of Japan; Yamamoto and Nagasawa 2015: 435, listed, East China and Yellow Seas.

Parabembras curta: Nakabo 2000: 614, Key, in part, Pacific coast of Japan; Shinohara et al., 2001: 318, listed, Tosa Bay; Nakabo 2002: 614 Key, in part, Pacific coast of Japan; Shinohara et al. 2005: 428, listed, Ryukyu Islands.

Bembradium roseum (not of Gilbert 1905): Shen and Wu 2011: 345, photo, Taiwan.

Material examined. FAKU 12176, 12280, 12371, 14289, 41439, 41441, 41443, 41445–41447, 106.0–193.1 mm SL (10 specimens), East China Sea, coll. Matsui and Takai, 20 Oct. 1949; FAKU 34911, 145.5 mm SL (1), Yawatahama, Ehime, Japan, Kishida, Mar. 1962; FAKU 35093, 114.8 mm SL (1), Tosa Bay, Kochi, Japan,. K. Amaoka, Mar. 1962; FAKU 37892, 37893, 37897, 143.9–154.1 mm SL (3), Shimonoseki, Yamaguchi, Japan, N. Taniguchi, 10 Jun. 1965; FAKU 99918, 99919, 123.3–148.2 mm SL (2), Kii Ohshima, Wakayama, Japan; FAKU 101901, 123.3 mm SL (1), Tsushima, Nagasaki, Japan, 31 Jul. 1973; FAKU 144461, 144462, 94.8–135.4 mm SL, Dong-gang, Pingtung, Taiwan, F. Tashiro and M. Y. Lee; NMMBA 2820, 86.7 mm SL, Kaohsiung, Taiwan; NMMBA 8359, 87.9 mm SL, Dong-gang, Pingtung, Taiwan, 17 Mar. 2005; NMMBA 20313, 117.3 mm SL, Dong-gang, Pingtung, Taiwan, 25 May 2013.

Diagnosis. *Parabembras curta* is distinguished from *P. robinsoni* in the absence of a symphyseal knob on the lower jaw (vs. distinct symphyseal knob in *P. robinsoni*), presence of a single preocular spine (vs. two preocular spines), and presence of two robust lachrymal spines (vs. a single robust lachrymal spine). It is further distinguished from *P. multisquamata*, in having 6–8 supraocular spines (vs. 9–11 supraocular spines in *P. multisquamata*); nine (rarely eight) spines in the first dorsal fin (vs. 10 spines); 34–39 pored lateral-line scales (vs. 40–44 pored lateral line scales).

Figure 1. Lateral view of the three species of *Parabembras*; **A** *P. curta*, FAKU 41447, 143.5 mm SL **B** *P. robinsoni*, NSMT-P 129791, 165.1 mm SL **C** *P. multisquamata*, holotype, MNHN-IC-2008-1516, 167.3 mm SL. White line indicates anus.

Description. Measurements are shown in Table 1. Body cylindrical, posteriorly weakly compressed, completely covered with ctenoid scales. Nasal spine simple, dorsoposteriorly directed. Anterior lachrymal with single robust spine, posterolaterally directed, in some specimens with small additional spine anteriorly; posterior lachrymal with sharp spine, posteroventrally directed. Single preocular spine present. Interorbital region narrow and weekly depressed, with 6–8 supraocular spines. Single postocular spine present, slightly larger than posteriormost supraocular spine. Suborbital ridge strongly or moderately developed, with three robust spines; tip of anteriormost spine below center of eye, second below posterior margin of eye, posteriormost below pterotic spine. Parietal spine robust and sharp, posteriorly directed. Three nuchal spines, one each on supratemporal, posttemporal, and supracleithrum, respectively; posttemporal in some specimens with additional spine. Pterotic with single sharp posteriorly directed spine. Preopercle with single robust posteriorly directed spine, in some specimens with supplementary spine; ventral margin of preopercle smooth. Opercle with upper and lower spines, directed slightly dorsoposteriorly and ventroposteriorly, respectively. Dermal flaps on head absent, except for flap on anterior nostril. Gill rakers blunt, usually four (in some specimens five) on upper limb; 11–13 (modally 12) on lower limb, including single (longest) raker at angle. Lateral line running parallel to dorsal contour of body, extending beyond caudal-fin base; 34–39 (modally 36) pored lateral line scales on body and 2–3 on caudal fin, each with single, robust tube.

Table 1. Counts and measurements of three species of *Parabembras*.

	Parabembras curtus		***P. robinsoni***		***P. multisquamus***		
	***n*=23**		***n*=9**		**Holotype**	**Paratypes (*n*=3)**	
	Range	**Mean**	**Range**	**Mean**		**Range**	**Mean**
Standard length (SL in mm)					167.3	146.4–186.9	
in % SL							
Head length	40.0–43.8	41.6	37.7–43.9	41.6	40.6	40.3–42.2	41.2
Snout length	9.7–11.0	10.4	10.4–12.4	11.2	10.6	10.1–10.7	10.4
Orbit diameter	11.3–14.2	12.5	11.7–14.1	12.6	12.0	12.3–13.9	13.0
Body depth 1	16.0–20.6	18.2	14.7–18.6	17.1	16.9	17.9–19.8	18.7
Body depth 2	15.2–18.1	16.6	13.6–16.2	14.8	16.1	16.5–17.4	17.0
Body width	15.9–19.6	17.8	13.9–18.8	16.2	15.1	14.6–16.8	15.8
Caudal peduncle depth	8.3–10.1	9.1	7.6–8.9	8.1	9.6	9.6–10.4	10.0
Upper jaw length	13.9–15.9	15.1	15.8–18.3	16.6	15.2	15.7–16.5	16.0
Predorsal fin length 1	37.8–41.2	39.3	37.4–41.3	39.2	40.3	38.1–40.9	39.6
Predorsal fin length 2	64.9–67.8	66.4	65.4–69.4	67.2	65.9	63.7–66.7	65.2
Preanal fin length	66.9–71.7	69.0	64.7–66.3	65.4	65.3	66.0–68.5	66.9
Preanal length	61.0–65.5	63.3	56.6–60.1	58.5	58.2	60.1–62.0	60.9
Prepelvic length	34.5–39.8	37.5	36.5–39.1	37.5	37.2	37.5–40.3	39.2
Pectoral fin length	22.5–28.4	26.3	22.6–27.3	25.4	26.4	24.2–28.5	26.6
Prepectoral fin length	36.9–40.9	38.4	38.8–42.2	40.0	38.9	38.9–39.6	39.3
Pelvic fin length	16.7–19.8	18.5	16.3–18.8	17.5	16.3	16.0–19.4	17.2
Pelvic fin spine length	9.5–14.0	11.5	9.6–11.5	10.5	10.6	10.2–13.0	11.5
Lengths of first dorsal fin							
1st dorsal-fin spine	2.4–3.9	2.9	1.7–4.4	2.7	2.6	2.1–3.0	2.6
2nd dorsal-fin spine	4.4–7.9	6.3	4.5–8.3	6.1	6.5	5.4–7.4	6.4
3rd dorsal-fin spine	10.0–14.0	11.8	8.3–12.3	10.2	11.1	10.6–11.3	11.0
4th dorsal-fin spine	14.4–20.6	16.5	11.6–15.3	14.0	14.6	14.7–14.7	14.7
5th dorsal-fin spine	15.0–20.9	17.7	12.5–15.8	14.1	14.8	13.7–15.1	14.4
Lengths of second dorsal fin							
1st dorsal-fin spine	13.3–17.3	15.2	10.6–14.1	12.2	11.1	10.4–12.5	11.3
1st dorsal-fin ray	15.4–18.1	16.6	13.1–15.9	15.0	15.7	14.9–16.7	16.0
1st anal-fin spine	4.0–7.1	5.6	3.4–5.1	4.1	5.1	5.2–5.7	5.5
2nd anal-fin spine	7.8–14.8	11.3	8.9–11.2	10.1	11.9	10.6–13.1	12.0
3rd anal-fin spine	8.1–11.1	9.3	7.9–10.1	9.2	10.1	9.1–11.2	10.1
1st anal-fin ray	12.1–16.9	14.2	12.2–14.2	13.3	13.9	13.3–15.5	14.3
Counts		Mode		Mode			Mode
Dorsal fin	VIII–IX-I, 8	IX-I, 8	X–XI-I, 8–9	XI-I, 9	X-I, 8	IX–X-I, 8	X-I, 8
Anal fin	III, 5	III, 5	III, 5	III, 5	III, 5	III, 5	III, 5
Pectoral fin	20–22	21	19–21	20	19	19–20	20
Pored lateral line scales	34–39	36, 37	38–41	40	44	40–44	43
Gill rakers	4–5+11–13	4+12	4–5+14–16	5+15	5+14	4–5+12	5+12

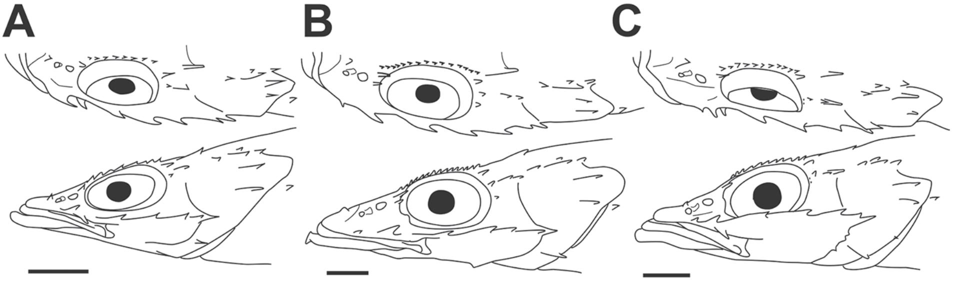

Figure 2. Lateral and dorsal views of the head of the three species of *Parabembras*; **A** *P. curta*, FAKU 41447, 143.5 mm SL **B** *P. robinsoni*, NSMT-P 129791, 165.1 mm SL **C** *P. multisquamata*, holotype, MNHN-IC-2008-1516, 167.3 mm SL. Bars equal to 10 mm.

Mouth large, slightly oblique; maxilla reaching anterior rim of pupil; posterior margin of maxilla with distinct notch. Upper half of maxilla fitting within groove below suborbital ridge. Symphyseal knob absent from lower jaw. Upper and lower jaws with villiform teeth arranged in a band; vomer V-shaped, with villiform teeth; tooth band on palatine narrow.

First dorsal fin originating above level of pectoral-fin base, with usually nine spines (rarely eight), gradually increasing in length to fifth spine. First and second dorsal fins well separated. Second dorsal fin with one spine and eight soft rays; first soft ray somewhat longer than spine. Second dorsal and anal fins opposite each other, nearly equal in length and height; origin of latter slightly posterior to that of former. Caudal fin rounded. Pectoral fin rounded, upper half somewhat longer than lower half; its tip not reaching to level of anus, usually with 20–22 rays (modally 21), the lower 3–8 rays unbranched.

Coloration. In fresh condition, head and body reddish orange, white ventrally; faint dark red saddle below first and second dorsal fins, respectively; fins red, interradial membranes pale red; posterior half of caudal fin dark red. In preserved specimens, head and body pale brown; fins pale gray without any markings.

Geographical distribution. Known from the western Pacific Ocean; Wakasa Bay of Sea of Japan and Kumano-nada, Pacific coast of Japan and Korea south to China and Taiwan (East China Sea, Yellow Sea, Bohai, and northern part of South China Sea) (Fig. 3). Benthic, on sandy mud substrate from depths of 60–141 m (Chu and Jin, 1963; Nakabo and Kai, 2013; present study).

Remarks. *Parabembras curta* was originally described as a member of *Bembras* by Temminck and Schlegel (1843) on the basis of the specimens collected in Japan 1823–1834 by Philipp von. Siebold and Heinrich Bürger. Boeseman (1947) reviewed the Siebold and Bürger's collection, and designated RMNH-D 682 as the lectotype and RMNH-D 2057 as paralectotype of the species. According to Boeseman (1947), the lectotype has nine spines in the first dorsal fin and the paralectotype has eight spines. The figure of the species given in the original description is characterized as having

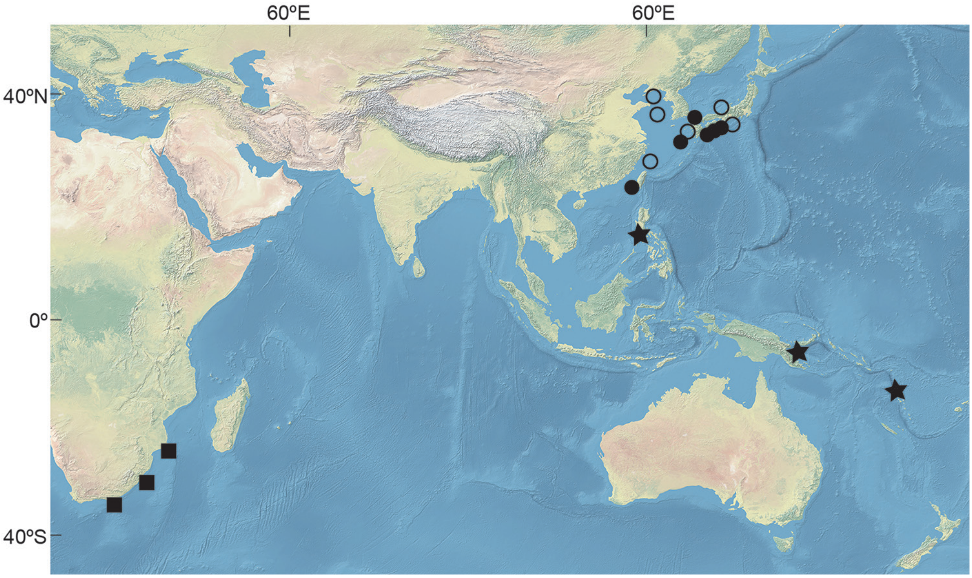

Figure 3. Distribution of the three species of *Parabembras* in the Indo-West Pacific. Circles, *P. curta*; squares, *P. robinsoni*; stars, *P. multisquamata.* Closed symbols - based on specimens examined in this study; open symbols - based on literature records. Map was made with layers from Natural Earth, free vector and raster map data at: http://naturalearthdata.com.

eight spines in first dorsal fin, one spine and eight rays in the second dorsal fin, a single preocular spine, seven supraorbital spines, and two robust lacrimal spines. The photo of RMNH-D 682 published by Yamaguchi and Machida (2003) indicates clearly the absence of a symphyseal knob on the lower jaw.

The short description of *P. curta* given by Günther (1860) agrees with the present specimens in the nine spines in the first dorsal fin. Jordan and Hubbs (1925), who established the family Parabembridae (originally as Parabembradidae), described *P. curta* as having nine spines in the first dorsal fin and two spines and seven rays in the second dorsal fin. Although the count of spines in the second dorsal fin is not usual for any three species recognized here, the counts of pored lateral line scales (37), gill rakers on lower limb (11) and supraocular spines (6) agreed well with the present specimens of *P. curta*. The descriptions of *P. curta* from the East China Sea given by Li (1955), Chu and Jin (1963) and Jin (2006) and that from Kochi, Japan by Kamohara (1952) are referable to the species identified here with reference to the counts of dorsal-fin spine (9) and lateral line scales (35–40). Lindberg and Krasyukova (1987) recorded *P. curta* on the basis of four specimens from Busan (Korea) and the East China Sea. They characterized the species as having nine spines in the first dorsal fin and 36–38 lateral line scales, which agrees with counts in the present specimens of *P. curta*. Suzuki and Kataoka (1997) characterized *P. curta* from Mie Prefecture, Japan as having 10 spines in the first dorsal fin. Although the count of dorsal–fin spines was rather similar to *Parabembras multisquamata* described below, the pectoral fin of their specimen does not reach to anus, matching the condition of the present specimens of *P. curta*. In addition, the established distributional range of *P. curta* is close to the locality of Suzuki and Kataoka's (1997) specimen. The short description of *P. curta* given by Ochiai (1984) apparently includes several species recognized here, because he assumed that *P. curta* was widely distributed in the Indo-West Pacific, and also presented a wide range in the count of dorsal-fin rays (IX–X-I, 7–9) (which apparently also includes *P. multisquamata* and *P. robinsoni*). The photograph provided by Ochiai (1984) agrees with the present specimens of *P. curta* in the short pectoral fin (not reaching to the anus) and absence of a symphyseal knob. The description of Shen (1993) apparently followed that of Ochiai (1984), but the photograph provided by him is referable to *P. curtus* recognized by the short pectoral fin (not reaching to the anus) and absence of a symphyseal knob. The keys and short descriptions of *P. curtus* presented by Nakabo (2000; 2002) also apparently followed Ochiai (1984). The images of *P. curta* and *Bembradium roseum* Gilbert, 1905 published by Shen and Wu (2011) are here both identified as *P. curta* in having nine spines in the first dorsal fin and three spines in the anal fin. However, their description of *B. roseum* does not agree with the specimen shown in their photograph which has 11 anal-fin rays.

The record of *P. curta* from the eastern Indian Ocean by Lin (1974: 26, western Indonesia) cannot be verified; specimens from these regions are needed to establish their identity. Although Krakstad et al. (2014: 74, 75) listed *P. curtus* from Myanmar, this record is not based on a species of *Parabembras*, but of *Bembras* (Peter Psomadakis, pers. comm.).

***Parabembras robinsoni* Regan, 1921**

Figs 1B, 2B

Parabembras robinsoni Regan, 1921: 418, KwaZulu-Natal, South Africa; Barnard 1927: 936; Smith 1949: 377, pl. 97, off Natal, South Africa; Smith 1961: 377, pl. 97, off Natal, South Africa; Smith 1965: 377, pl. 97, off Natal, South Africa; Knapp 1986: 482, pl. 29, fig. 154.1, Durban to southern Mozambique, South Africa; Schneider et al. 2005: 218, listed, Mozambique.

Parabembras curtus (not of Temminck and Schlegel 1843): Gilchrist 1922: 75, South Africa; Ochiai 1976: 105, pl. E. Afr-97, east coast of South Africa.

Parabembras sp.: Everett et al. 2015: 89, listed, Kenya, Tanzania, Mozambique.

Material examined. BMNH 1921.3.1.19 (holotype of *P. robinsoni*, photo only), 24–35 km off Umvoti River, KwaZulu-Natal, South Africa [ca. 29°32'S, 31°36'E], depth 120–130 fathoms [219–238 m], R. Robinson, 1921; MCZ 130275, 127.0 mm SL (1), off Mozambique, 25°26'S, 34°19'E, 356 m depth, RS Algoa-014, 21 June 1994 (3D CTs only); NSMT-P 129786–129792, 126.7–176.1 mm SL (9 specimens), east coast of South Africa, 25°21'S, 34°20.5'E 326 m depth, 6 Dec. 1970.

Diagnosis. *Parabembras robinsoni* is distinguished from its congeners in having usually 11 spines in the first dorsal fin (vs. 8–9 in *P. curta* and 9–10 in *P. multisqua-*

mata), a distinct symphyseal knob in the lower jaw (vs. symphyseal knob absent in *P. curta* and *P. multisquamata*), two preocular spines (vs. single in *P. curta* and *P. multisquamata*), and single lachrymal spine (two in *P. curta* and *P. multisquamata*).

Description. Measurements are shown in Table 1. Body cylindrical, posteriorly moderately compressed, completely covered with ctenoid scales. Anterior lachrymal with single robust spine, posterolaterally directed, in some specimens with small additional spine anteriorly; posterior lachrymal without spine. Two preocular spines present. Interorbital region narrow and slightly depressed, with more than 12 small spines, forming a serrated ridge. Single small postocular spine present. Suborbital ridge strongly or moderately developed, with three robust spines, tip of anteriormost spine below center of eye, second below posterior margin of eye; posteriormost below pterotic spine. Parietal spine sharp, posteriorly directed. Three nuchal spines, one each on supratemporal, posttemporal, and supracleithrum, respectively; posttemporal sometimes with additional spine. Pterotic with two sharp spines posteriorly directed. Posterior rim of orbit armed with small spines. Preopercle with single robust spine, posteriorly directed; usually with supplementary spine; ventral margin of preopercle smooth. Opercle with upper and lower spines, slightly directed dorsoposteriorly and posteriorly, respectively. Dermal flaps on head absent, except for flap on anterior nostril. Gill rakers blunt, usually 4–5 on upper limb; 14–16 (modally 15) on lower limb, including single (longest) raker at angle. Lateral line running parallel to dorsal contour of body, extending beyond caudal-fin base; 38–41 (modally 39) pored lateral-line scales on body and 2–3 on caudal fin, each with single, robust tube.

Mouth large, slightly oblique; maxilla reaching level of anterior rim of pupil; posterior margin of maxilla weakly notched. Upper half of maxilla fitting within groove below suborbital ridge. Lower jaw with distinct symphyseal knob. Upper and lower jaws with villiform teeth in a band; vomer V-shaped with villiform teeth; tooth band on palatine narrow.

First dorsal fin originating above level of pectoral-fin base, usually with eleven spines (in some specimens ten), gradually increasing in length to fifth spine. Last spine of first dorsal fin separated from penultimate spine without membrane, positioned midway between penultimate spine of first dorsal fin and insertion of second dorsal fin. Second dorsal fin with one spine and 8–9 soft rays; first soft ray slightly longer than spine. Second dorsal and anal fins directly opposite each other, nearly equal in length and height. Caudal fin rounded. Pectoral fin usually with 19–21 rays (modally 20), lower 4–7 rays unbranched; its rounded upper half somewhat longer than lower half, slightly extending beyond level of anus.

Coloration. In fresh condition, head and body reddish orange, white ventrally; fins red, interradial membranes pale red; distal margins of dorsal and anal fins dark red; posterior half of caudal fin dark red [based on pl. E. Afr-97 of Ochiai (1976)]. In preserved condition, head and body dark brown; fins pale gray; distal margin of second dorsal, anal and caudal fins dark brown.

Geographical distribution. Western Indian Ocean, from Durban to at least southern Mozambique, along the east coast of South Africa at depths of 200–600 m (Knapp 1986). According to Everett et al. (2015), the species may be distributed along the East African coast north to Kenya; however, these records need confirmation.

Remarks. *Parabembras robinsoni* was originally described by Regan (1921), characterized as having 10 spines in the first and one spine and nine soft-rays in the second dorsal fin. However, the last spine of the first dorsal fin, which is positioned between the penultimate ray of the first dorsal fin and the insertion of the second dorsal fin, is present in the holotype (BMNH 1921.3.1.19), which has eleven dorsal-fin spines, a distinct symphyseal knob in the lower jaw and a single lachrymal spine; hence, the present specimens are identified as *P. robinsoni*.

Barnard (1927) and Smith (1949, 1961, 1985) reported *P. robinsoni* from off the coast of KwaZulu-Natal, South Africa as having ten or eleven spines in the first dorsal fin. The short description by Knapp (1986) also characterized *P. robinsoni* as having ten or eleven spines in the first dorsal fin and a symphyseal knob in the lower jaw. These characters agree well with the present specimens of *P. robinsoni*. In contrast, Gilchrist (1922) described *P. curta* from South Africa and considered *P. robinsoni* as a junior synonym of *P. curta*. However, he described the species as having two preocular spines, agreeing with the present specimens of *P. robinsoni*, but not with *P. curta*. Similarly, Ochiai (1976) described *P. curta* from the east coast of South Africa. His photograph clearly shows *P. robinsoni*, judging by the presence of a distinct symphyseal knob in the lower jaw. Ochiai assumed that *P. curta* was widely distributed in the Indo-West Pacific, but apparently he confused *P. curta* and *P. robinsoni*. Probably due to this report, some subsequent authors mistakenly reported an occurrence of *P. curta* in the Indian Ocean (e.g., Nakabo 2000, 2002; Yamada et al. 2007).

***Parabembras multisquamata* sp. n.**

http://zoobank.org/9342A016-DC81-4F49-A88E-FA17F64D42B3

Figs 1C, 2C

Parabembras curtus (not of Temminck and Schlegel 1843): Fricke 2015, 4, fig. 8, Morobe Province, Papua New Guinea.

Holotype. MNHN-IC-2008-1516, 167.3 mm SL, 15°4'12"S, 166°57'0"E, Big Bay, Espiritu Santo, Vanuatu, 408–444 m depth, R/V Alis, expedition name: SANTO 2006, Station: AT106, 15 Oct. 2006.

Paratypes. Four specimens. MNHN-IC-1984-0687, 170.1 mm SL, 13°49'1.2"N, 120°51'0"E, off southwestern Luzon, Philippines, 299–320 m depth, expedition name: MUSORSTOM 2; Station: 26cp4, 23 Nov. 1980; MNHN-IC-2008-2443, 2009-0115, 158.3–186.9 mm SL, 15°4'21"S, 166°51'46.8"E, Big Bay, Espiritu Santo, Vanuatu, 350–400 m depth, R/V Alis, expedition name: BOA1; Station: CP2416, 6 Sep. 2005; NTUM 10690, 146.4 mm SL, Papua New Guinea, Morobe Province, 28 km east of Lae, 06°45'03.90"S, 147°14'40.44"E – 06°45'18.24"S, 147°14'03.26"E, 360 m depth, R/V Alis, expedition name: PAPUA NIUGINI; Station: CP3999, 10 Dec. 2012.

Diagnosis. *Parabembras multisquamata* is distinguished from *P. robinsoni* in having two lachrymal spines and no symphyseal knob on the lower jaw. It is most similar to *P. curta*, but is clearly distinguished from the latter in having usually 10 first dorsal-fin spines (vs. 8 or 9 spines in *P. curta*), 9–11 supraocular spines (vs. 6–8 in *P. curta*), and 40–44 pored lateral line scales (vs. 34–39 in *P. curta*).

Description. Measurements are shown in Table 1. Data of the holotype are given first, followed by data of the paratypes, in parentheses, if different from holotype. Body cylindrical, posteriorly weakly compressed, completely covered with ctenoid scales. Nasal spine simple, dorsoposteriorly directed. Anterior lachrymal with single robust spine, posterolaterally directed, with small additional spine anteriorly (without an additional spine in MNHN-IC-1984-0687); posterior lachrymal with sharp spine, directing posteroventrally. Single preocular spine present. Interorbital region narrow and weekly depressed, armed with 11 (9–11) supraocular spines. Single postocular spine present, somewhat larger than posteriormost supraocular spine. Suborbital ridge strongly developed (moderately developed), with three (three or four) robust spines; tip of anteriormost spine below center of eye, second below posterior margin of eye, third below pterotic spine (posteriormost on margin of preopercle). Three nuchal spines; one each on supratemporal, posttemporal, and supracleithrum, respectively. Pterotic with two sharp spines posteriorly directed. Posterior rim of orbit armed with small spines. Preopercle with single robust and several small supplementary spines, posteriorly directed; ventral margin of preopercle with three (0–5) tiny spines. Opercle with upper and lower spines, slightly dorsoposteriorly and ventoposteriorly directed, respectively. Dermal flaps on head absent, except for flap on anterior nostril. Gill rakers blunt, usually 5 (4–5) on upper limb; 14 (12–13) on lower limb, including single (longest) raker at angle. Lateral line running parallel to dorsal contour of body, extending beyond caudal-fin base; 44 (40–44) pored lateral-line scales on body and 2 (2–3) on caudal fin, each with single, robust tube.

Mouth large, slightly oblique; maxilla reaching anterior rim of pupil; posterior margin of maxilla with distinct notch. Upper half of maxilla fitting within groove below suborbital ridge. Symphyseal knob absent from lower jaw. Upper and lower jaws with villiform teeth arranged in a band; vomer V-shaped, with villiform teeth; tooth band on palatine narrow.

First dorsal fin originating above level of pectoral-fin base, usually with 10 spines (nine in MNHN-IC-2009-0115), gradually increasing in length to fifth (forth or fifth) spine. First and second dorsal fins well separated. Second dorsal fin with one spine and 8 soft rays; first soft ray somewhat longer than spine. Second dorsal and anal fins opposite each other, nearly equal in length and height; anterior insertion of latter slightly posterior to that of former. Caudal fin rounded. Pectoral fin rounded, upper half somewhat longer than lower half; its tip extending beyond level of anus, with 19 rays (19–21) of which lower 7 (6–7) rays unbranched.

Coloration. In fresh specimens [based on fig. 8 in Fricke (2015), NTUM 10690], head and body red, white ventrally; first dorsal fin dark red margined with black; second dorsal fin red with black marking; posterior half of caudal fin dark red; pectoral fin bright red; pelvic fin pale red. In preserved condition, head and body pale brown; first dorsal fin margined with black; second dorsal fin with dark brown marking.

Geographical distribution. Known from the western Pacific Ocean, off southwestern Luzon, Philippines, Morobe Province of Papua New Guinea, and Espiritu Santo, Vanuatu. The new species was collected at depths of 299–444 m (Fig. 3).

Etymology. The name *multisquamata* is derived from Latin *multus* meaning many and *squamatus* meaning scaled, in reference to the high number of pored lateral line scales. The name is an adjective, its ending following the feminine gender of the generic name *Parabembras*.

Remarks. Fricke (2015) reported *P. multisquamata* as *P. curtus* (non Temminck and Schlegel 1843) from Morobe Province of Papua New Guinea on the basis of a single specimen, NTUM 10690, which is now one of the paratypes of *P. multisquamata*. Judging from the collection data, the record of *P. curta* from off southwestern Luzon, Philippines by Fourmanoir (1985: 46, as *P. curtus*) was based on MNHN-IC-1984-0687, one of the paratypes of *P. multisquamata*.

Key to species of *Parabembras*

1 Lower jaw with a distinct symphyseal knob; lachrymal with single robust spine [western Indian Ocean] .... ***Parabembras robinsoni***
– Lower jaw without a symphyseal knob; lachrymal with 2 robust spines **2**
2 First dorsal fin usually with 10 (rarely 9) spines, head with 9–11 supraocular spines, pored lateral line scales 40–44, pectoral fin extending beyond the level of anus [southwestern Pacific Ocean and the Philippines] .... ***Parabembras multisquamata***
– First dorsal fin with 8 or 9 spines, head with 6–8 supraocular spines, pored lateral line scales 34–39, pectoral fin not reaching to the level of anus [northwestern Pacific Ocean] .... ***Parabembras curta***

Discussion

Parabembras multisquamata is most similar to *P. curta* in having two lachrymal spines and no symphyseal knob on the lower jaw, but is clearly distinguished as described above. These two species differ further in some morphometric characters, including the preanal length and the first spine of the second dorsal fin (Fig. 4). Furthermore, the pectoral fin of *P. multisquamata* extends beyond the level of the anus (vs. not reaching to the level of anus in *P. curta*). The PCA using 20 measurements (eight were eliminated due to the lack of data in some of the specimens) resulted in the rough separation of three species. The first and second principal components accounted for 34.4 % and 18.3 % of the variation. PC1 was heavily loaded on caudal peduncle depth, body depth 2, and length of second anal-fin spine, providing separation between *P. robinsoni* and the other two species (Fig. 5). PC2 was heavily loaded on length of second anal-fin

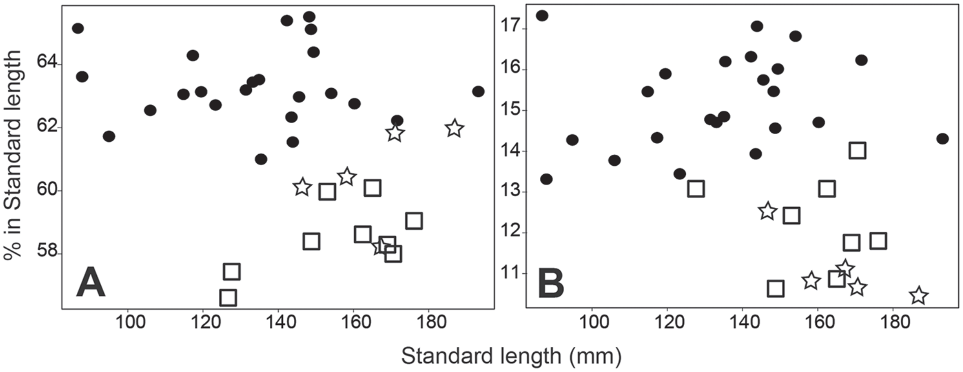

Figure 4. Comparison of selected morphometric characters of species of *Parabembras*; **A** proportion of pre-anal length **B** first spine of second dorsal fin. Circles, *P. curta*; squares, *P. robinsoni*; stars, *P. multisquamata.*

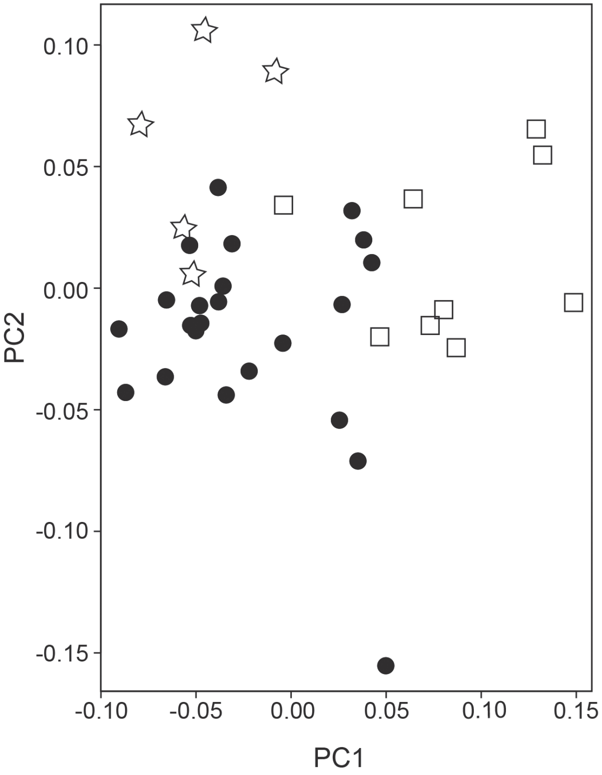

Figure 5. Plots of the first two principal components scores based on 20 body measurements of the three species of *Parabembras*. Circles, *P. curta*; squares, *P. robinsoni*; stars, *P. multisquamata*.

spine, body width, and body depth 1, providing separation between *P. multisquamata* and the other two species. These results also support the existence of three species in *Parabembras*. The distributional ranges of the three species are not overlapped, suggesting that they speciated allopatrically.

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RESEARCH ARTICLE

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A new species of sea urchin associating clingfish of the genus *Dellichthys* from New Zealand (Teleostei, Gobiesocidae)

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Abstract

A new species of clingfish, *Dellichthys trnskii* **sp. n.** is described on the basis of 27 specimens, 11.9–46.0 mm SL, collected from intertidal and shallow coastal waters of New Zealand. It is distinguished from its only congener, *D. morelandi* Briggs, 1955 by characters of the cephalic sensory system and oral jaws, snout shape, and colouration in life. A rediagnosis is provided for *D. morelandi*, which is shown to exhibit sexual dimorphism in snout shape.

Keywords

Taxonomy, marine fishes, Acanthomorpha, sexual dimorphism

Introduction

The family Gobiesocidae contains over 160 species within 50 genera of predominately small-bodied marine fishes found in coastal areas of the Atlantic and Indo-Pacific Oceans (Briggs 1955; Conway et al. 2015), from the intertidal zone to ~500 meters (Hastings and Conway 2017). Seven species also are known to inhabit freshwater streams in the Neotropics (Briggs and Miller 1960; Conway et al. 2017a). Commonly referred to as clingfishes, members of this family generally exhibit a well-developed ventral adhesive disc (formed by elements of the paired-fin girdles (Guitel 1888)), with which they can attach to smooth or even heavily structured substrates with great tenacity (Wainwright et al. 2013; Ditsche et al. 2014).

Many species of clingfishes are reported to live in close association with echinoderms (Pfaff 1942; Teytaud 1971). This relationship may be obligate, as in the association between clingfishes of the genus *Discotrema* and certain crinoids (Briggs 1976; Fishelson 1966, 1974), or more facultative and dependent on life stage (Sakashita 1992; Gonçalves et al. 2002). For example, juveniles of the New Zealand urchin clingfish *Dellichthys morelandi* live directly underneath or in close proximity to the echinoid *Evechinus chloroticus* (Dix 1969, 1970). This association provides juveniles of *D. morelandi* with both protection from predators and also food, as confirmed by the presence of tube feet and/or pedicellaria in the stomachs of individuals dissected for diet analyses (Dix 1969; Russell 1983). Individuals of *D. morelandi* that have become too large to seek refuge beneath the spines of *E. chloroticus* instead occupy crevices between or under rocks or among shell debris (Paulin and Roberts 1992; Francis 2012).

Recent ichthyological surveys targeting clingfishes in intertidal and shallow subtidal areas along the coast of Northland (New Zealand) produced multiple individuals of *Dellichthys* from directly beneath or in close proximity to the sea urchin *E. chloroticus*. Subsequent investigation revealed that these specimens represent two species; one *D. morelandi* and the other an undescribed species, which is described herein.

Materials and methods

Specimens used in this study were obtained from the following museum collections: Australian Museum, Sydney (**AMS**); Auckland War Memorial Museum, Auckland (**AIM**); Museum of New Zealand Te Papa Tongarewa, Wellington (**NMNZ**); and the Biodiversity Research and Teaching Collections, Texas A&M University, College Station (**TCWC**).

Head and body measurements reported follow Conway et al. (2014) and are expressed as percent of standard length (**SL**) or head length (**HL**). Adhesive disc papillae terminology follows Briggs (1955). Cephalic superficial neuromast row terminology follows Conway et al. (2017b) and cephalic lateral line pore terminology follows Shiogaki and Dotsu (1983), except that we also use numbers to refer to individual pores following Conway et al. (2017b).

Select specimens were cleared and double stained (**C&S**) for bone and cartilage investigation using the protocol of Taylor and Van Dyke (1985). Select specimens were reversibly stained using cyanine blue following Saruwatari et al. (1997) to aid examination of adhesive disc papillae. Specimens or parts thereof were observed and photographed using a ZEISS SteREO Discovery V20 stereomicroscope equipped with a ZEISS Axiocam MRc5 digital camera. Digital images taken with this set up were typically stacked using the ZEISS Axiovision software. Computed tomography (**CT**) scans of select specimens were also obtained at the Karel F. Liem BioImaging Center (Friday Harbor Laboratories, University of Washington) using a Bruker (Billerica, MA) SkyScan 1173 scanner with a 1 mm aluminum filter at 60 kV and 110 µA on a 2048 × 2048 pixel CCD at a resolution of 8.8 µm. Specimens were scanned simultaneously while inside a 50 ml plastic Falcon tube (Corning, NY), in which they were wrapped with cheesecloth moistened with ethanol (70 %) to prevent movement during scanning. The resulting CT data were visualized, segmented, and rendered in Horos (http://www.horosproject.org) and Amira (FEI). All digital images were processed using Adobe Photoshop and Adobe Illustrator.

Genomic DNA was extracted from muscle tissue or fin clips (stored in 95% ETOH) using a DNeasy Blood and Tissue Extraction Kit (Qiagen, Inc.) in accordance with the manufacturer's protocols. A segment of the cytochrome c oxidase subunit I (COI) and the 12s ribosomal RNA (12S) was amplified using the primers LCO1490/ HC02198 (Folmer et al. 1994) and L1091/H1478 (Kocher et al. 1989), respectively. Parameters for PCR amplification followed Conway et al. (2017a). Genetic distances (uncorrected *p*-distances) were calculated based on COI and 12S sequences using PAUP v.4.0b10 (Swofford 2000).

Systematics

Dellichthys trnskii sp. n.

http://zoobank.org/1D5D5875-116E-4F15-9E65-322BE259F2DA
Figs 1, 2A, 3, 4A, 5A, 6, 7A–B, 8A–C
New English Name: Trnski's Clingfish

Holotype. AIM MA73570, 22.8 mm SL, New Zealand, Northland, Tutukaka, Pacific Bay, 35°37'07.2"S, 174°32'03.8"E, 0–2 meters depth, 8 March 2016, T. Trnski, I. Middleton, K.W. Conway, S. Hannam, & G. Short.

Paratypes. All New Zealand. *Auckland:* **NMNZ P.028060**, 4 (1 CT [https://doi.org/10.17602/M2/M40584]), 20.1–29.7 mm SL; **NMNZ P.060626**, 2 (C&S), 21.0–25.0; Hauraki Gulf, Matatuahu Point, Tawharanui Peninsula, 0–5 meters depth (36°23'00.0"S, 174°49'00.0"E), 8 April 1992. *Bay of Plenty:* **NMNZ P.035572**, 1, 46.0 mm SL; Rurima Islets, 7–10 meters depth (37°49'47.0"S, 176°52'38.0"E), 02 June 1998. *Marlborough:* **NMNZ P.025671**, 2, 42.0–45.6 mm SL; **NMNZ P.060627**, 1 (C&S), 41.8 mm SL; Gorse Bay, Port Underwood (41°18'27.1"S, 174°09'39.7"E), 25 September 1989. *Hawke's Bay:* **NMNZ P.057592**, 1, 32.7 mm SL; Bare Island (39°49'54.0"S, 177°01'30.0"E), 09 December 1991. – **NMNZ P.057600**, 1, 43.3 mm SL; south of Aramoana, 0–3 meters depth (40°09'42.0"S, 176°50'18.0"E), 19 January 1991. *Northland:* **AIM MA4341**, 1, 45.8 mm SL, Poraenui Point, Bay of Islands (35°11'34"S, 174°4'8"E), 15 December 1983. – **AIM MA6395**, 1, 11.9 mm SL, Kerikeri Inlet, Bay of Islands, 7 meters depth (35°12'0.0"S, 174°02'43.0"E), 28 Jan 1972. – **AIM MA7070**, 1, 33.0 mm SL, Te Puna off Mataka, Bay of Islands (35°09'0.0"S, 174°06'12.0"E), 20 March 1988. – **AIM MA73571**, 2 (ethanol preserved DNA vouchers), 17.0–20.0 mm SL; **TCWC 17264.03**,

Figure 1. *Dellichthys trnskii*, AIM MA73570, holotype, male, 22.8 mm SL; New Zealand: Northland, Pacific Bay, Tutukaka Coast.

1 (C&S), 18.0 mm SL, same as holotype. – **AIM MA75372**, 1, 18.8 mm SL, Rawhiti, Taupiri Bay (35°16'58.4"S, 174°17'38.0"E), 10 March 2016. – **AIM MA73573**, 1, 21.3 mm SL, Bland Bay, 0–3 meters depth (35°20'47.8"S, 174°21'57.6"E), 11 March 2016. – **NMNZ P.057601**, 1, 31.3 mm SL; north side of the Matapouri Peninsula, 0–8 meters depth (35°33'15.0"S, 174°30'00.0"E), 09 April 1992. – **TCWC 17171.04**, 1 (ethanol preserved DNA voucher), 25.5 mm SL, Tutukaka, rocky bay between Tutukaka reserve and Kukutauwhao Island (35°36'40.7"S, 174°32'29.8"E), 1 March 2015. *Wellington:* **NMNZ P.048189**, 1, 45.0 mm SL; Wellington Port, overseas passenger terminal (41°17'19.6"S, 174°47'09.5"E), 23 November 2001. – **NMNZ P.048197**, 1, 37.0 mm SL; Wellington Port, Burnham Wharf (41°18'42.0"S 174°48'12.0"E), 20 November 2001.

Other material. AMS I.34453-005, 1, 20.0 mm SL; New Zealand: locality unknown.

Diagnosis. *Dellichthys trnskii* is diagnosed by the following combination of characters: snout broad, short (length less than or equal to interorbital distance); upper and lower jaws equal in length or lower jaw only slight shorter than the upper; upper jaw teeth not visible or only few teeth visible in gap between upper and lower lip at tip of jaws when jaws are closed; patch of teeth on lingual surface of premaxilla roughly rectangular, with ~50 small conical teeth; skin fold on surface of snout directly posterior to fold of upper lip; postorbital lateral line canal pore 2 located directly above

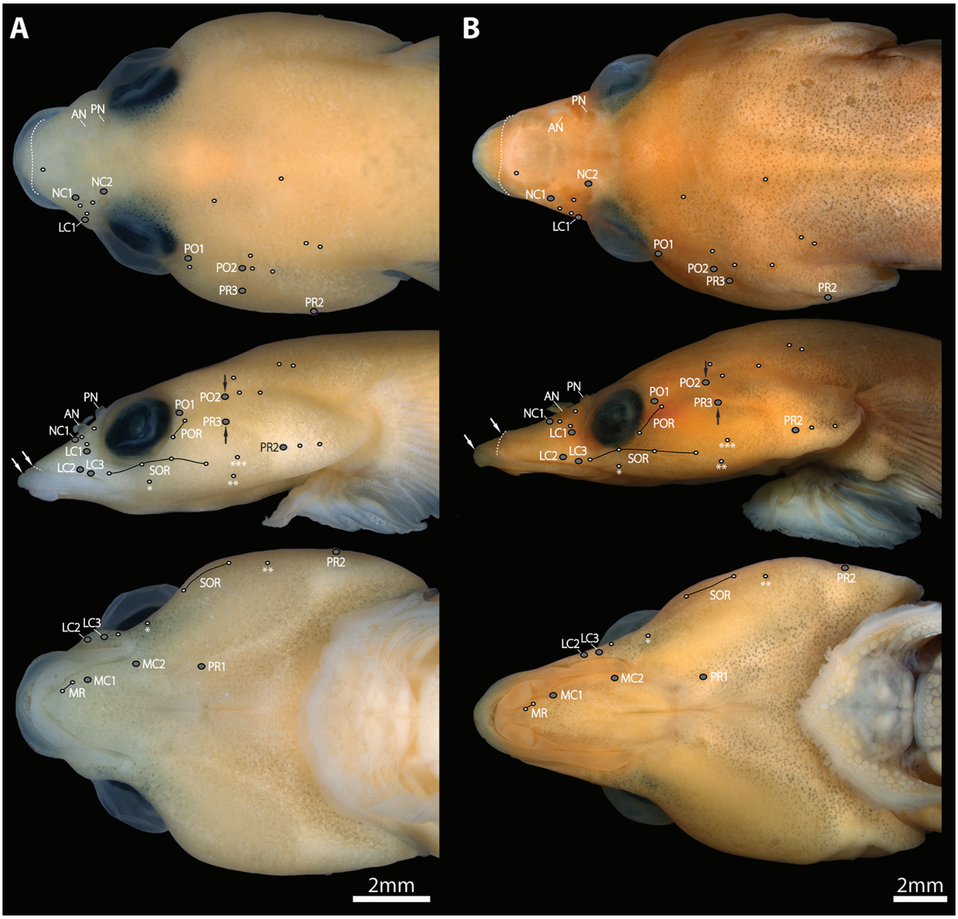

Figure 2. Head (in dorsal, lateral and ventral view) in members of *Dellichthys* highlighting position of cephalic lateral line canal pores (grey circles) and superficial neuromasts (white circles) on the left side of the head, and skin fold on snout. **A** *Dellichthys trnskii*, AIM MA73573, paratype, 21.3 mm SL **B** *Dellichthys morelandi*, TCWC 17264.02, 34.2 mm SL. Black arrows point to location of postorbital canal pore 2 (upper arrow) and preopercular canal pore 3 (lower arrow). White arrows point to location of posterior margin of upper lip (anterior arrow) and anterior margin of skin fold on snout (posterior arrow). White dashed line follows margin of skin fold on snout in dorsal and lateral view. Superficial neuromasts arranged in rows are connected by a thin black line. Superficial neuromasts on surface of body not highlighted. Abbreviations: AN, anterior nostril; LC1-3, lachrymal canal pores 1–3; MC1–3, mandibular canal pores 1–2; MG, mandibular row of superficial neuromasts; NC1–2, nasal canal pores 1–2; PN, posterior nostril; PO1–2, postorbital canal pores 1–2; POR, postorbital row of superficial neuromasts; PR1–3, preopercular canal pores 1–3; SOR, suborbital row of superficial neuromasts.

preopercular lateral line canal pore 3; tip of snout and lower jaw pale pink in life; dorsal and lateral surface of head light yellow to green in life; body pale orange to yellow in life; and median fins transparent and without faint brown reticulate markings in life.

Description. General body shape as in Figure 1. Morphometric characters listed in Table 1. Head large, slightly dorsoventrally compressed. Body moderately dorsoventrally

Table 1. Select morphometric characters for *Dellichthys trnskii* (n=7) and *D. morelandi* (n=12).

	Dellichthys trnskii				***Dellichthys morelandi***		
	Holotype	**Range**	**Mean**	**St. Dev.**	**Range**	**Mean**	**St. Dev.**
Standard Length (SL)	22.8	20.1–31.7			31.0–65.5		
In % of SL							
Head length (HL)	41.6	40.4–45.5	42.1	1.8	38.3–43.6	41	1.6
Body depth	15.3	14.2–16.4	15.2	0.8	12.3–15.5	13.7	1
Predorsal length	72.8	72.8–80.1	75.4	2.6	74.3–79.2	76.3	1.6
Preanal length	75.4	73.7–79.1	78.5	1.8	73.8–80.5	76.7	1.9
Preanus length	62.3	62.2–66.3	63.6	1.8	62.2–71.2	66.1	2.6
Anus to disc	8.8	8.8–12.6	10.4	1.3	11.2–15.2	13.1	1.3
Anus to anal fin	17.5	17.3–24.5	19.2	2.7	10.5–15.2	12.8	1.8
Caudal peduncle length	10.1	7.7–10.1	9.1	0.8	7.2–9.4	8.2	0.7
Caudal peduncle depth	10.1	9.7–11.8	10.5	0.7	8.4–10.3	9.4	0.5
Disc length	24.1	22.8–27.8	25.9	1.9	22.6–25.9	24.3	1
Disc width	24.5	22.0–25.9	23.8	1.3	20.4–23.5	21.9	1.1
In % of HL							
Head depth at orbit	31.6	25.2–31.6	28.5	2.1	21.3–24.6	23.4	1
Head width at orbit	45.3	36.1–45.3	40.6	3	32.5–39.3	35.3	2.3
Head width at widest point	68.4	58.5–68.4	62.7	4.2	51.1–65.3	55.9	4.3
Interorbital width	26.3	20.5–27.7	23.9	3.3	17.9–23.2	19.9	2
Snout length	28.4	23.9–28.8	26.7	1.8	25.6–33.7	31.2	2.3
Eye diameter	22.1	18.8–23.5	20.9	1.7	13.9–19.8	16.3	1.8

compressed anteriorly, becoming increasingly laterally compressed posteriorly at region of dorsal and anal fins. Widest point of head wider than widest point of body (immediately behind head). Body width tapering gradually posteriorly. Eye large, positioned on dorsolateral surface of head; orbit visible in ventral view. Centre of eye closer to tip of snout than to posterior margin of operculum. Snout short, broad; anterior margin rounded. Transverse skin groove present across dorsal surface of snout; skin anterior to groove thin and transparent (Fig. 2A). Anterior nostril a small tubular opening, with short, thin blade-like flap extending from posterior margin. Posterior nostril tubular, situated along anterdorsal margin of orbit. Gill membranes united and free from isthmus.

Mouth terminal, small; posterior tip of upper jaw reaching imaginary vertical line through anterior margin of orbit when mouth closed. Upper lip narrow; thickest along lateral margin of upper jaw; thinnest at snout tip. Lower lip thin at jaw symphysis; expanded into fleshy lobes adjacent to symphysis. Premaxilla with outer row of larger conical teeth with strongly recurved tips (Figs 3B, 4A, 5A) and medial, roughly rectangular patch of ~50 smaller conical teeth on lingual surface posterior to outer row of larger teeth (Fig. 5A). Dentary with broad patch of conical teeth with recurved tips anteriorly, tapering to single row of larger conical teeth posteriorly (Fig. 4A). Pharyngeal jaws comprising patch of 16–18 small conical teeth with slightly recurved tips on pharyngobranchial toothplate 3 and two rows of 5–8 small conical teeth with slightly recurved tips along

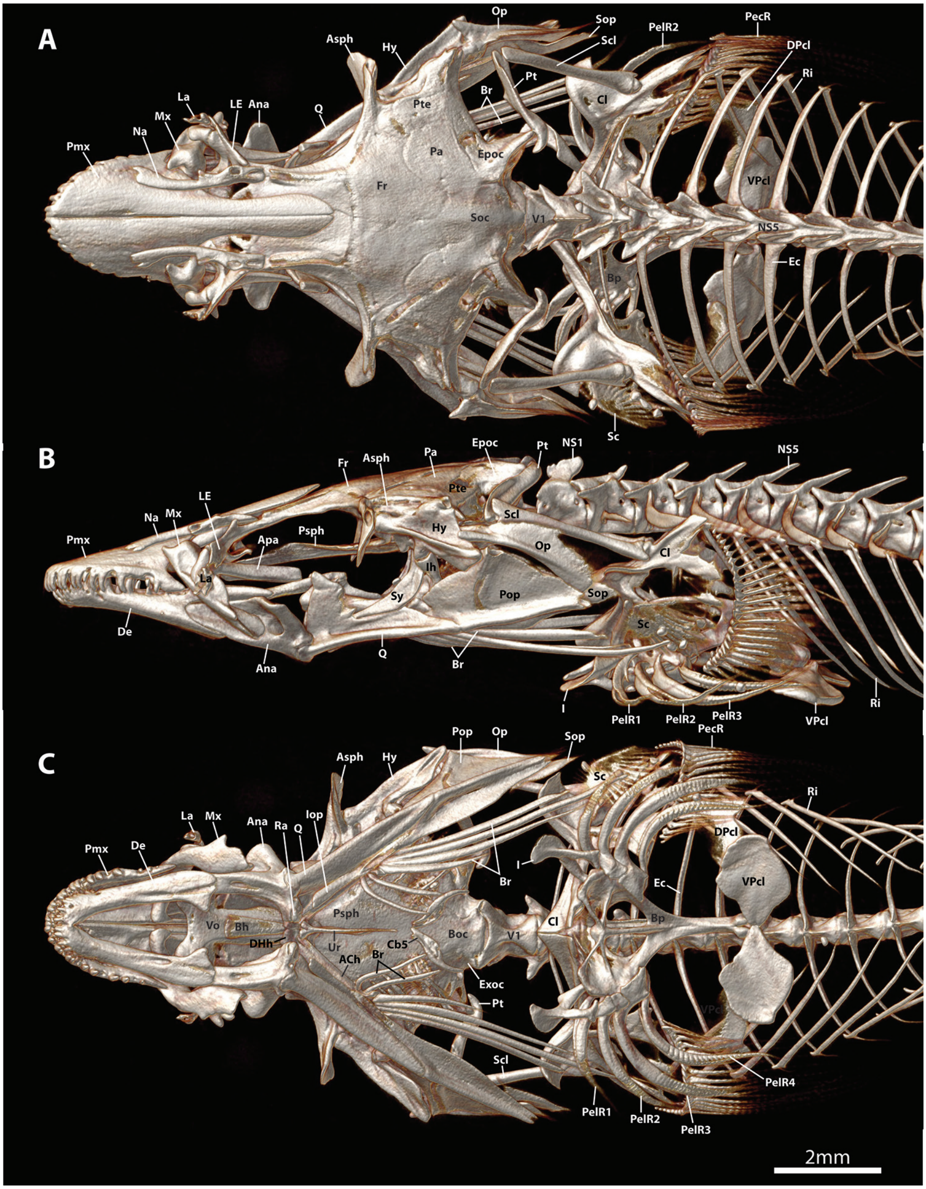

Figure 3. CT scanned anterior skeleton, including cranium, paired-fin girdles and abdominal region of vertebral column, of *Dellichthys trnskii*, NMNZ 028060, paratype, 25.0 mm SL. **A** Dorsal view **B** Lateral view **C** Ventral view. Single scale bar shared by **A–C**. Abbreviations: ACh, anterior ceratohyal; Ana, anguloarticular; Apa, autopalatine; Asph, autosphenotic; Bh, basihyal; Boc, basioccipital; Bp, basipterygium; Br, branchiostegal rays; Cb5, ceratobranchial five; Cl, cleithrum; De, dentary; DPcl, dorsal postcleithrum; Ec, epicentral; Epoc, epioccipital; Exoc, exoccipital; Fr, frontal; Hy, hyomandibular; I, spinous pelvic-fin ray; Ihc, interhyal; Iop, interopercle; La, lachrymal; LE, lateral ethmoid; Mx, maxilla; Na, nasal; NS, neural spine; Op, opercle; Pa, parietal; PecR, pectoral-fin ray; PelR, pelvic-fin ray; Pmx, premaxilla; Pop, preopercle; Psph, parasphenoid; Pt, posttemporal; Pte, pterotic; Q, quadrate; Ra, retroarticular; Ri, rib; Sc, scale; Scl, supracleithrum; Soc, supraoccipital; Sop, subopercle; Sy, symplectic; Ur, urohyal; V, vertebral centrum; VPcl, ventral postcleithrum.

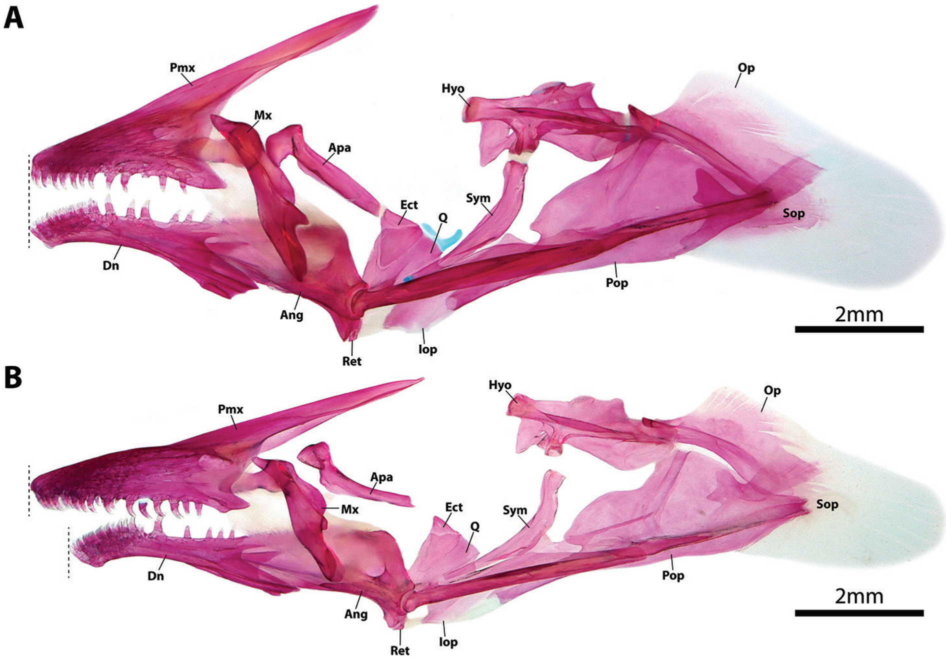

Figure 4. Hyopalatine arch and opercular series (right side in lateral view [image reversed]) in members of *Dellichthys*. **A** *D. trnskii*, NMNZ P.062699, paratype, 41.8 mm SL **B** *D. morelandi*, NMNZ P.018388, 39.0 mm SL. Dashed lines indicate anterior extent of upper and lower jaws. Abbreviations: Ang, anguloarticular; Apa, autopalatine; Dn, dentary; Ect, ectopterygoid; Hyo, hyomandibular; Iop, interopercle; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ret, retroarticular; Sop, subopercle; Sym, symplectic.

ceratobranchial 5. 10–12 gill rakers located along anterior and posterior edge of ceratobranchials 2–3 and anterior edge of ceratobranchial 4; 7 gill rakers located along anterior edge of ceratobranchial 1. Gill filaments associated with ceratobranchials 1–4 (3.5 gill filaments of Briggs (1955)); ceratobranchial 1–3 each with holobranch; hemibranch only on ceratobranchial 4. Basihyal elongate, widest anteriorly (Fig. 3C); anterior edge tipped with cartilage. Branchiostegal rays 6; two anteriormost rays articulating medially with hyoid bar along anterior ceratohyal; posterior rays articulating with hyoid bar laterally, including 3 along posteriormost part of anterior ceratohyal and 1 straddling junction between anterior and posterior ceratohyals (Fig. 3C). Anteriormost branchiostegal rays shorter than posterior rays; orientated with posterior tips directed towards ventral midline. Two posteriormost branchiostegal rays approximately twice as long as short anterior rays; orientated with posterior tips directed towards posterior. Intervening rays intermediate in length; orientated with posterior tips directed towards posterior.

Cephalic lateral-line system with 2 pores in nasal canal; 2 pores in postorbital canal; 3 pores in lachrymal canal; 3 pores in preopercular canal; 2 pores in mandibular canal (Fig. 2A). Postorbital canal pore 2 located directly above preopercular canal pore 3. Mandibular and preopercular canals continuous; connected via unossified canal;

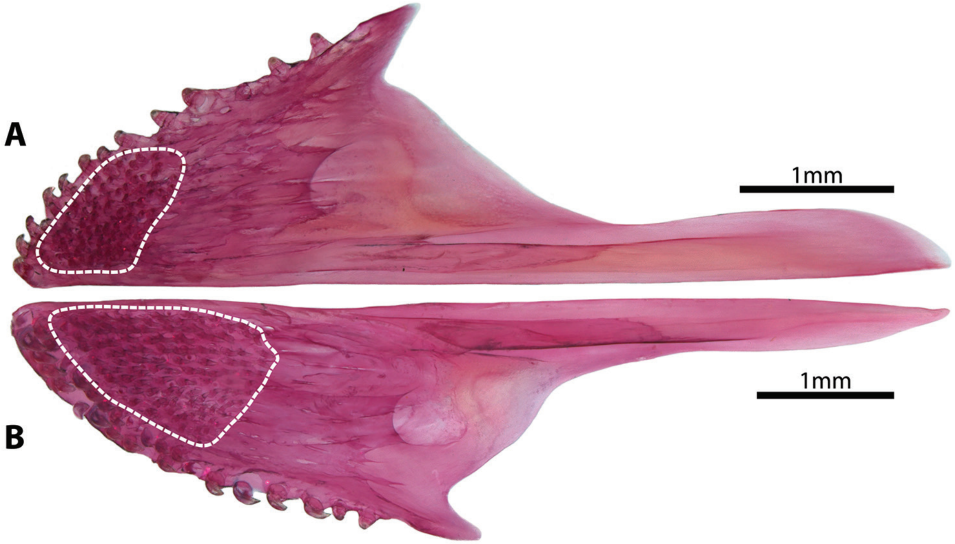

Figure 5. Premaxilla (right side in ventral view [image reversed]) in members of *Dellichthys*. **A** *D. trnskii*, NMNZ P.062699, paratype, 41.8 mm SL **B** *D. morelandi*, NMNZ P.018388, 39.0 mm SL.

anteriormost pore of preopercular canal (PR1) located at center of unossified canal between anguloarticular and preopercle (Fig. 2A). Superficial neuromasts on head isolated or arranged in rows (Fig. 2A). 4 superficial neuromasts in suborbital row; 2 superficial neuromasts in postorbital row; 2 superficial neuromasts in mandibular row.

Dorsal-fin rays 9. Anal-fin rays 7 (1), 8 (2) or 9 (1). Principal caudal-fin rays 5+5, dorsal procurrent rays 6 (2) or 7 (2), ventral procurrent rays 5 (1), 6 (2) or 7 (1). Pectoral-fin rays 22 (3) or 23 (1). Pelvic-fin rays I,4. All fin rays unbranched and segmented. Caudal fin rounded, tips of principal caudal fin rays extended slightly beyond fin margin. Caudal-fin skeleton comprised of upper and lower hypural plates; epural and parhypural poorly ossified, triangular and similar in size (Fig. 6D). Dorsal-fin origin opposite anal-fin origin. First dorsal-fin pterygiophore inserted between neural spines of vertebrae 15/16. First anal-fin pterygiophore inserted between hemal spines of vertebrae 15/16. Total number of vertebrae 30 (3) or 31 (1), consisting of 13 abdominal and 18 (3) or 19 (1) caudal vertebrae (Fig. 6). Ribs 10, associated with vertebrae 3–12. Epicentrals 17 (3), associated with vertebrae 2–18, or 21, associated with vertebrae 2–22.

Adhesive disc large, double (Fig. 7A); anterior and posterior margin weakly crenulated. Disc region A with 5–6 transverse rows of papillae. Disc region B with 6–7 transverse rows of papillae. Disc region C with 4–5 rows of papillae. Papillae of disc region A decreasing in diameter towards outer margin of disc. Papillae of disc region B and C decreasing in diameter towards outer margin of inner disc. Dorsal postcleithrum a thin irregular shaped bone; larger than ventral postcleithrum (Fig. 7B). Ventral postcleithrum irregular in shape; lateral edge rounded; medial edge roughly triangular, with point directed toward ventral midline (Fig. 7B). Fimbrae along posteroventral margin

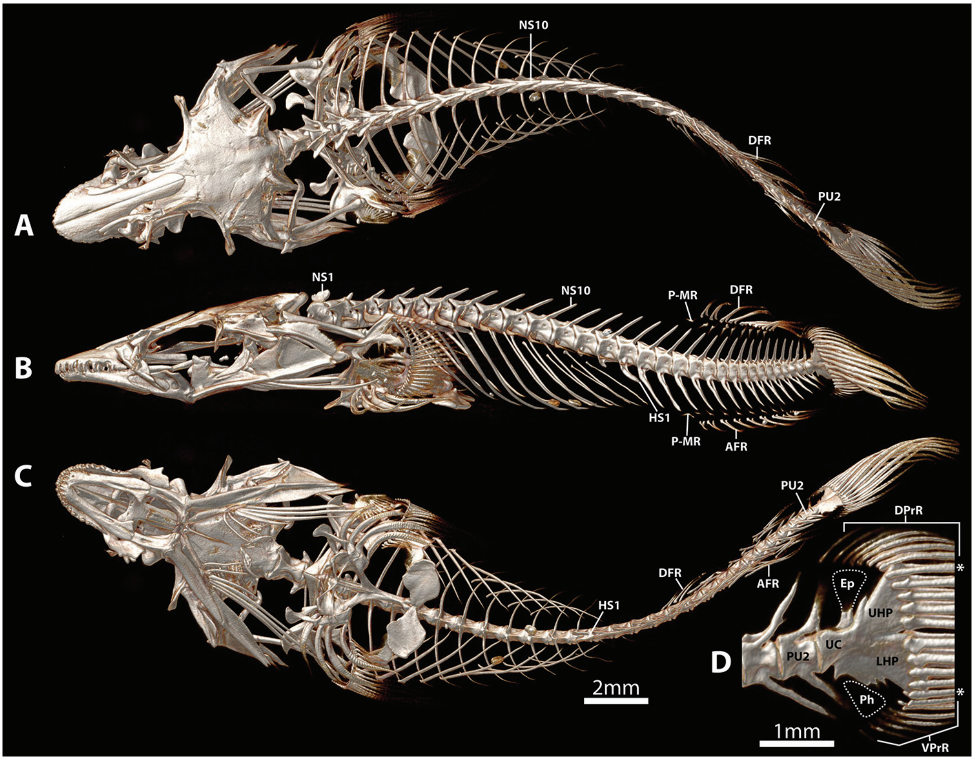

Figure 6. CT scanned skeleton of *Dellichthys trnskii*, NMNZ P.028060, paratype, 25.0 mm SL. **A** Dorsal view **B** Lateral view **C** Ventral view **D** Caudal fin skeleton, lateral view. Asterisks indicate position or upper- and lowermost principal caudal-fin rays in D. Outline of poorly ossified portion of epural and entire parhypural indicated by white dotted line in D. Single scale bar shared between A-C. Abbreviations. AFR, anal-fin ray; DFR, dorsal-fin ray; DPrR, dorsal procurrent caudal-fin ray; Ep, epural; HS1, first hemal spine (14th vertebral centrum); LHP, lower hypural plate; NS, neural spine, number indicates associated vertebral centrum; P-MR, proximal-middle radial; PrR PU2, second preural centrum; UC, ural centrum; UHP, upper hypural plate; VPrR, ventral procurrent caudal-fin ray.

of dorsal postcleithrum and posterior margin of ventral postcleithrum well-developed. Skin associated with last pelvic-fin ray attaching to base of pectoral fin opposite 5th lowermost pectoral-fin ray. Skin over base of ventral pectoral-fin rays smooth.

Colouration. In alcohol, body background colour pale yellow. Median fins pale yellow to white along bases, transitioning to hyaline along distal margins. Paired fins hyaline; papillae on adhesive disc translucent white. In formalin and shortly after initial transfer to alcohol (Fig. 1), body background colour pale orange to yellow with darker orange markings along dorsal midline and ventral midline posterior to adhesive disc. Snout and lips orange. Orange to light brown stripe on lateral side of head posterior to orbit. Dorsal and anal fins orange along base, transitioning to white along distal margins. Base and center of caudal fin pale orange, transitioning to white along distal margins. Pectoral fin hyaline. Distal margin of pelvic fin whitish; papillae on adhesive disc light orange.

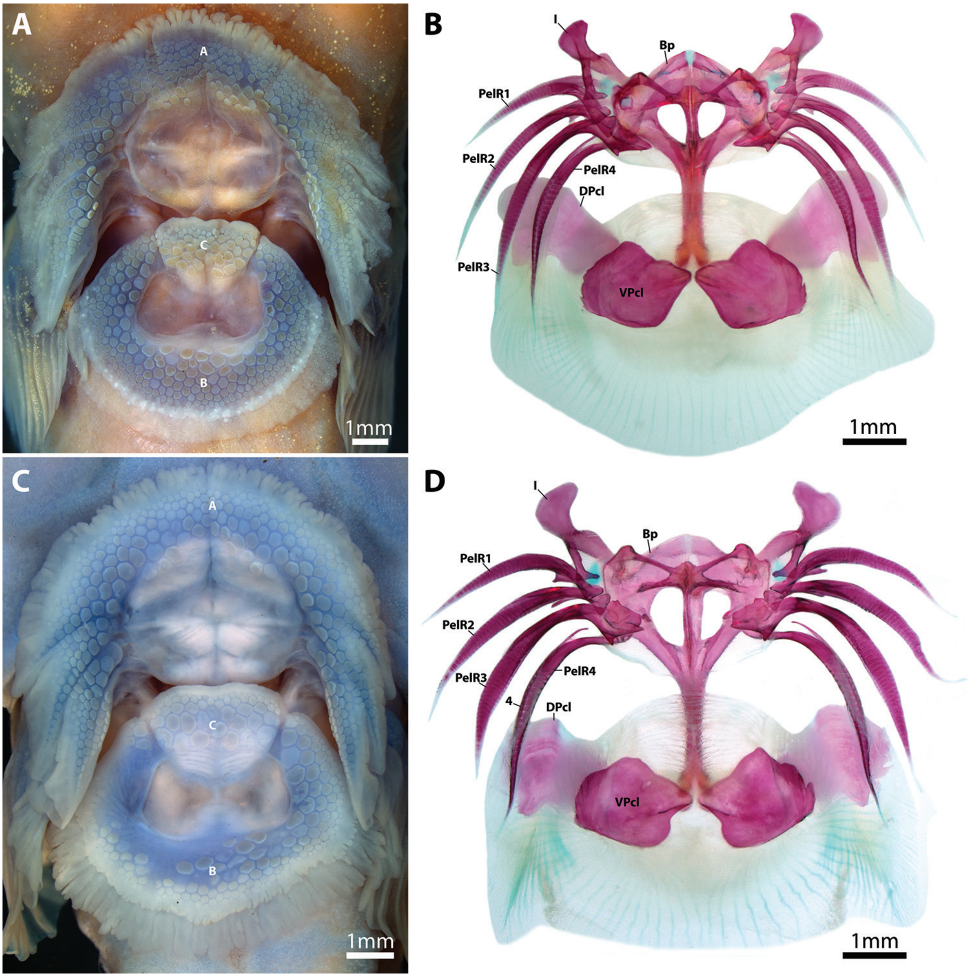

Figure 7. Surface features (**A, C**) and internal supporting skeleton (**B, D**) of the adhesive disc in species of *Dellichthys* in ventral view (anterior to top of page). **A** *D. trnskii*, AIM MA4341, 45.8 mm SL **B** *D. trnskii*, NMNZ P.062699, paratype, 41.8 mm SL **C** *D. morelandi*, TCWC 17269.03, 37.1 mm SL **D** *D. morelandi*, NMNZ P.018388, 39.0 mm SL. Abbreviations: A, disc region A; B, disc region B; Bp, basipterygium; C, disc region C; DPcL, dorsal postcleithrum; I, pelvic-fin spine; PelR1–4, pelvic-fin rays 1–4; VPcL, ventral postcleithrum.

In life, background colour translucent orange to pale yellow (Fig. 8A–C). Lateral body surface with faint to distinct irregular white to pale blue lines that may or may not connect with counterparts along dorsal midline. In some individuals (potentially female), irregular lines replaced by irregular rows of small white to pale blue spots (Fig. 8C). Light brown pigment surrounding nerve cord and darker content in stomach visible through body. Dorsal surface of head translucent light yellow to pale green with three or four white to pale blue lines that become more obvious anteriorly. Lateral surface of head posterior to orbit with two white to pale blue lines

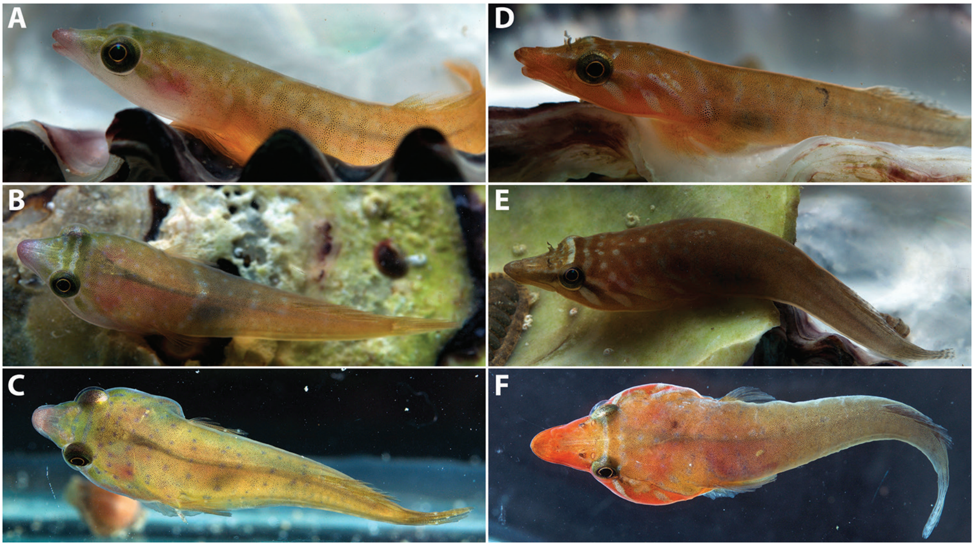

Figure 8. *Dellichthys trnskii* (**A–C**) and *D. morelandi* (**D–F**) photographed in an aquarium soon after collection. **A–B** AIM MA73570, holotype, male, 22.8 mm SL; Pacific Bay, Tutukaka Coast **C** AIM MA73571, paratype, female, 20.0 mm SL; Pacific Bay, Tutukaka Coast **D** TCWC 17264.02, male, 33.8 mm SL; Pacific Bay, Tutukaka Coast **E** TCWC 17264.02, potential female, 29.0 mm SL; Pacific Bay, Tutukaka Coast **F** TCWC 17269.03, male, 37.1 mm SL; Rawhiti, Taupiri Bay.

flanking a central light brown to pale green region (equivalent to orange to light brown stripe on lateral side of head posterior to orbit described above for specimens in formalin). In some individuals (potentially female), white to pale blue lines on dorsal and lateral surfaces of head are replaced by rows of small white to pale blue spots. Tip of snout and adjacent portions of lips pink. Iris orange. Fins clear to translucent orange/yellow.

Distribution. *Dellichthys trnskii* is endemic to New Zealand coastal waters, currently known only from shallow (0–7 meters in depth) waters along the northeastern coast of both the North Island (Auckland, Bay of Plenty, Hawke's Bay, Northland, and Wellington) and South Island (Marlborough Sounds) (Fig. 9). Its occurrence further south may be confirmed by further sampling and by a better understanding of the differences between the two species.

Notes on biology. At the type locality, *D. trnskii* was found primarily under rocks or boulders covered with filamentous algae or low macroalgae often in close proximity to the sea urchin *Evechinus chloroticus*. Small dense objects, possibly sand grains, are visible in the pharyngeal cavity and gut of the CT scanned paratype (NMNZ P.028060, 25.0 mm SL; Figs 3, 6). A single ctenoid scale also is lodged in the opercular opening of this individual (Fig. 3). Whether this scale was ingested or entered the opercular opening subsequent to capture is difficult to confirm. The specimen was collected with a large number of associated sub-tidal species including triplefins, some of which could have shed scales in the bag.

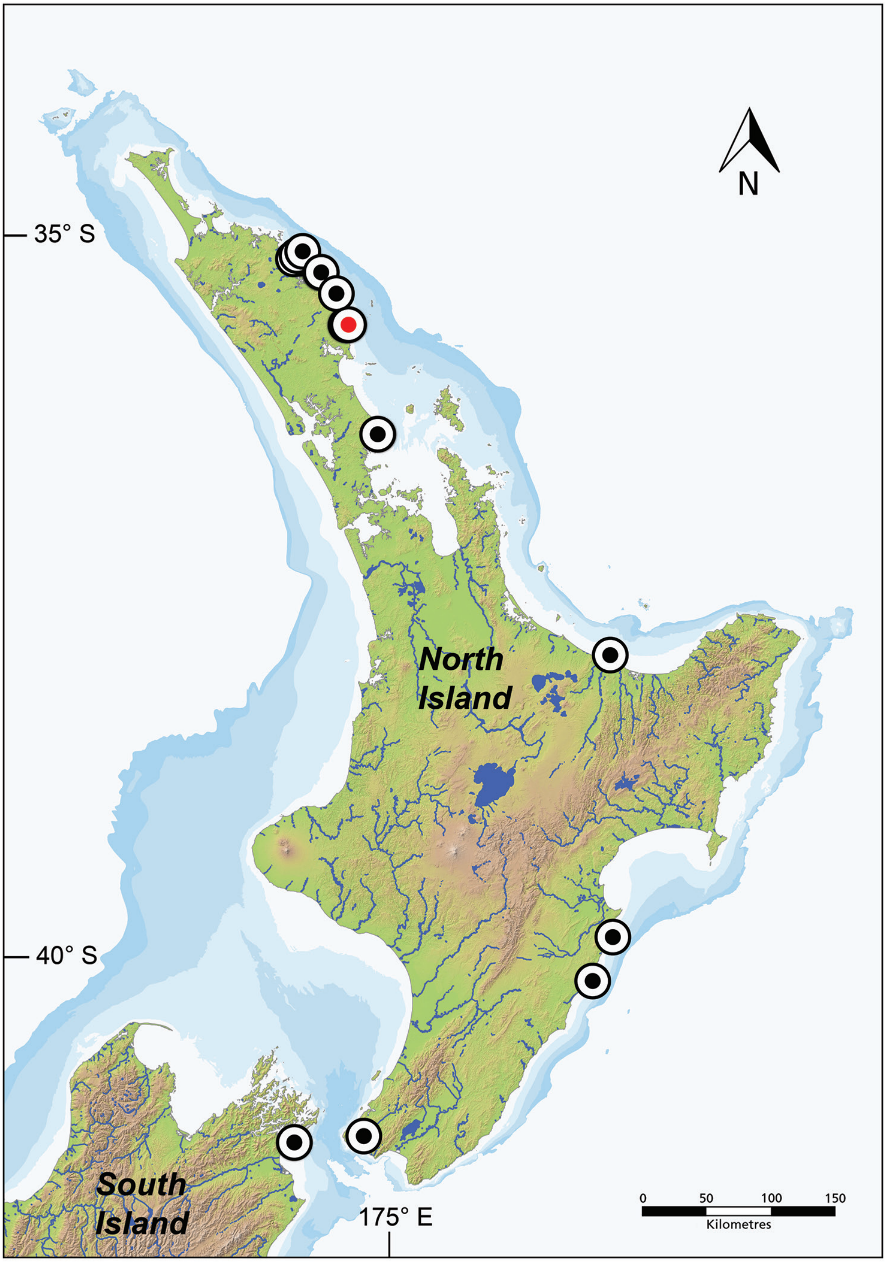

Figure 9. Distribution of *Dellichthys trnskii*. Type locality marked with a red dot.

Sexual dimorphism. No obvious sexual dimorphism is present in the available material. Potential sexual dichromatism is described above in the section on colouration.

Etymology. Named for Tom Trnski, who played a key role in the discovery of the new species by collecting in depths beyond the reach of the first author. A noun in the genitive.

Genetic Distances. The sequences of COI (684bp) obtained from two specimens of *D. trnskii* (Genbank numbers [GB#] MF621939-40) were identical and differed from sequences obtained from six specimens of *D. morelandi* (GB# MF621941-44, MF318544-45) by 11.7 % (uncorrected *p*-distance). Similarly, the sequences of 12S (365bp) obtained from three specimens of *D. trnskii* (GB# MF621933-35) were identical and differed from sequences obtained from five specimens of *D. morelandi* (GB# MF318559-60, MF621936-38) by 3.4% (uncorrected *p*-distance).

Comparisons. *Dellichthys trnskii* is most easily distinguished from *D. morelandi* by features of the colour pattern in life (Fig. 8), including a pale orange to yellow background colour on the body (vs. light brown to dark orange, red or purplish), areas between white to pale blue markings (most commonly stripes) on dorsal and lateral surface of head light yellow to green (vs. brown to dark orange or red), tip of snout and lower jaw pale pink (vs. brown to dark orange or red), and the absence (vs. presence) of faint brown reticulate markings on the median fins.

Dellichthys trnskii is further distinguished from *D. morelandi* by features of the oral jaws, including having the upper and lower jaws equal in length or the lower jaw only slight shorter than the upper, with few upper jaw teeth visible in the gap between the upper and lower lip when the jaws are closed (vs. upper jaw notably longer than lower jaw, with many upper jaw teeth visible in the gap between the upper and lower lip when the jaws are closed) (Fig. 4), a small, roughly rectangular patch of ~50 small conical teeth on the lingual surface of the premaxilla that flanks the posterior margin to the larger conical teeth along the outer margin of the bone (vs. large, roughly triangular patch of ~90 small conical teeth that extends over much of the anterolingual surface of the premaxilla) (Fig. 5). *Dellichthys trnskii* also can be distinguished from *D. morelandi* by its slightly shorter snout (snout length 24–29 % HL vs. 26–34 % HL in *D. morelandi*), the length of which is equal to or less than the interorbital distance (vs. snout length greater than interorbital distance), and by having the transverse skin fold on the surface of snout located directly posterior to the fold of the upper lip (vs. transverse skin fold on the surface of the snout separated from the fold of the upper lip by a broad band of thin, transparent skin). Finally, *D. trnskii* is distinguished from *D. morelandi* by the location of postorbital lateral line canal pore 2, which is located directly above preopercular lateral line canal pore 3 (vs. postorbital lateral line canal pore 2 anterior to preopercular lateral line canal pore 3) (Fig. 2).

Remarks. Briggs (1955) erected *Dellichthys* for the sole inclusion of *D. morelandi*, which he considered to be an “interesting species with no known close relatives” (Briggs 1955: 15). We assign the new species to *Dellichthys* because it exhibits all of the diagnostic characters listed by Briggs (1955:14), including: a narrow upper lip, separated by a broad frenum at tip of snout; small, sharp, conical teeth arranged in a deep patch on both the upper and lower jaw, tapering to a single row of larger, strongly recurved, “canine-like” teeth posteriorly; a relatively high number of narrow pointed gill-rakers on the second gill arch (10–12 in *D. trnskii*; 14 listed by Briggs for *D. morelandi*, 1955); a poorly developed fleshy pad at lowest part of pectoral-fin base; and ventral postcleithrum with a “characteristic” shape in ventral view (i.e., lateral margin rounded and medial margin roughly triangular; Briggs 1955: fig. 44).

Briggs (1955: 14) also listed the absence of the subopercle as diagnostic for *Dellichthys* and considered the opercle to form the terminal element of the operculum in *D. morelandi*. Our investigation of the osteology of *Dellichthys morelandi* and *D. trnskii* has revealed the subopercle to be present (Figs 3A,B, 4). In both cases, the subopercle is comprised of a small, heavily ossified anterior part at the point of articulation with the opercle and preopercle, and a very poorly ossified posterior portion, represented by a thin, yet extensive, lamina of dermal bone that does not take up alizarin red S when cleared and double stained (Fig. 4) nor render well in reconstructions of the CT scan data (e.g., Fig. 3). The poorly ossified posterior margin to the subopercle in *D. morelandi* and *D. trnskii* differs markedly from the heavily ossified and often spine-like posterior margin to the subopercle present in other gobiesocids (e.g., see fig. 12 in Conway et al. (2017c)) and we consider this unique condition (not absence) of the subopercle to be diagnostic for *Dellichthys*.

Though Briggs (1955) provided a detailed diagnosis for *Dellichthys*, derived from multiple external and internal morphological features, the diagnosis provided for *D. morelandi* (also on pg. 14) is relatively short and lists characters that apply to both *D. morelandi* and *D. trnskii.* A rediagnosis for *D. morelandi* is provided below.

Dellichthys trnskii is sympatric with *D. morelandi,* at least along the coast of Northland, and specimens of the two species were commonly collected from within close proximity, in some cases from under the same rock. Paulin and Roberts (1992: 52) described the head and body colour of *D. morelandi* as "purple or cream with blue spots and a band of pale colour across the nape". Stewart (2015: 1545) used the same description for juveniles of *D. morelandi* but described adults as "more olive grey-brown, sometimes flushed with red to orange around ventral part of head." Given that *D. morelandi* and *D. trnskii* occur together and are similar in appearance, we suspect that these previous published descriptions of live colouration in *D. morelandi* are based on observations of both species, with purple specimens representing *D. morelandi* (e.g., see Francis 2012: 54) and cream specimens representing *D. trnskii* (e.g., see Fig. 8C). We note here that the cream coloured specimen figured in the account for *D. morelandi* in Stewart (2015: 1545, fig. 218.2) is instead a small specimen of *Trachelochismus melobesia*.

Dellichthys morelandi **Briggs, 1955**

Urchin Clingfish

Material examined. All New Zealand. *Gisborne*: **NMNZ P.001574**, holotype, 35.8 mm SL; Lottin Point. *Auckland*: **AIM MA995**, 1, 38.8 mm SL; Waitemata Harbour, Torbay Reef (36°41'42.0"S, 174°45'42.0"E), 13 May 1968. – **AIM MA5414**, 5, 28.0–36.2 mm SL; Waitemata Harbour, Okoromai Bay, Whangaparoa Peninsula, 22 January 1985. – **AIM MA27860**, 1 (DNA voucher), 18.7 mm SL; Waterfall Bay, Manukau Harbour (37°01'44.4"S, 174°32'17.9"E), 9 April 2008. *Chatham Islands*: **AIM MA 93927**, 1, 45.4 mm SL; Waitangi Ellice Point (43°56'36.0"S, 176°33'54.0"W), 28 March 1995. *Northland*: **AIM MA5198**, 2, 35.2–36.0 mm SL; Whangaruru, Bland Bay (35°20'24.0"S, 174°22'24.0"E), 22 February 1984. – **AIM MA5331**, 3, 27.5–42.7 mm SL; Bay of Islands, Urapukapuka Island, Albert Passage (35°13'18.0"S, 174°14'36.0"E), 22 August 1984. – **AIM MA5345**, 2, 31.5–32.7 mm SL; Cape Wiwiki, Bay of Islands (35°09'36.0"S, 174°07'36.0"E), 23 August 1984. – **AIM MA7024**, 5, 22.8–60.5 mm SL; Te Puna off Mataka, Bay of Islands (35°09'0.0"S, 174°06'12.0"E), 20 March 1988. – **AIM MA77665**, 1, 51.6 mm SL; Deep Water Cove, Bay of Islands (35°11'42.0"S, 174°18'0.0"E), 8 September 1992. – **AIM MA656096,** 1, 27.4 mm SL; Three Kings Islands, Great Island (34°09'08.9"S, 172°07'50.5"E), 18 April 2013. – **NMNZ P.018388**, 15 (2 C&S), 29.0–46.4 mm SL; Motukokako Island (35°09'00.0"S, 174°20'00.0"E), 8 February 1986. – **TCWC 17173.03**, 1, 21.0 mm SL; Matapouri, Mermaid Pool (35°33'32.1"S, 174°30'51.3"E), 2 March 2015. – **TCWC 17174.03**, 1, 23.7 mm SL; Tutukaka, Dolphin Bay (35°37'33.4"S, 174°32'33.4"E), 2 March 2015. – TCWC 17264.02, 3, 20.0–33.8 mm SL; Tutukaka, Pacific Bay (35°37'07.2"S, 174°32'03.8"E), 8 March 2016. – **TCWC 17264.02**, 3, 21.0–35.0 mm SL. –**TCWC 17269.03**, 1, 37.1 mm SL; Rawhiti, Taupiri Bay (35°16'58.4"S, 174°17'38.0"E), 10 March 2016. – **TCWC 17615.04**, 3, 18.2–32.0 mm SL; **TCWC 17615.14**, 2 (C&S), 18.5–22.0 mm SL; Tutukaka, rocky bay between Tutukaka reserve and Kukutauwhao Island (35°36'40.7"S, 174°32'29.8"E), 11 March 2016. *Southland*: **AIM MA6548**, 1, 42.8 mm SL; Chalky Sound (46°03'0.0"S, 166°31'0.0"E), 23 May 1986. Wellington: **NMNZ P.030622**, 4, 28.1–65.5; Castlepoint, Wairarapa (40°54'00.0"S, 176°14'00.0"E), 14 December 1992. – **NMNZ P.030626**, 5 (2 CT, 1 male [https://doi.org/10.17602/M2/M37807], 1 female [https://doi.org/10.17602/M2/M37808]), 41.4–61.4; same as NMNZ P.030622, 11 November 1992.

Diagnosis. *Dellichthys morelandi* is diagnosed by the following combination of characters: snout spatulate, long (length greater than interorbital distance); lower jaw shorter than upper jaw; teeth at tip of upper jaw visible in gap between upper and lower lip at tip of jaws when jaws are closed; patch of teeth on lingual surface of premaxilla roughly triangular, with ~90 small conical teeth; skin fold on surface of snout located at approximately one quarter of the distance from snout tip to anterior margin of eye, widely separate from fold of upper lip by a broad band of thin, transparent skin; postorbital lateral line canal pore 2 located anterior to imaginary horizontal line through preopercular lateral line canal pore 3; dorsal and lateral surface of head light brown to bright orange or red in life; body light brown to dark orange, red or purplish in life; faint brown reticulate markings on median fins in life.

Remarks. Briggs (1955) described *D. morelandi* based on 14 specimens all from Lottin Point (East Cape). Though we have examined more specimens than were available to him, the morphometric and meristic characters reported herein (Table 1) are consistent with those in the original description.

Briggs (1955:14) made several observations on the snout of *D. morelandi*, which he described as “protruding, spatulate” and “distinctive”. Briggs (1955) made no mention of sexual dimorphism in relation to the snout of *D. morelandi* but based on the material that we have examined there is a clear difference in snout shape between the sexes, with males possessing wider snouts than females when viewed from above (Fig. 10). In addition to a wider snout, males also exhibit a wider head than females, which

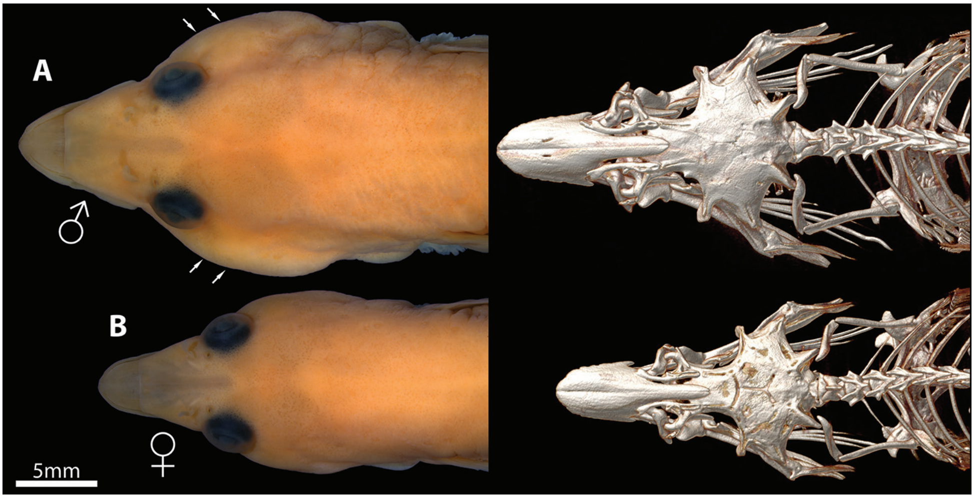

Figure 10. Alcohol preserved specimen (left) and corresponding CT (right) of a male and female of *Dellichthys morelandi*, NMNZ P.030626 **A** male, 60.0 mm SL **B** female, 42.0 mm SL. White arrows point to expanded cheek region of male in A.

may be related to an increase in the size of the muscles of the adductor mandibulae complex. These differences in snout and head profile between the sexes do not appear to be mirrored in the cephalic skeleton, which is similar in males and females (Fig. 10). Sexual dimorphism in head and snout shape has been reported for a number of gobiesocids (e.g., Guitel 1888; Pfaff 1942; Sakashita 1992), is likely related to male nest guarding and parental care (e.g., Coleman 1998; Pires and Gibran 2011), and is probably more widespread than known currently within this fascinating group of fishes.

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RESEARCH ARTICLE

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Species rediscovery or lucky endemic? Looking for the supposed missing species *Leistus punctatissimus* through a biogeographer's eye (Coleoptera, Carabidae)

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Abstract

Is it correct to look for a supposedly missing species by focusing research at the type locality? A species can be declared extinct because for an unusual amount of time it has not been seen again; however, in the frame of the climate change it is likely that a supposedly missing species is a lucky survivor not seen because it was not searched for in the correct environment. We used the strictly endemic Leistus punctatissimus Breit, 1914 (Coleoptera, Carabidae) as the case study for testing the latter hypothesis vs. the type locality approach. On the basis of past unsuccessful searches in the Dolomites (a mountain range in the eastern Alps, Italy) driven by the type locality approach, a study area was selected where climate change may have exerted environmental constraints on endemic species. Five pitfall traps were used in each of seven sample sites, at an average altitude of 2600 m a.s.l., within a high altitude alpine plateau covered by scarce patchy vegetation. Leistus punctatissimus was rediscovered, far from its type locality, after one hundred years since its first collection. It was part of a group of species well adapted to the extreme ecological factors of the alpine environments above the vegetation line. Following a biogeographical approach (i.e., the biogeographer's eye rather than the collector's eye) it was possible to find an endemic species of the alpine ecological landscape in places from where it probably had never disappeared. The supposed refugial area was a nunatak during the last glacial period, where Leistus punctatissimus found suitable habitat conditions, and from where it alternated between downward and uphill changes in its distribution range after the last glacial period, under the effect of climate change. From such a perspective, it can be concluded that the type locality may be the wrong place to look for a supposedly extinct species.

Keywords
climate change, endemism, ice ages, glacial periods, nunatak, mountain ecosystems, species rediscovery, Wallacean extinction

Introduction

When a species is "rediscovered" there are at least three reasons it was supposed to have disappeared (Scheffers et al. 2011): i) it disappeared as a consequence of a declaration of extinction by the researcher who rediscovered it; ii) when for any of several reasons it has been unseen for an unusually lengthy period of time; or iii) when it was collected for the second time only long after the collection of the type. A fourth reason has been proposed by Ladle et al. (2011), the lack of appropriate ecological and biogeographical knowledge because the species is only known from few specimens in museum collections. It is reasonable to suppose that the latter is the most probable explanation when dealing with relict species confined to high altitude environments.

Leistus punctatissimus Breit, 1914 is an ideal case study, because it is a relict species known for more than a hundred years on the basis of a female specimen lacking the abdomen (Breit 1914) and a male specimen dating back to the same epoch but described only recently (Assmann and Heine 1993) on the basis of which more complete knowledge of its morphology was obtained. From the date of the first collection on the Rolle Pass (Italy) by Anton Otto in 1902 (Breit 1914), the presence of the species has not been confirmed despite of extensive searches by Brandmayr and Zetto Brandmayr (1988), who focussed on a large altitudinal gradient of several environments from the bottom valleys to the talus slopes at high altitudes in the area surrounding Rolle Pass. A second research expedition was made along the same gradient in the years 2007–2012 (Pizzolotto et al. 2014, Pizzolotto et al. 2016) with the aims of detecting faunistic variations possibly occurring after the 1988 expedition and of sampling new habitats seeking for the presence of the beetle, but again, no trace of it was found.

The new research described in this paper was intended to determine if the distribution range of *L. punctatissimus* is other than what is arguable that based on the type locality (see Ladle et al. 2011), or if the distribution range has changed as a consequence of the climate change, as documented by the uphill shift (Pizzolotto et al. 2014) of two microthermal endemic species *Nebria germari* Heer, 1837 and *Trechus dolomitanus* Jeannel, 1931, once abundant in the area around Rolle Pass (Brandmayr and Zetto Brandmayr 1988).

Methods

New environments were sampled in the years 2013–2014 following the hypothesis that the collection made by Anton Otto (Breit 1914) was the result of a fortuitous find, maybe at the limit of the distribution range of *L. punctatissimus*. We moved from the idea that climate change may have restricted the species' geographic range much earlier, perhaps immediately after its discovery, according to the first well known temperature increase during the 1920s, as highlighted by the CRUTEM4 database (Jones et al. 2012).

The new sample sites had to show ecological features different from the sites sampled in the past, while at the same time they had to be characterised by features consistent with the presence of an endemic alpine species. Thus, we looked for the presumed missed species at higher altitude than in the past, in environments characterised by extreme ecological conditions, and covering an area large enough to ensure the long-term survival of viable populations also during ice age episodes.

Our choice was directed by the topography of the mountains around the Rolle Pass and fell on the Altopiano delle Pale di S. Martino (Figure 1), a karstic rock "desert" surrounded by several dolomite pinnacles approximately 3,000 m high. Seven sample sites were selected having an average uphill shift of five hundred metres, at an average altitude of 2600m a.s.l., within a landscape typical of high altitude alpine environments where the vegetation cover is mostly composed of few pioneer species taking root on a thin lithosol patchily covering the rocks.

Five sites were selected in correspondence with the vegetation type mainly characterising the study area, which is classified in the eighth group (rocky habitats) of the NATURA 2000 (N2k) habitats (European Commission 2013), mainly a mosaic of limestone pavements habitat type (code 8240, N2k) and small patches of vegetation belonging to the calcareous and calcschist screes habitat type (code 8120, N2k). One site was selected on a talus slope covered with vegetation belonging to *Thlaspietea rotundifolii* Br.-Bl. in Br.-Bl. et Jenny 1926, code 8120, N2k, which characterises 10 % of the study area landscape. Another sampling site was selected on closed turfs (code 6170, N2k) within a small snowbed, which is a geomorphological element made by the seasonal accumulation of snow into small to large depressions; such landforms characterise 10 % of the area.

Five pitfall traps were placed in each site. A preservative mixture of wine vinegar oversaturated with table salt was used at the start of sampling and each time after the traps were emptied. Due to the low temperatures it was possible to empty the traps two or three times during July and September of each year.

Results

Ground beetle samples

In the seven sample sites twelve species of ground beetles were found, mostly endemic of the Dolomites (n = 7; 58 %) and with short wings (i.e., brachypterous, n = 8; 67 %). Among these *L. punctatissimus* was collected for the first time after more than one hundred years since its first collection and description. Three specimens were found in the pitfall traps, two females and one male, all deteriorated due to bad weather conditions during trapping.

Figure 1. The study area "Altopiano delle Pale" was a karstic rock "desert" surrounded by several dolomite pinnacles, the one visible in this picture is the Rosetta Mount (2743 m a.s.l.) westward from the photographer. Behind it, to the right, the dark Lagorai mountain chain. The vegetation patchily colonised the study area exploiting the scarce presence of a thin lithosol. The "good" season usually lasts from the end of June to the beginning of September.

Among the sampled taxa, two species have wider distributions, *Bembidion glacialis* (Heer, 1837) and *Pterostichus morio* (Duftschmid, 1812), known from the Alps, the northern part of the Apennines, and Carpathian Mountains, while two species, *Notiophilus biguttatus* (Fabricius, 1779) and *Amara erratica* (Duftschmid, 1812), have European and Palaeartic distribution range, respectively.

The species most frequently found in the study area were *Nebria germari* (100% of the sampled sites), *N. diaphana* (K. Daniel & J. Daniel, 1890), *Carabus bertolinii* Kraatz, 1878, *C. creutzeri* Fabricius, 1801 (all in 86 % of the sites; n = 6), and *Trechus dolomitanus* (n = 4; 57 % sites).

The highest diversity was found in the snowbed environment, where 83 % of the sampled species (n = 10) were collected, while the talus slope environment harbours 50 % of all species recorded. In all the sites except one, the patchy pioneer vegetation site, species richness was less than the 50 % of the sampled species. All the species collected except *A. erratica* have zoophagous diet.

Temperature trends

The average temperature trend at the Rolle Pass is given in Figure 2, where it is compared with the northern hemisphere temperature increase during the last century (CRUTEM4 database), and with the CRUTEM4 average of 1902. Especially in the last four decades, the average values show a strong increase, but a preliminary warming of the area may have occurred even before this, beginning at least during the 1930s when measurements first began at the Rolle Pass, as is evident in Figure 2.

Palaeogeographic reconstruction

The map presented in Figure 3 shows the presumable distribution of ice cover during the last glacial age (Würmian) and the possible "overwintering" sites of *L. punctatissimus* on the Pale di S. Martino high plateau. In Figure 4 the same area is redrawn as it is during the present time, where the remaining small glaciers are reduced to nearly invisible spots. The distribution of the beetle was reconstructed on the basis of Pizzolotto et al. (2014), who found in the same area an uphill shift of the distribution range of several species as a consequence of the climate change. The described uphill shift can be used to reconstruct the distribution ranges also of former periods as in Figure 4, where the putative distribution of *L. punctatissimus* is restricted to the plateau, while it was wider than now at the beginning of the last century. .

Discussion

The paths rising to the Dolomites plateaus have a long history, being visited by tourists since the mid-nineteenth century (Gilbert and Churchill 1864). However, there is no certainty of knowing whether or indeed how many entomologists went so far. It is a matter of speculation whether Anton Otto in 1902 had preferred a convenient walk around the Pass, where he found a pair of specimens of *Leistus punctatissimus*, or whether he intentionally went climbing on the surrounding mountains.

After thorough searches following the footsteps of Anton Otto, which lead to no further findings of *L. punctatissimus*, it was hypothesised that the core of the distribution range could have been linked to the environmental conditions shaped by the effect of the ice age.

From a biogeographical point of view, a species narrowly distributed inside an alpine landscape, above the tree line of a southern European mountain chain, is seen as

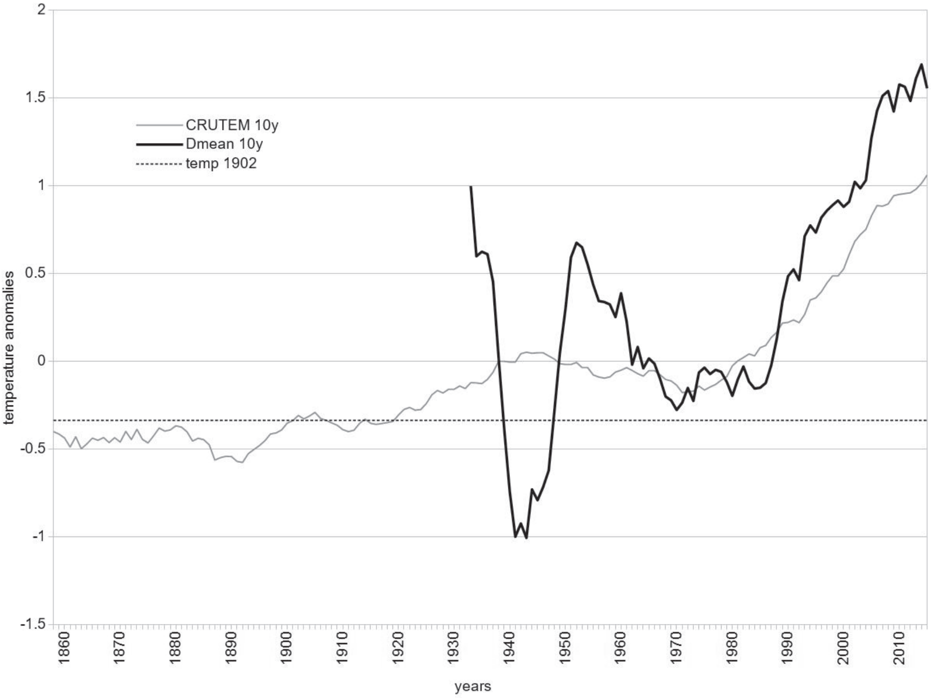

Figure 2. Trends of global and local ten years running average temperature anomalies. The local (Rolle Pass) temperature trend (bold black line, based on the Meteotrentino database, see Data Accessibility) consistently with the global temperature trend (based on CRUTEM4 database) is expressed as temperature anomalies from the base period 1961–90 (see Jones et al. 2012). The horizontal dotted line shows the average global temperature anomaly in 1902, after this year the global trend cross the line downwards only one time. During the last 30 years, global and local trends are consistent with the climate change hypothesis.

the product of evolution and area restriction moulded by the ice ages. Consequently, the species should be looked for within areas possibly free from ice cover, corresponding to a nunatak or a peripheral glacial refugium (Holderegger and Thiel-Egenter 2009). Conversely, following the "collector's eye" the same species should be looked for at or near the type locality. Indeed *L. punctatissimus* was found as a very rare species among a group of twelve species in the Dolomites, most of these stenoendemic and brachypterous. Among these, worthy of a mention are *Nebria germari* and *N. diaphana*, which inhabit high altitude environments colonised by small patches of vegetation in the Dolomites (Brandmayr and Zetto Brandmayr 1988, Pizzolotto et al. 2014). From a general point of view, based on biogeographical and autoecological features of our sampled carabid fauna, the Pale di S. Martino plateau is recognised as a relevant nunatak in the eastern Alps at least during the last glaciation. At the same time, the Rolle Pass played the role of a northern threshold in the pathway of distribution for the short-distance re-immigrating species, arriving from the "massifs de refuge" of the southern Alps (see Holdhaus 1954).

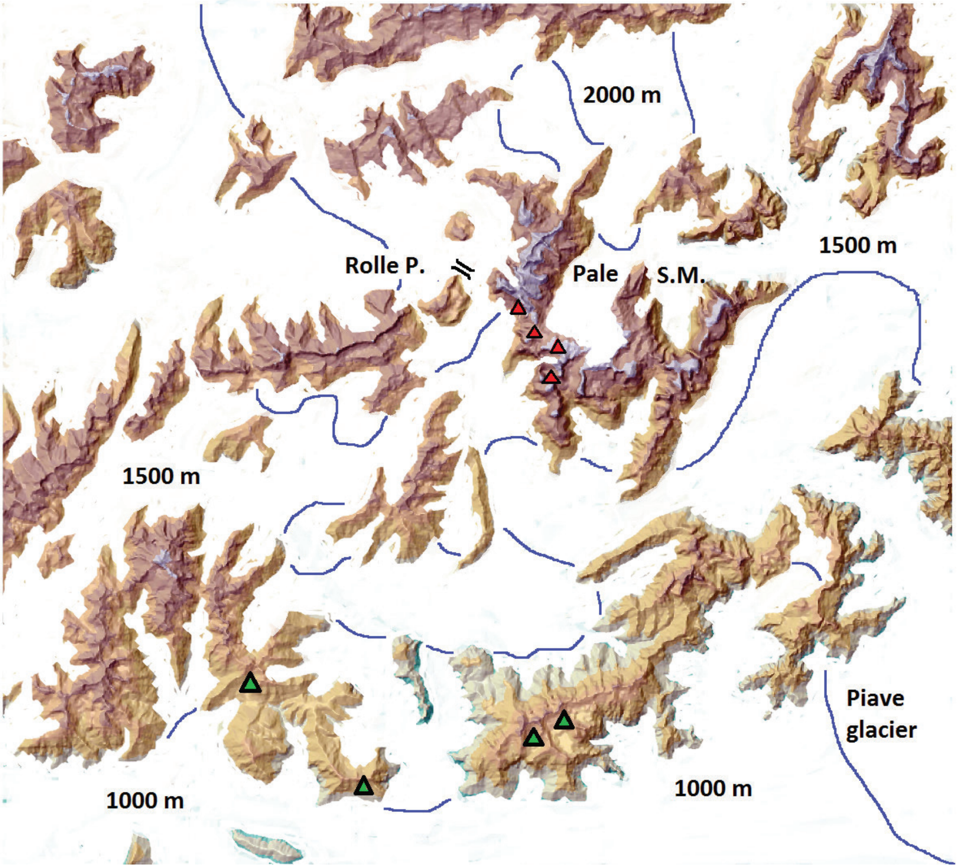

Figure 3. The possible distribution of *Leistus punctatissimus* during the last ice age maximum, (red triangles). Green triangles: northern "sentinels" of *Duvalius breiti*, a relict of the "Massifs de refuge". The blue lines indicate the approximate height of the alpine "inlandsis" of the Dolomites around the Rolle Pass. Reconstructed after the map of Pellegrini et al., 2004. The Pale di San Martino massif represents one of the largest nunatak area near the Rolle Pass.

Assmann (1997) suggested that the absence of specimens of *L. punctatissimus* from pitfall trap samples taken in the Rolle Pass area was simply due to successful avoidance of the traps by members of this species. Even if Perrault (1982) placed *L. punctatissimus* in synonymy with *L. ovipennis* Chaudoir, 1867, the latter does not occur at Rolle Pass, so that no taxonomic issue could explain the disappearance of *L. punctatissimus*. However Assmann and Heine (1993) provided morphological data supporting these two as separate species, an opinion shared also by Farkac (2005).

It is likely that *L. punctatissimus* is another case of "Wallacean extinction" (Ladle and Jepson 2008), which refers to a species poorly documented because the survey of its populations has been discouraged by the severe environmental conditions researchers had to face (see also Ladle et al. 2011). Our results highlight that, rather than focusing

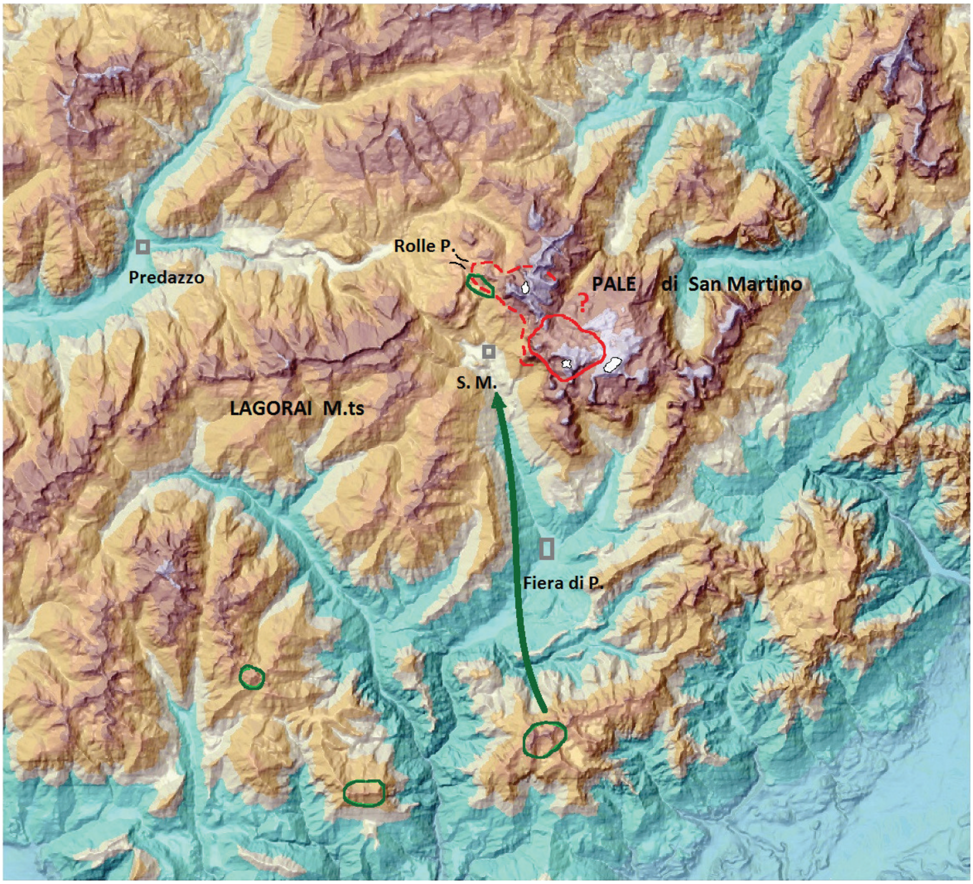

Figure 4. Present distribution area of *Leistus punctatissimus* (continuous red line) and putative western boundaries of the same around year 1900 (broken red line). The eastern boundaries of the area remain uncertain. The glaciers as present today are represented by white spots with black borders. Green areas: presently known distribution of *Duvalius breiti*. The green arrow indicates the possible re-immigration pathway of this species towards Rolle Pass. S. M.: San Martino di Castrozza.

on the type locality, it is better to derive the possible habitat preference of the supposedly missed species on the basis of its biogeographical history, and then to derive the possible bioclimatic zone which is expected to harbour the target species. It appears that a biogeographical approach is more informative than a purely geographical one in these cases. This situation is comparable to the history of a relict species of the "massifs de refuge" studied by Holdhaus (1954), the microphthalmic carabid beetle *Duvalius breiti* (Ganglbauer, 1900), found at the Rolle Pass by Brandmayr and Zetto Brandmayr (1988).

The question that remains controversial is whether our first searches might have been misled by the consequences of climate change. This would imply an early contraction of the species' distribution range, perhaps immediately after its discovery according to global warming data, which after the beginning of the 20th century shows a clear upward trend (Figure 2, see the 1920's temperature line). However the species is strictly stenoendemic, so that it responds to local temperature trends, and the local temperature trend shows that a time of climate cooling occurred between the discovery of *L. punctatissimus* and the 1980s expeditions (Figure 2, during the 1940s). It would be possible to hypothesise that during that cooling time, the species could have expanded rather than contracted its distribution range.

A reasonable explanation is that this cooling time was too short for the species to respond. Expanding this reasoning based on the theories of Vincent et al. (2005), one could hypothesise that the shrinking of the *L. punctatissimus* distribution range began at the end of the Little Ice Age when the temperature factor became more critical than the lack of snow precipitations.

Again, seeking the species on the basis of its biogeographical features provided the searching clue consistent with the actual distribution of the species, which was rediscovered within an environment of approximately 2600 metres altitude, where the favourable season for insect activity is a short cold spring (compared with the bottom valley climate), and the vegetation is at the upper limit of survival. These are environmental features generally in line with the autoecological features of an endemic species of the Alps, which lead us to consider the initial discovery by Anton Otto as a fortuitous finding, while our first failures were the result of an erroneous "geographically driven" research.

Another question requiring an answer is about the origin of the species. Following Habel et al. (2010), we can hypothesise that *L. punctatissimus* is a relict species that evolved, after the recolonization from the Pontic-Mediterranean glacial refugia, from a group of *Leistus* which lead to the allopatric differentiation of eight species (Assmann and Heine 1993). The speciation was a consequence either of the Holdaus Line effect (Drees et al. 2010), or of the disjunction of a population along the northward recolonising route. Assmann and Heine (1993) outlined that the distribution range of *L. punctatissimus* was known to be very small, only the region around the Rolle Pass, an area which had been covered by ice during the last glaciation. On this basis they hypothesised that the species should has come from a refugial landscape like, for instance, *Duvalius breiti*, and it should be considered as a short-distance re-immigrant (Holdhaus 1954).

As it is not easy to reconstruct the kinship among *L. punctatissimus* and those eight species, and given the very narrow distribution range of each, it could be hypothesised that *L. punctatissimus* is a species which evolved *in situ*. This opens new perspectives for biogeographical studies of the Oriental Dolomites, because these mountains may have played the role of nunatak, while the same is not arguable from a mere geographical or geomorphological analysis.

The survival on nunataks is likely for other ground beetles also. This is especially true for Nebriine species to which also *Leistus punctatissimus* belongs (e.g. *Oreonebria atrata*: see Holdhaus 1954; *Oreonebria bremii* and *O. bluemlisalpicola*: see distribution maps in Szallies and Huber 2014). Moreover, several other ground beetle species survived on permafrost ground conditions the last glacial period in Central Europe as revealed by strikingly differentiated populations (e.g. Homburg et al. 2013, Drees et al. 2016). Therefore, it seems to be likely that many ground beetle species are able to survive under low temperature conditions than previously thought (cf. discussions in Drees et al. 2016).

Permanent monitoring of the study area will inform us if the population of *L. punctatissimus* is in a stable or in a contracting state in light of climate change, while a daring entomological exploration of the peaks crowning the S. Martino valley will led to the reconstruction of its actual distribution range, telling us if the species evolved *in situ* or if it re-immigrated from southern glacial refugia.

Conclusions

Leistus punctatissimus is likely a nunatak survivor that "overwintered" on the extremely large nunatak of the Pale di San Martino and its karstic alpine upland. In the post-glacial period it alternated between downwards and uphill changes of the distribution range, colonising the southern slope of the Rolle Pass and its large debris and stone fields during the postglacial retreat of the ice.

The last of such "area pulses" happened during the small ice age of the eighteenth and nineteenth centuries. During this epoch, *L. punctatissimus* and *Duvalius breiti* populations lived together in the erosion landscapes and debris channels of the southern slopes of the Rolle Pass. Shortly thereafter the extremely microthermophilous *Leistus* species was forced to leave the open habitats around the Rolle treeline, whereas the more thermophilous (and hygrophilous) *Duvalius* species survived in humid erosion channels and along, stone-rich runlets.

Last, but not least, in the new perspective of global warming: it should be kept in mind that a type locality of the past century could not be the appropriate collecting target.

Data accessibility

All topographic and environmental GIS layers generated for this study are available from the cartographic databases of the Trento Province (http://www.territorio.provincia.tn.it/portal/server.pt/community/s_i_a_t/255/s_i_a_t/18995), and the Veneto Region (http://idt.regione.veneto.it/app/metacatalog/).

All climatic data used for this study are available from the CRUTEM4 database (https://www.metoffice.gov.uk/hadobs/crutem4/), and the Meteotrentino, i.e. the Trento Province database for climatic data (http://www.meteotrentino.it/dati-meteo/stazioni/elenco-staz-hydstra.aspx?id=168).

Acknowledgements

We thank Alessandro Minelli for critically reading the paper, Thorsten Assmann and David Kavanaugh for reviewing the paper. Their advices strongly improved the scientific quality of the paper. This research is part of the project "Dolomites Global Change" supported by the regional park "Parco di Paneveggio e Pale di S. Martino" (Trento, Italy). It was supported also by the Italian Ministry for the University within the project "PRIN 2009 (prot.200947YRB9_001) - Impatto del cambiamento climatico su comunità animali e vegetali".

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RESEARCH ARTICLE

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An illustrated key to the genera of Eumeninae from China, with a checklist of species (Hymenoptera, Vespidae)

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Abstract

An illustrated key to the currently recognized genera of the subfamily Eumeninae (Vespidae) from China is presented together with a list of 267 species and subspecies, belonging to 51 genera. *Nortozumia* van der Vecht, 1937 is reported for the first time from China. Two replacement names are proposed for junior primary homonyms: *Ancistrocerus rufofrustius* Tan & Carpenter, **nom. n.** replacing *Ancistrocerus rufopictus* (Kostylev) and *Orientalicesa confasciatus* Tan & Carpenter, **nom. n.** replacing *Orientalicesa unifasciatus* (von Schulthess, 1934).

Keywords

homonym, illustrated key, new record, Oriental, Palaearctic

Introduction

Eumeninae or potter wasps are the largest subfamily of the Vespidae with 3773 valid species in 205 genera (Carpenter 1986; Zhou et al. 2011; Tan et al. 2015, 2018a; Pannure et al. 2016; Carpenter unpubl.). Eumeninae have a cosmopolitan distribution and are morphologically very diverse. The generic classification of Eumeninae is chaotic and has a troubled taxonomic history. The extreme splitting haphazardly pursued during much of the 20th century has contributed much to this current state (Hermes et al. 2014). Clearly, the situation with the generic classification will have to be rationalized by future synonymy of numerous taxa after their phylogeny is better known (Carpenter and Cumming 1985; Carpenter and Garcete-Barrett 2003; Hermes et al. 2014). The need for taxonomic work on Eumeninae is underlined by the lack of adequate and well-illustrated keys, both to genera and to species (Pannure et al. 2016). The few generic keys available concern one region or a country: Yamane (1990) revised the Japanese fauna of Eumeninae with a key to 18 genera, Carpenter and Garcete-Barrett (2003) presented a key to the genera of Neotropical Eumeninae and Pannure et al. (2016) included a key to the 31 eumenine genera known from South India. We present the first illustrated key to genera of Eumeninae from a major area encompassing two faunal regions and the first complete key to genera of Chinese Eumeninae. It is a major step to facilitate the classification of Chinese Eumeninae. Nevertheless, the status of several genera remains problematical; only a combined approach using molecular, biological, and morphological data will make it possible to decide their taxonomic position.

The Chinese Eumeninae were first catalogued by Liu (1936–1937) resulting in a list of 57 species divided among nine genera. Unfortunately, his research stopped after his only revision (*Pareumenes*; Liu 1941). Lee (1982a, 1985) published the most recent key to the genera of Eumeninae in China, including only 25 genera (for 65 species and 13 subspecies). Finally, Zhou et al. (2011) listed 45 genera present in China and included 172 species and 50 subspecies. Several scattered papers have been published on Chinese Eumeninae, but a thorough inventory is lacking (Zhou et al. 2012, 2013; Li and Chen 2014a, 2014b, 2015, 2016a, 2016b; You et al. 2013; Ma et al. 2016, 2017; Nguyen and Xu 2014; 2015; 2017; Yeh and Lu 2017; Tan et al. 2018a). The illustrated key to the genera of Chinese Eumeninae presented here includes 51 genera and the checklist contains 267 species and subspecies in total. One genus (*Nortozumia* van der Vecht, 1937) is reported as new to China. Two replacement names are proposed for junior primary homonyms: *Ancistrocerus rufofrustius* Tan & Carpenter, nom. n. replacing *Ancistrocerus rufopictus* (Kostylev) and *Orientalicesa confasciatus* Tan & Carpenter, nom. n. replacing *Orientalicesa unifasciatus* (von Schulthess, 1934).

Material and methods

Specimens were collected by hand net or with Malaise traps. The studied specimens are deposited in the collections of College of Life Sciences, Northwest University, Xi'an (**NWUX**); Northwest A&F University Entomological Museum, Yangling, Shaanxi (**NWAY**); Zhejiang University Hymenoptera Museum, Hangzhou (**ZJUH**); General Station of Forest Pest Management, State Forestry Administration, Shenyang (**GSFA**); American Museum of Natural History, New York (**AMNH**); Naturalis Biodiversity Center, Leiden (**RMNH**); Museum national d'Histoire naturelle, Paris (**MNHN**); and Senckenberg Deutsches Entomologisches Institut, Müncheberg (**SDEI**).

Morphological terminology follows Carpenter and Cumming (1985), Yamane (1990), and Carpenter and Garcete-Barrett (2003). Observations and descriptions were made with an Olympus SZX11 stereomicroscope and fluorescent lamps. Photographic images were made with Keyence VHX-5000 digital microscope (NWUX, Xi'an), Olympus SZX 12 stereomicroscope with analySIS Soft Imaging System software (RMNH, Leiden), and Microptics-USA/Visionary Digital photomicrographic system, developed by Roy Larimer, multiple layers stacked using Helicon Focus (AMNH, New York).

Key to genera of Eumeninae from China

1 Tergum I more or less petiolate, slender and its apical half parallel-sided or slightly narrowed posteriorly (1a); tergum I usually at least twice as long as wide (but in e.g., *Pseudozumia* slightly longer than wide); tergum II twice maximum width of tergum I in dorsal view, but approx. 1.5 × in *Pseudozumia* **2**

– Tergum I robust and its apical half widened posteriorly (1aa); tergum I much less than twice as long as wide; tergum II at most twice as wide as tergum I........ **18**

Figure 1. Metasomal terga I-II, dorsal view: **a** *Eumenes m. mediterraneus* (Kriechbaumer) (left 1), *Pseudozumia indica* (de Saussure) (left 2), *Calligaster cyanoptera* de Saussure (middle) **aa** *Antepipona deflenda lepeletieri* (Blüthgen) (right 2), *Symmorphus foveolatus* (Gussakovskij) (right1).

2 Middle tibia with two spurs (2a) **3**

– Middle tibia with one spur (2aa) **5**

Figure 2. Part of middle leg: **a** *Discoelis zonalis* (Panzer) **aa** *Pseumenes depressus annulatus* van der Vecht.

3 Propodeum with valvula distinctly protruding, elongate and rectangular (3a), orifice acutely pointed dorsally (3b) .... ***Zethus* Fabricius**

– Propodeum with valvula not protruding (3aa), orifice rounded dorsally (3bb) **4**

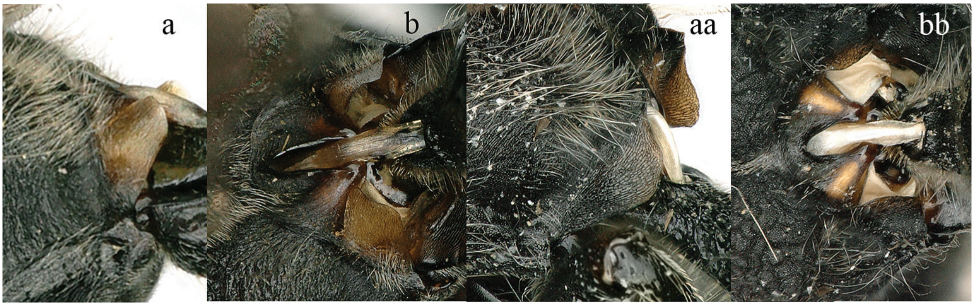

Figure 3. Part of propodeum lateral view (**a, aa**) and caudal view (**b, bb**): **a, b** *Zethus velamellatus* Tan **aa, bb** *Discoelis zonalis* (Panzer).

4 Maxillary palpus 3-segmented (4a); tergum I more than twice as long as wide, longitudinally striate (4b); tegula posteriorly acute (4c) .... ***Calligaster* de Saussure**

– Maxillary palpus 4-segmented (4aa); tergum I less than twice as long as wide, punctate (4bb); tegula posteriorly truncate (4cc)............ ***Discoelius* Latreille**

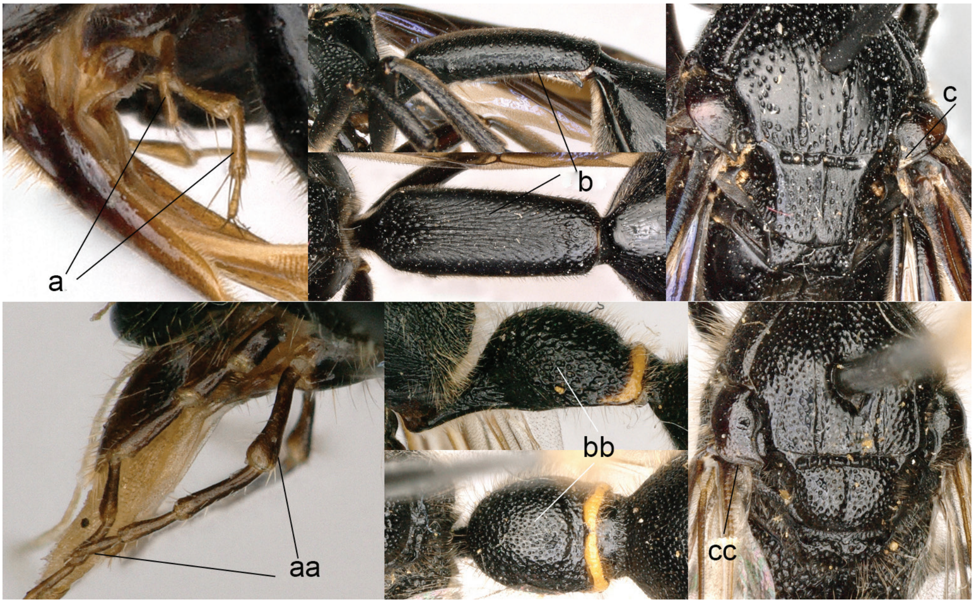

Figure 4. Labial palpi (**a, aa**) and metasomal segment I (**b, bb**): **c, cc** part of mesosoma, showing tegula: **a–c** *Calligaster cyanoptera* de Saussure **aa–cc** *Discoelis zonalis* (Panzer).

5 Propodeal valvula relatively short, rounded, submarginal carina distinctly protruding (5a); frons distinctly longer than clypeus; second submarginal cell narrow anteriorly, vein 1-M and vein 2-M meeting almost at right angle (5b)............... **6**

– Propodeal valvula elongate, rectangular, submarginal carina not protruding (4aa); frons shorter than clypeus; second submarginal cell wide anteriorly, vein 1-M and vein 2-M meeting at obtuse angle (5bb) **8**

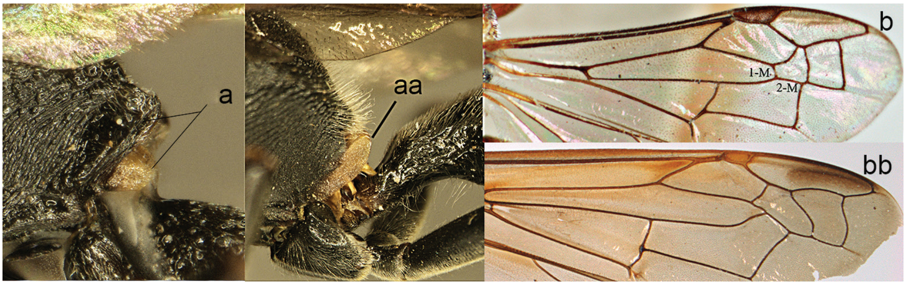

Figure 5. Propodeum (**a, aa**) and part of forewing (**b, bb**): **a** *Leptomicrodynerus tieshengi* Giordani Soika **b** *Labus spiniger* de Saussure (right upper) **aa** *Coeleumenes* sp. (middle) **bb** *Delta campaniforme esuriens* (Fabricius).

6 Female with fovea anterior to mid-ocellus (6a); metanotum monodentiform mesally (6d); metasomal petiole abruptly swollen apically in lateral view (6c); tegula not exceeding parategula posteriorly (6b); anterior face of pronotum smooth (6e) .... ***Labus* de Saussure**

– Female without fovea on vertex (6aa); metanotum obtuse mesally (6dd); metasomal petiole not conspicuously swollen in lateral view (6cc); tegula more or less exceeding parategula posteriorly (6bb); anterior face of pronotum distinctly punctuate laterally (6ee) 7

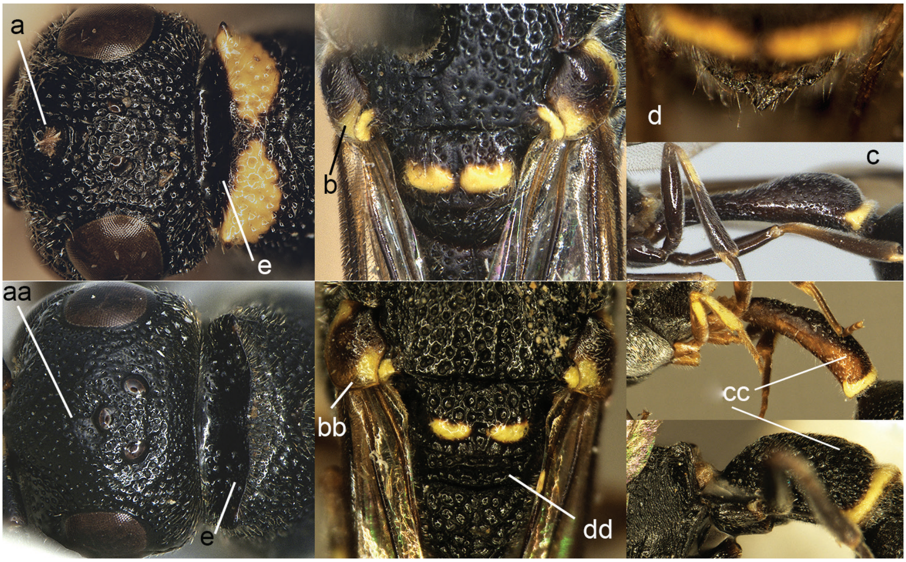

Figure 6. Head and pronotum (**a, e, aa, ee**), part of mesonotum in dorsal view (**b, bb, dd**), metanotum magnified (**d**), and metasomal segment I in lateral view (**c, cc**): **a–e** *Labus spiniger* (de Saussure) **aa, ee, lower cc** *Leptomicrodynerus tieshengi* Giordani Soika **bb, dd, upper cc** *Cyrtolabulus suavis* van der Vecht.

7 Mesoscutum distinctly longer than wide (7a), apical margin of tergum I wider than half width of TII (7b); parategula short, almost absent, tegula distinctly exceeding parategula (7c) .... ***Leptomicrodynerus* Giordani Soika**

– Mesoscutum distinctly wider than long (7aa); apical margin of tergum I narrower than half width of tergum II (7bb); parategula normal, tegula slightly exceeding parategula (7cc) .... ***Cyrtolabulus* van der Vecht**

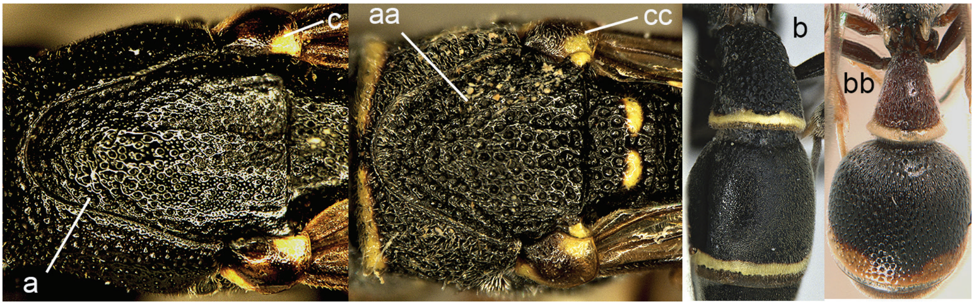

Figure 7. Mesosoma (**a, c, aa, cc**) and metasoma (**b, bb**). **a–c** *Leptomicrodynerus tieshengi* Giordani Soika **aa, cc** *Cyrtolabulus suavis* van der Vecht **bb** *Cyrtolabulus exiguus* (de Saussure).

8 Propodeum dorsally with elongate fovea from which a carina runs to orifice, usually with dentiform projections above valvulae (8a); axillary fossa narrower than long, slit-like (8b); tegula with narrow posterior lobe which about equals parategula posteriorly (8c) **9**

– Propodeum without fovea or dentiform projections (8aa); axillary fossa oval, broader than long (8bb); tegula short, convex and not equalling parategula posteriorly (8cc), or long, with narrow posterior lobe which surpasses parategula posteriorly **14**

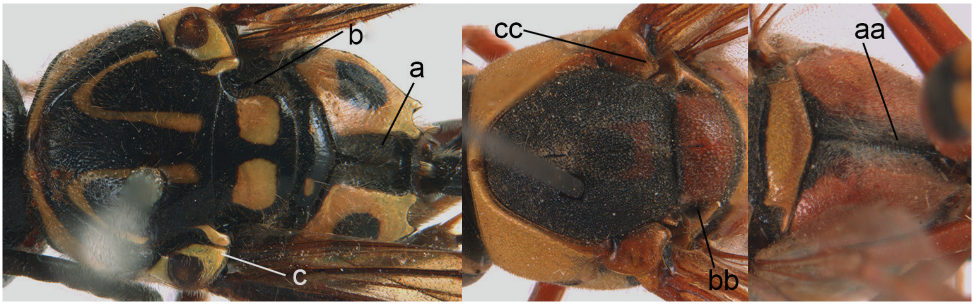

Figure 8. Mesosoma, dorsal view. **a–c** *Pseumenes d. depressus* (de Saussure) **aa–cc** *Delta campaniforme gracile* (de Saussure).

9 Mesepisternum with epicnemial carina present (9a) **10**
– Mesepisternum with epicnemial carina absent (9aa) **13**

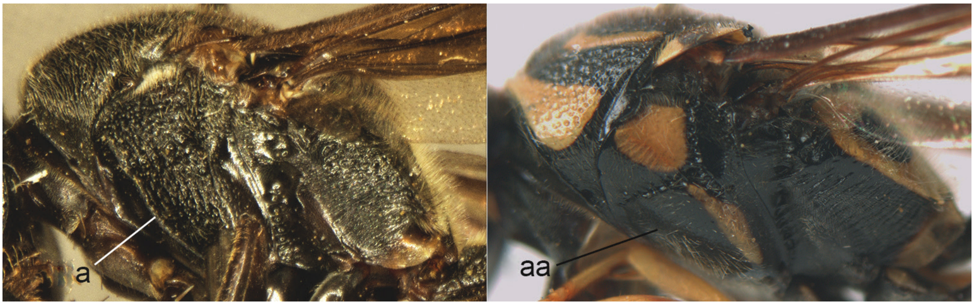

Figure 9. Mesosoma, lateral view. **a** *Nortozumia* sp. **aa** *Pseumenes d. depressus* (de Saussure).

10 Metasomal petiole with transverse carina basally (10a, a') **11**
– Metasomal petiole not carinate (10aa, aa') **12**

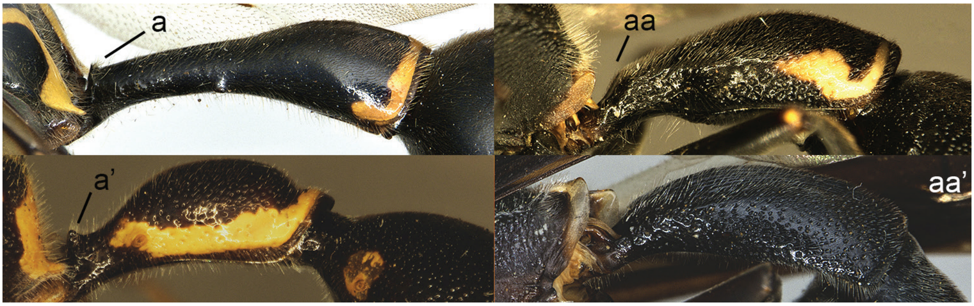

Figure 10. Metasomal segment I in lateral view. **a** *Ectopioglossa s. samariensis* (Giordani Soika) **a'** *Nortozumia pulchella* (Smith) **aa** *Coeleumenes* sp. **aa'** *Pseudozumia indica paulonotata* Giordani Soika.

11 Tergum I with its lateral margins fused ventrally; sternum I reduced to posterior crescentic sclerite (11a); [mesonotum and propodeum smooth between fine punctures] .... ***Ectopioglossa* Perkins**
– Tergum I with lateral margins not meeting ventrally, sternum I visible along entire petiole length (11aa) ....***Nortozumia* van der Vecht** (new record)

Figure 11. Metasomal segment I, ventral view. **a** *Ectopioglossa s. samariensis* (Giordani Soika) **aa** *Nortozumia pulchella* (Smith).

12 Mesoscutum with a pair of prescutellar longitudinal groove (12a); forewing with parastigma longer than pterostigma (12b); sternum I irregularly rugose posteriorly, with rugae running in longitudinal direction (12c) .... ***Pseudozumia* de Saussure**

– Mesoscutum without prescutellar longitudinal groove (12aa); forewing with parastigma shorter than pterostigma (12bb); sternum I smooth basally, its posterior two thirds transversely striate or smooth (12cc) .... ***Coeleumenes* van der Vecht**

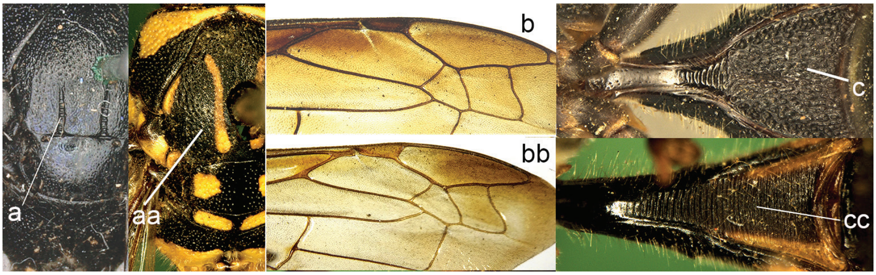

Figure 12. Part of dorsal mesosoma (**a, aa**), part of forewing (**b, bb**) and ventral metasomal segment I (**c, cc**). **a** *Pseudozumia i. indica* (de Saussure) **b** *Pseudozumia indica borneana* Giordani Soika **c** *Pseudozumia* sp. **aa–cc** *Coeleumenes impavidus* (Bingham).

13 Forewing with parastigma longer than pterostigma (13a); sternum I gradually widened backwards with regular transverse striae (13b); female with cephalic fovea (13c); hind tibia with number of short spines on its outside (13d) .... ***Pareumenes* de Saussure**

– Forewing with parastigma shorter than pterostigma (13aa); sternum I narrower basally, more or less fused with tergum I, posteriorly short, triangular and without ruga (13bb); female without cephalic fovea (13cc); hind tibia without spines on its outside (13dd) .... ***Pseumenes* Giordani Soika**

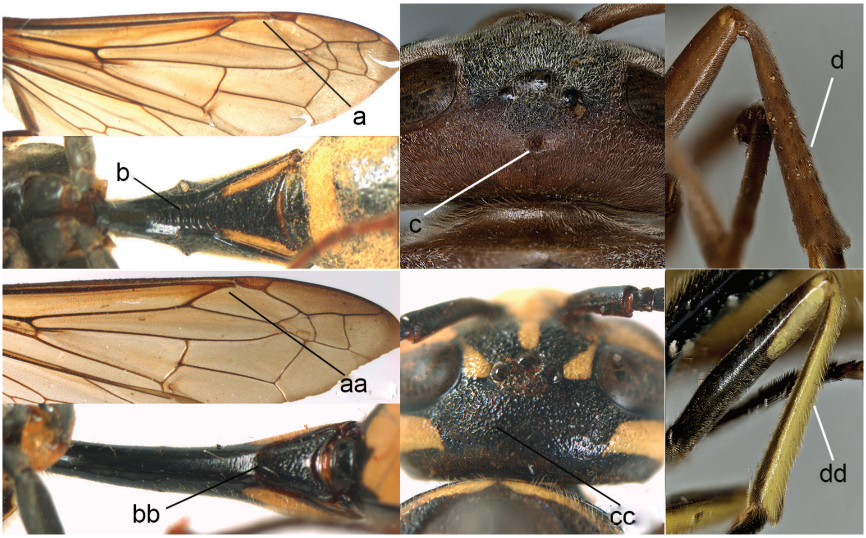

Figure 13. Forewing (**a, aa**), metasomal sternum I (SI) (**b, bb**), head in dorsal view (**c, cc**) and hind tibia (**d, dd**). **a–b** *Pareumenes quadrispinosus conjunctus* Liu **c, d** *Pareumenes s. sansibaricus* (von Schulthess) **aa–cc** *Pseumenes d. depressus* (de Saussure); dd. *Pseumenes depressus annulatus* van der Vecht.

14 Tergum I impunctate or with only a few small punctures (14c); propodeum inclining posteriorly into a slope (14a); tergum II without lamella separated by preapical thickening, sometimes with pale border (14b) **15**

– Tergum I with dense, coarse punctation (14cc); propodeum less inclined posteriorly (14aa); tergum II with apical lamella more or less separated from disc by preapical thickening (14bb) **17**

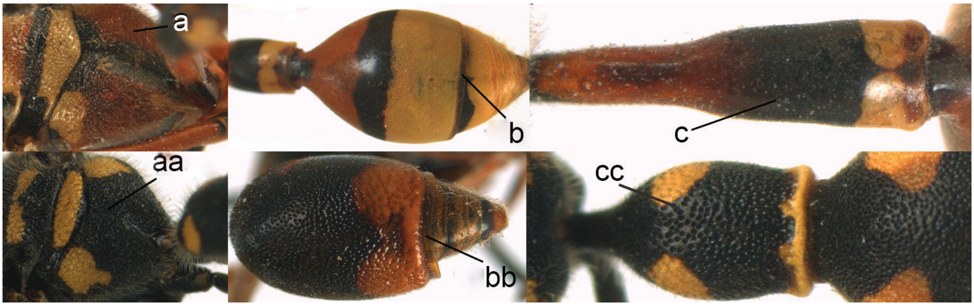

Figure 14. Propodeum (**a, aa**), metasomal tergum II (TII) (**b, bb**) and metasomal tergum I (TI) (**c, cc**). **a–c** *Delta campaniforme esuriens* (Fabricius) **aa, cc** *Eumenes c. coarctatus* (Linnaeus) **bb** *Eumenes kiangsuensis* Giordani Soika.

15 Clypeus apically rounded (15a); temple in dorsal view as long as eye (15b)... .... ***Katamenes* Meade-Waldo**

– Clypeus apically truncate or emarginated (15aa); temple in dorsal view shorter than eye (15bb)..**16**

Figure 15. Head in frontal (**a, aa**) and dorsal view (**b, bb**). **a, b** *Katamenes sesquicinctus* (Lichtenstein) **aa, bb** *Delta campaniforme gracile* (de Saussure).

16 Tergum I slightly longer than mesosoma, with section after spiracles shorter than section before spiracles (16a); male: terminal sternum with a longitudinal groove (16b)... ***Delta* de Saussure**

– Tergum I much longer than mesosoma, with section after spiracles longer than section before spiracles (16aa); male: terminal sternum without groove (16bb) ....***Phimenes* Giordani Soika**

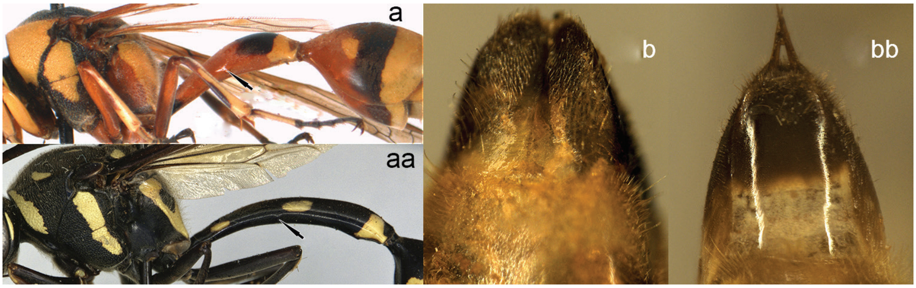

Figure 16. Mesosoma and part of metasoma (**a, aa**), terminal sternum of male (**b, bb**). **a, b** *Delta campaniforme gracile* (de Saussure), arrow = spiracle **aa, bb** *Phimenes f. flavopictus* (Blanchard).

17 Pronotum with pretegular carina absent (17b); parastigma of forewing shorter than half of pterostigma (17a); female: apical margin of clypeus emarginated (17c); propodeum lateral margin rounded, without distinct border with posterior face; male: apical antennal segment medium-sized and curved (17d)...........***Eumenes* Latreille**

– Pronotum with pretegular carina present (17bb); parastigma of forewing longer than half of pterostigma (17aa); female: apical margin of clypeus truncated (17cc); propodeum lateral side distinctly separated from its posterior face; male: apical antennal segment small and straight (17dd) ....***Oreumenes* Bequaert**

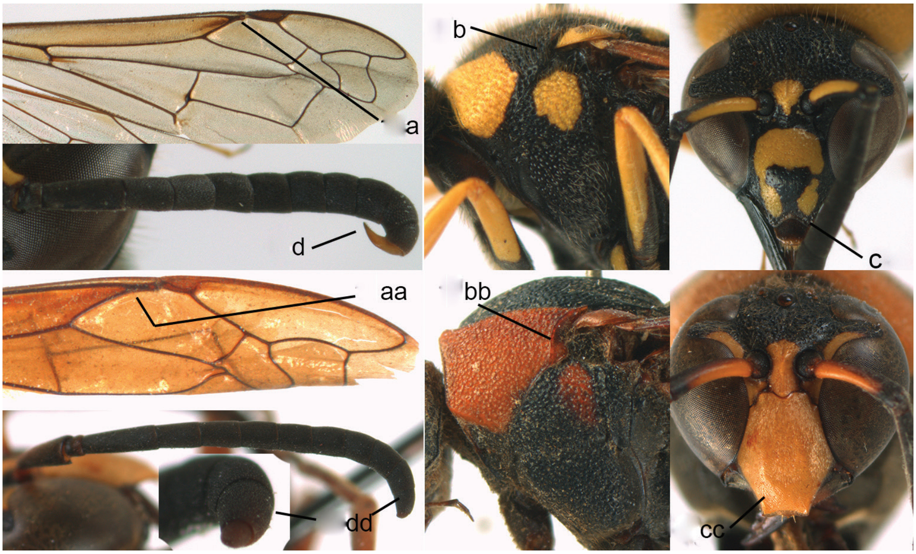

Figure 17. Forewing (**a, aa**), mesosoma in lateral view (**b, bb**), head in frontal view (**c, cc**) and antenna (**d, dd**). **a–d** *Eumenes c. coarctatus* (Linnaeus) **aa–dd** *Oreumenes decoratus* (Smith).

18 Tegula evenly rounded posteriorly and usually not reaching apex of parategula (18a); male antenna apically spiralled (18b) **19**

– Tegula protruding posteriorly, emarginate or truncate adjoining parategula (18aa); male antenna apically hooked or simple (18bb) **22**

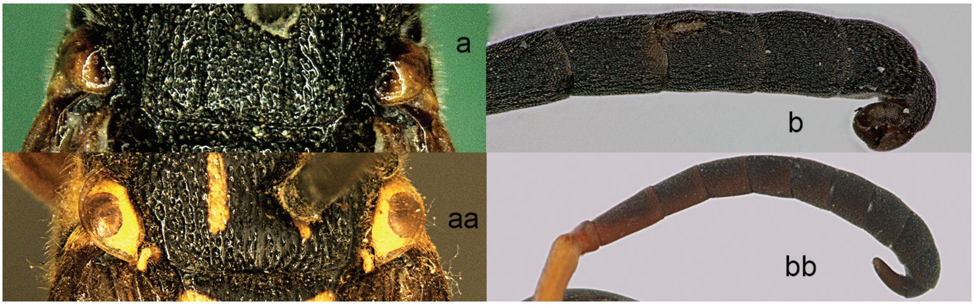

Figure 18. Part of mesosoma (**a, aa**) and antennae (**b, bb**). **a** *Onychopterocheilus mochii* (Giordani Soika) **b** *Pterocheilus p. phaleratus* (Panzer) **aa** *Stenodyneriellus guttulatus* (de Saussure) **bb** *Euodynerus d. dantici* (Rossi).

19 Labial palpi 3-segmented, in female segment II and III both broadly flattened, fringed with setae, forming a psammophore (19a); sterna II-V in male usually with central apical brush (19b).. **20**

– Labial palpus 4-segmented, in female cylindrical, without psammophore (19aa); sterna II-V in male usually without central apical brush (19bb) **21**

Figure 19. Part of mouthparts showing labial palpus (**a, aa**) and metasomal sterna (SII-VII) of male (**b, bb**). **a** *Onychopterochilus mochii* (Giordani Soika) **b** *Pterocheilus p. phaleratus* (Panzer) **aa–bb** *Odynerus albopictus* (de Saussure).

20 Maxillary palpus 5- (20a) or 6- (20a') segmented; female: labial palpus segment II thick basally, segment II, III not curved (20b); male: mandible with penultimate tooth often without deep excision, and axis of penultimate tooth is at an oblique angle relative to main axis of mandible and approximately parallel to axis of apical tooth (20c); body <9 mm .... ***Pterocheilus* Klug**

– Maxillary palpus 6-segmented (20aa); female: labial palpus segment II and III slender, flat and curved (20bb); male: mandible with distance between second and third tooth broad (20cc) or deeply and broadly excised, and axis of penultimate tooth is at approximately a right angle relative to the main axis of the mandible and relative to the apical tooth (20cc'); body >10 mm......... .... ***Onychopterocheilus* Blüthgen**

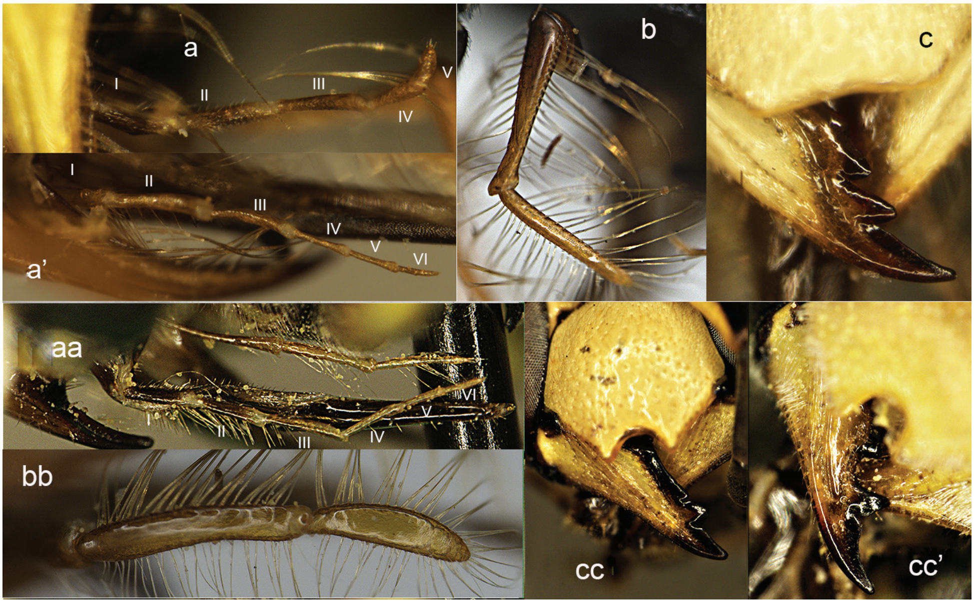

Figure 20. Maxillary palpus (a, a' and aa), labial palpus of female (**b, bb**) and mandibles of male (**c, cc, cc'**). **a–c** *Pterocheilus p. phaleratus* (Panzer) **a'** *Pterocheilus c. chobauti* Dusmet; **aa–bb** *Onychopterocheilus mochii* Giordani Soika **cc** *Onychopterocheilus pallasii* (Klug) **cc'** *Onychopterocheilus* sp.

21 Propodeum with lateral carinae well developed (21a); female without cephalic foveae (21b); vertex weakly longitudinally rugose posteriorly (21b); temples and mesosoma with very fine pubescence; male sterna II-VI with conspicuous fringe of setae (21c) .... ***Tropidodynerus* Blüthgen**

– Propodeum with lateral carinae weak or absent (21aa); female with cephalic foveae; vertex not rugose; temples and mesosoma with long setae (21bb); male sterna without fringe of setae (21cc) .... ***Odynerus* Latreille**

Figure 21. Propodeum (**a, aa**), head in dorsal view (**b, bb**) and sterna (**c, cc**). **a, b** *Tropidodynerus f. flavus* (Bingham) **c** *Tropidodynerus hostis* (Nurse) **aa–cc** *Odynerus albopictus* (de Saussure).

22 Anterior face of pronotum with two close and deeply impressed pits, which may be approximated, or with series of elongate foveae (22a); tegula broad, wider than long, not surpassing parategula (except *Jucancistrocerus*) (22b); propodeum valvula bilamellate (with submarginal carina produced into pointed lamella apically and valvula enlarged and free posteriorly from submarginal carina) (22c)... **23**

– Anterior face of pronotum without deep pits or foveae (except punctures) (22aa, aa'); submarginal carina, propodeum valvula and tegula variable **28**

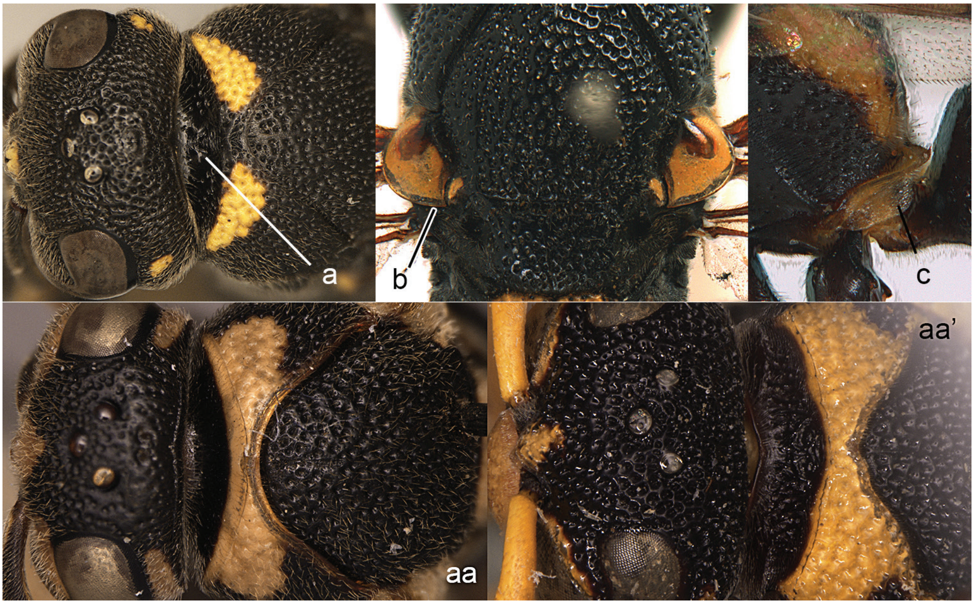

Figure 22. Head and pronotum in dorsal view (**a, aa, aa'**), part of mesosoma in dorsal view (**b**) and propodeum lateral view (**c**). **a, c** *Stenodynerus c. chinensis* (de Saussure) **b** *Stenodynerus frauenfeldi* (de Saussure) **aa** *Stenodyneriellus* sp. **aa'** *Brachyodynerus magnificus* (Morawitz).

23 Tergum I with two transverse carinae (23a) or with one (23a') **24**

– Tergum I without transverse carinae (23aa) **27**

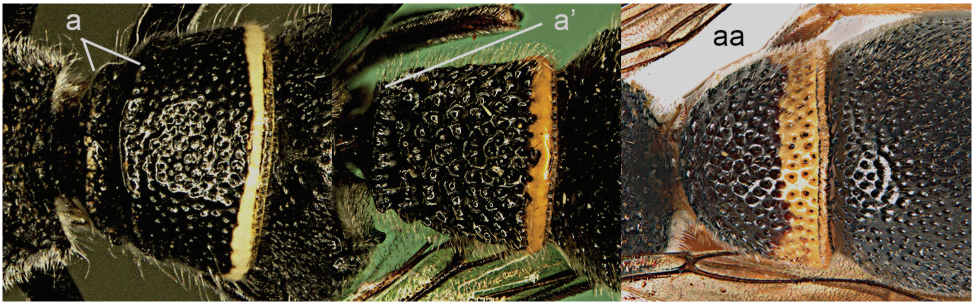

Figure 23. Metasomal tergum I. **a** *Subancistrocerus sichelii* (de Saussure) **a'** *Pseudonortonia abbreviaticornis* Giordani Soika **aa** *Stenodynerus chinensis* (de Saussure).

24 Tegula densely punctate, sieve-like, surpassing parategula posteriorly (24a); propodeal dorsum without extending horizontal area (24b); pretegular carina absent (24c); [carina of tergum I indistinct in some species] .... ***Jucancistrocerus* Blüthgen**

– Tegula usually finely punctate (24aa); propodeal dorsum extending horizontally, forming shelf-like area behind metanotum (24bb); pretegular carina present (24cc) **25**

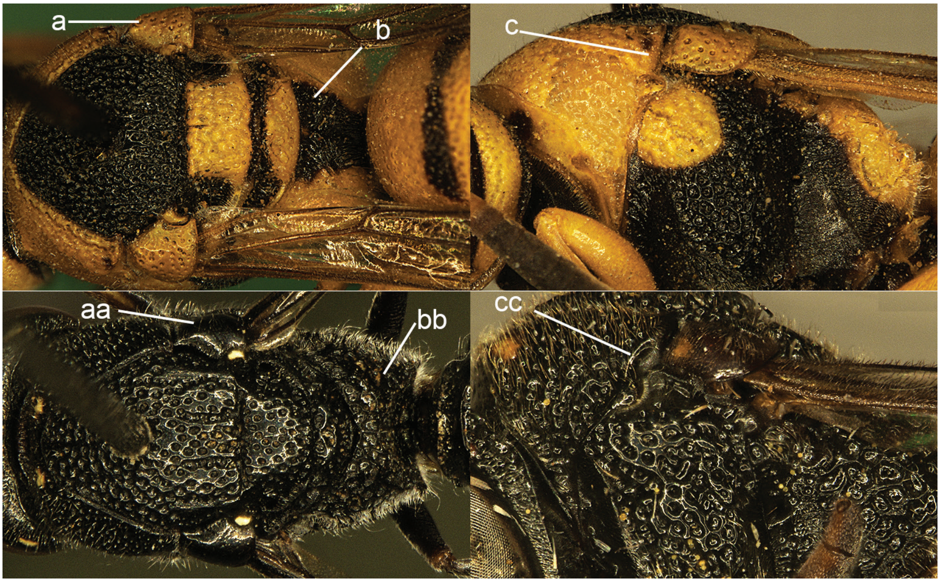

Figure 24. Mesosoma in dorsal view (**a, b, aa, bb**) and in lateral view (**c, cc**). **a–c** *Jucancistrocerus (Eremodynerus) atrofasciatus* (Morawitz) **aa–cc** *Pseudonortonia abbreviaticornis* Giordani Soika.

25 Tergum I with two carinae, tergum wider than long in dorsal view, both carinae relatively close near each other (25a)........***Subancistrocerus* de Saussure**

– Tergum I with one (25aa) or two carinae (25aa'); **if** with two carinae, then tergum I longer than wide in dorsal view, more or less petiole-like and distance between both carinae relatively large...**26**

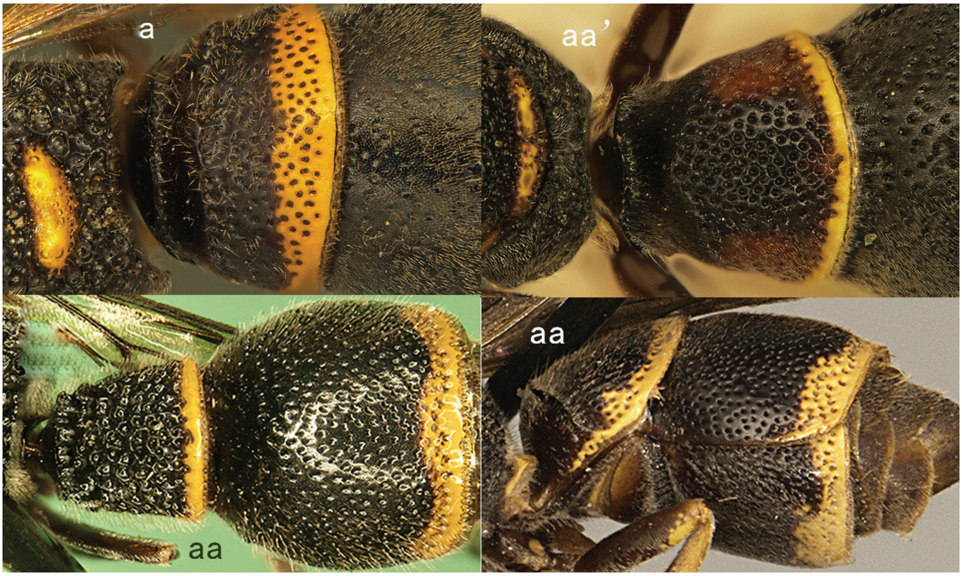

Figure 25. Metasomal tergum I in dorsal view. **a** *Subancistrocerus domesticus* **aa** (left). *Pseudonortonia abbreviaticornis* Giordani Soika **aa** (right). *Parancistrocerus samarensis* (von Schulthess) **aa'** *Pseudonortonia* sp.

26 Anterior face of pronotum with foveae separated (26a); tergum II usually smooth basally, forming an acarinarium (26b); metasoma sessile, tergum I nearly as wide as tergum II (26b') .... ***Parancistrocerus* Bequaert**

– Anterior face of pronotum with contiguous foveae (26aa); tergum II ridged basally, not forming an acarinarium; tergum I in dorsal view longer than wide, tergum II much wider than tergum I (26bb)................***Pseudonortonia* Giordani Soika**

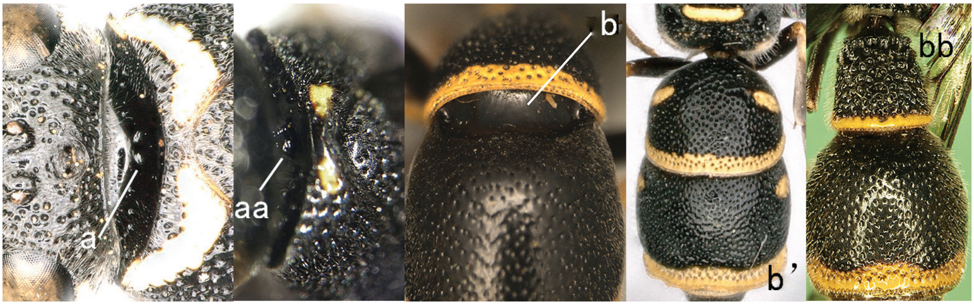

Figure 26. Anterior face of pronotum (**a, aa**); metasomal segments I and II (**b, b', bb**). **a, b'** *Parancistrocerus toltecus* **b** *Parancistrocerus samarensis* (von Schulthess) **bb** *Pseudonortonia abbreviaticornis* Giordani Soika.

27 Tergum I relatively short, gradually widened, with its lateral sides divergent in dorsal view (27a); vertex strongly depressed, forming an acute triangle with face (27b, arrowing part); in female, apical margin of clypeus truncated and with two longitudinal carinae (27c); anterior face of pronotum with foveae coalesced (27b) ....***Paraleptomenes* Giordani Soika**

– Tergum I relatively long, roughly parallel-sided in dorsal view (27aa); vertex normal, not forming an acute triangle with face (27bb); apical margin of clypeus emarginate and without carina (27cc); anterior face of pronotum with foveae separated (22a). [Note: if tergum I of *Parancistrocerus* spp. has an indistinct transverse carina, then it is difficult to separate them from *Stenodynerus*; *Parancistrocerus* spp. usually have an acarinarium on tergum II basally and tergum I more or less lengthened medially in dorsal view, while *Stenodynerus* spp. have tergum II ridged basally and tergum I medio-dorsally without elongation] .... ***Stenodynerus* de Saussure**

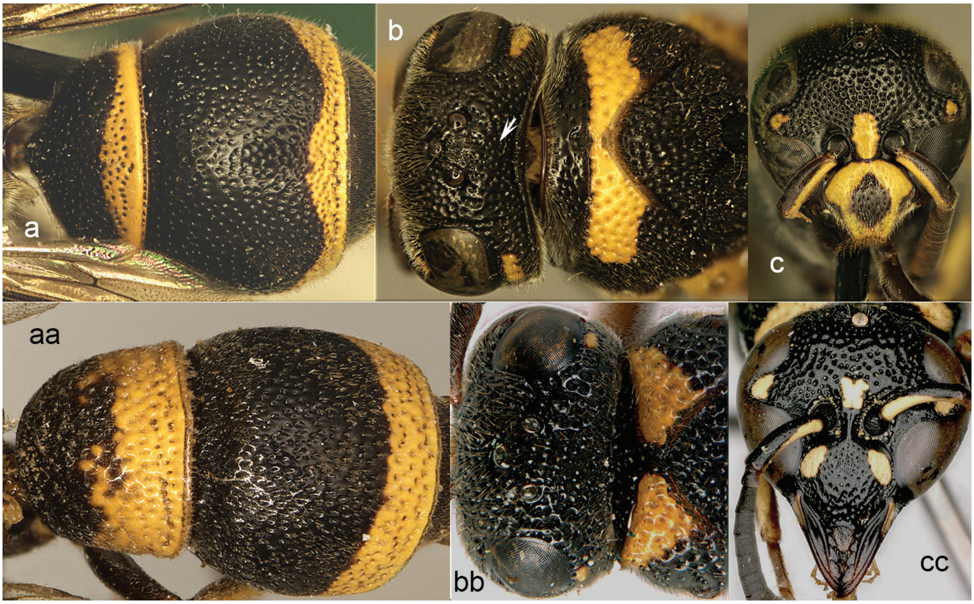

Figure 27. Metasoma in dorsal view (**a, aa**), head and pronotum in dorsal view (**b, bb**, white-arrow pointing to the depression) and in frontal view (**c, cc**). *Paraleptomenes kosempoensis* (von Schulthess) **aa–cc** *Stenodynerus chinensis* (de Saussure).

28 Tergum I transversely carinate (28a) **or** horizontal and vertical faces of tergum clearly separated (*Pararrhynchium*, 28a') **29**

– Tergum I evenly curved, without transverse carina (28aa) **34**

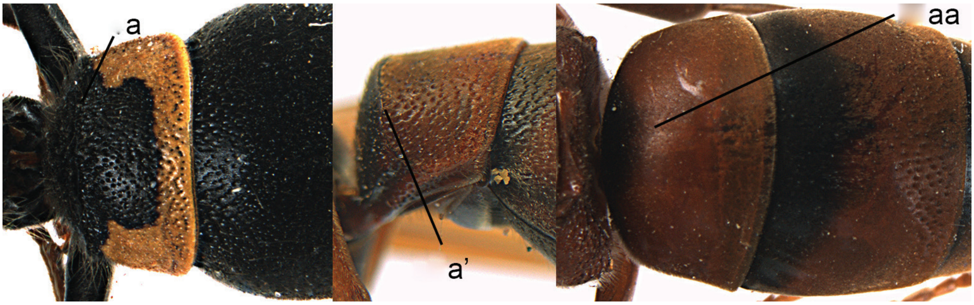

Figure 28. Metasomal tergum I (TI) in dorsal view (**a, aa**) and in lateral view (**a'**). **a** *Ancistrocerus parietinus* (Linnaeus) **a'** *Pararrhynchium ornatum sauteri* (Schulthess) **c** *Rhynchium carnaticum* (Fabricius).

29 Tergum I with broad medio-longitudinal furrow posterior to transverse carina (29a); notauli clearly indicated (29b); male antenna simple apically (29c) .... ***Symmorphus* Wesmael**

– Tergum I without medio-longitudinal furrow (29aa); notauli absent or nearly so (29bb); male antenna hooked apically (29cc)..**30**

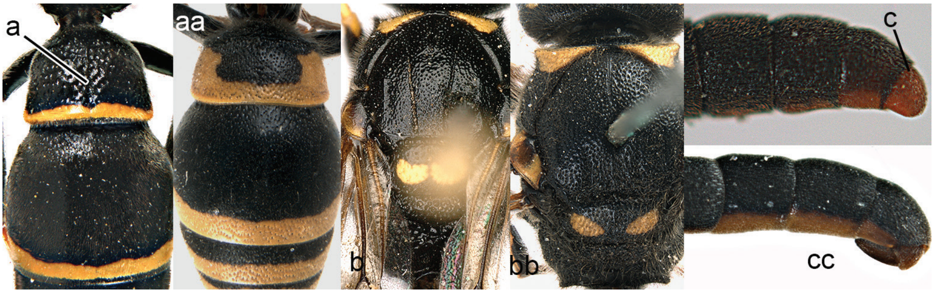

Figure 29. Metasomal terga I-II (**a, aa**) and mesosoma (**b, bb**) in dorsal view, distal segments of antenna (**c, cc**). **a, c** *Symmorphus bifasciatus* (Linnaeus) **b** *Symmorphus elegans* **aa–cc** *Ancistrocerus parietinus* (Linnaeus).

30 Parastigma of forewing with more than half the length of pterostigma, measured along posterior part, often nearly equal (30a)....................................**31**

– Parastigma half the length of pterostigma or less, measured along posterior part (30aa) **33**

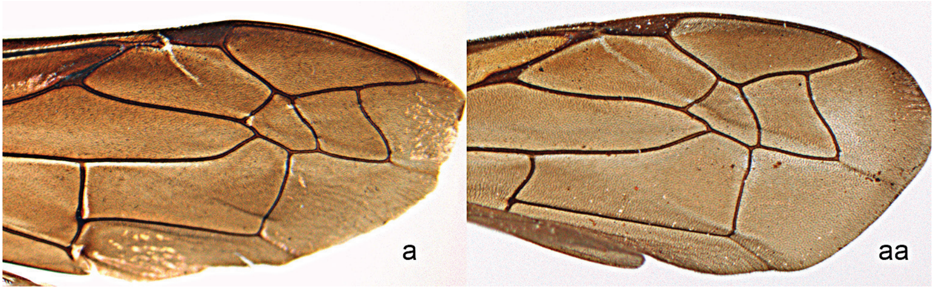

Figure 30. Forewing. **a** *Orancistrocerus a. aterrimus* (de Saussure) **aa** *Pararrhynchium o. ornatum* (Smith).

31 Tergum II with well-developed apical lamella (31a) .... ***Lissodynerus* Giordani Soika**

– Tergum II lacking an apical lamella (31aa)..**32**

Figure 31. Metasoma in lateral view. **a** *Lissodynerus s. septemfasciatus* (Smith) **aa** *Orancistrocerus a. aterrimus* (de Saussure).

32 Clypeus wide ventrally and slightly emarginated medio-ventrally (32a); male: terminal sternum without teeth basally (32b).... ***Orancistrocerus* van der Vecht**

– Clypeus narrower ventrally and deeply emarginated medio-ventrally (32aa); male: terminal sternum with 2–3 teeth basally (32bb) .... ***Archancistrocerus* Giordani Soika**

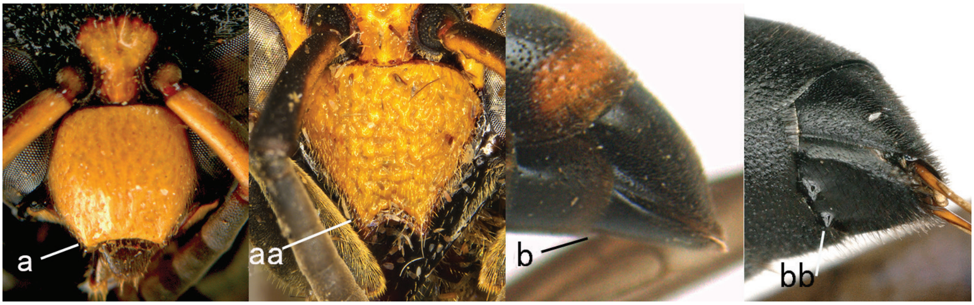

Figure 32. Clypeus (2 left) and distal part of male metasoma in lateral view (2 right). **a, b** *Orancistrocerus drewseni opulentissimus* (Giordani Soika) **aa** *Archancistrocerus diffinis* Giordani Soika, holotype **bb** *Archancistrocerus* sp.

33 Axillary fossa narrower than long, slit-like (33b); humeri ("shoulder") rounded (33a); propodeal dorsum strongly extending horizontally, forming shelf-like area behind metanotum (33c) .... ***Pararrhynchium* de Saussure**

– Axillary fossa oval, broader than long (33bb); humeri angular or pointed (33aa); propodeal dorsum slightly extending behind metanotum, below level of metanotum (33cc) .... ***Ancistrocerus* Wesmael**

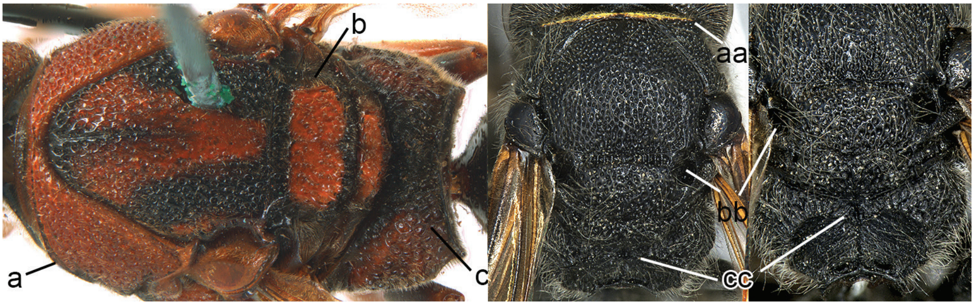

Figure 33. Mesosoma in dorsal view (left and middle) and dorso-caudal view (right). **a–c** *Pararrhynchium ornatum sauteri* (Schulthess) **aa–cc** *Ancistrocerus trifasciatus shibuyai* (Yasumatsu).

34 Metanotum with serrate bilobed ridge (34a, a') **35**

– Metanotum low toothed (34aa), including blunt or rounded off ridge or flat... **36**

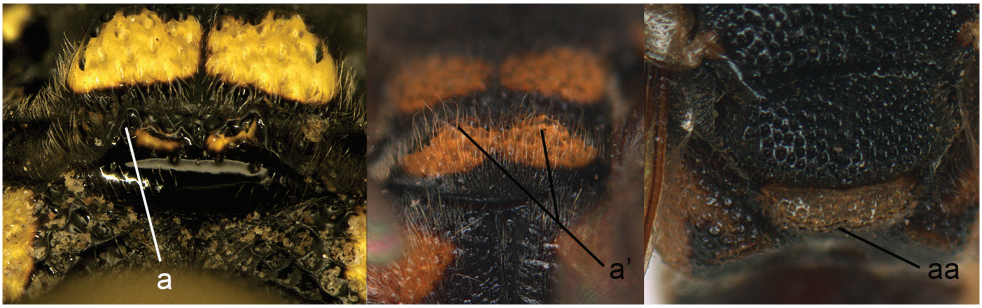

Figure 34. Metanotum. a. *Antepipona asiamontana* Gusenleitner; **a'** *Apodynerus f. formosensis* (von Schulthess) **aa** *Euodynerus trilobus* (Fabricius).

35 Clypeus higher than wide (35a); metanotum with truncate teeth; mid-anterior face of pronotum smooth and with short transverse rugae (35b); tergum I distinctly narrower than tergum II (35c); male terminal antennal segment small (35d) ....***Apodynerus* Giordani Soika**

– Clypeus wider than high (35aa); mid-anterior face of pronotum usually densely punctate and with an upper trace of transverse carina (35bb); tergum I slightly narrower than tergum II (35cc); male terminal antennal segment relatively large (35dd) ....***Antepipona* de Saussure**

Figure 35. Head in frontal view (**a, aa**), metasoma in dorsal view (**c, cc**), anterior face of pronotum (**b, bb**) and antenna (**d, dd**). **a–d** *Apodynerus troglodytes* (de Saussure) **aa, cc** *Antepipona silaos* (de Saussure) **bb** *Antepipona menkei* Giordani Soika; dd. *Antepipona rufescens* (Smith).

36 Tergum II with lamella behind transverse band (36a) **37**

– Tergum II without lamella behind transverse band, at most with narrow border (36aa). Note: few *Euodynerus* spp. may possess a distinct lamella on tergum II (see 45a), they can be separated from *Leptochilus* by having tergum I not depressed subapically (depressed in *Leptochilus*); and differs from *Gribodia*, *Stenodynerellus* and *Epsilon* by having oval axillary fossa, broader than long (slit-like, narrower than long in *Gribodia*, *Stenodynerellus* and *Epsilon*)........**40**

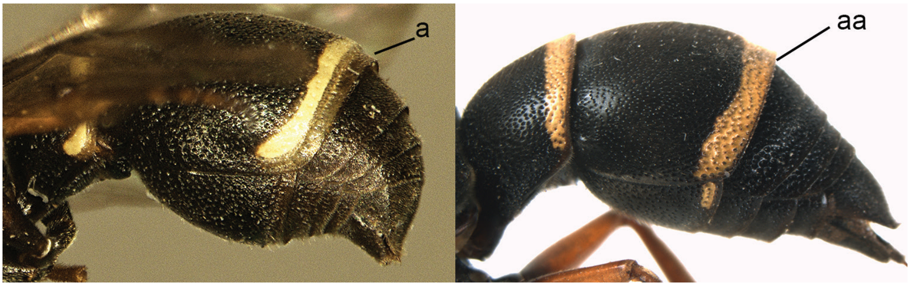

Figure 36. Metasoma in lateral view. **a** *Leptochilus m. medane* (Gribodo) **aa** *Anterhynchium flavomarginatum micado* (Kirsch).

37 Tergum I depressed subapically, gradually widened with lateral sides divergent in dorsal view (37 aa); propodeum with submarginal carina projecting as rounded lobe above valvula, bilamellate (37bb); epicnemial carina absent (37cc); axillary fossa oval, broader than long (37dd)...***Leptochilus* de Saussure**

– Tergum I not depressed subapically, usually with lateral sides roughly parallel in dorsal view (37aa); propodeum with submarginal carina not differentiated from valvula, mono-lamellate (37bb; except *Epsilon*); epicnemial carina present (37cc); axillary fossa narrower than long, slit-like (37dd)...................**38**

Figure 37. Metasomal tergum I (**a, aa**) in dorsal view, propodeum in lateral view (**b, bb**), mesosoma in lateral view (**c, cc**) and metanotum in dorsal view (**d, dd**). **a–d** *Leptochilus m. mauritanicus* (Lepeletier) **aa** *Gribodia confluenta* (Smith) **bb, cc** *Stenodyneriellus guttulatus* (de Saussure) **dd** *Stenodyneriellus* sp.

38 Palpal formula 5:3 (38a); male vertex sometimes with large and deep depression (38b); propodeum without shelf-like protruding part and with lateral carinae well developed (38c); [metanotum angulated, second submarginal cell with second recurrent vein nearly or completely interstitial with third submarginal cell; terga I-V each with apical lamella] ...... ***Gribodia* Zavattari**

– Palpal formula 6:4 (38aa); male vertex without large and deep depression (38bb); propodeum with shelf-like protruding part (38cc) or absent (38cc') **39**

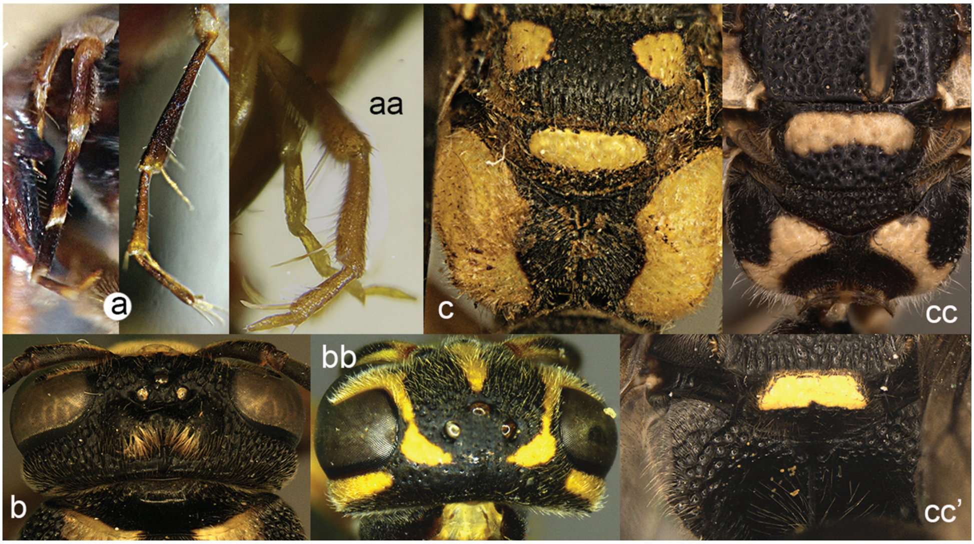

Figure 38. Maxillary palpus (**a** left) and labial palpus (**b** right), mouthpart palpi (**aa**), head in dorsal view (**b, bb**), part of mesosoma in dorso-caudal view (**c, cc, cc'**). **a–c** *Gribodia* sp. **aa, bb** *Stenodyneriellus guttulatus* (de Saussure) **cc** *Stenodyneriellus* sp. **cc'** *Epsilon dyscherum* (de Saussure).

39 Clypeus longer than wide, apical margin usually truncate (39a); propodeum with submarginal carina not differentiated from valvula (39b); propodeum usually with dorsal surface at about same level as metanotum, lateral margin rounded; metanotum usually smoothly convex (39c); terga I-V each with apical lamella (39d); second submarginal cell with second recurrent vein variable.. ***Stenodyneriellus* Giordani Soika**

– Clypeus longer than wide, apical margin emarginate (39aa); propodeum with submarginal carina projecting as rounded lobe above valvula (39bb); propodeum without raised shelf-like part, lateral margin carinate; metanotum angulated (39cc); only tergum II with lamella (39dd); second submarginal cell with second recurrent vein nearly or completely interstitial with third submarginal cell (39ee) .... ***Epsilon* de Saussure**

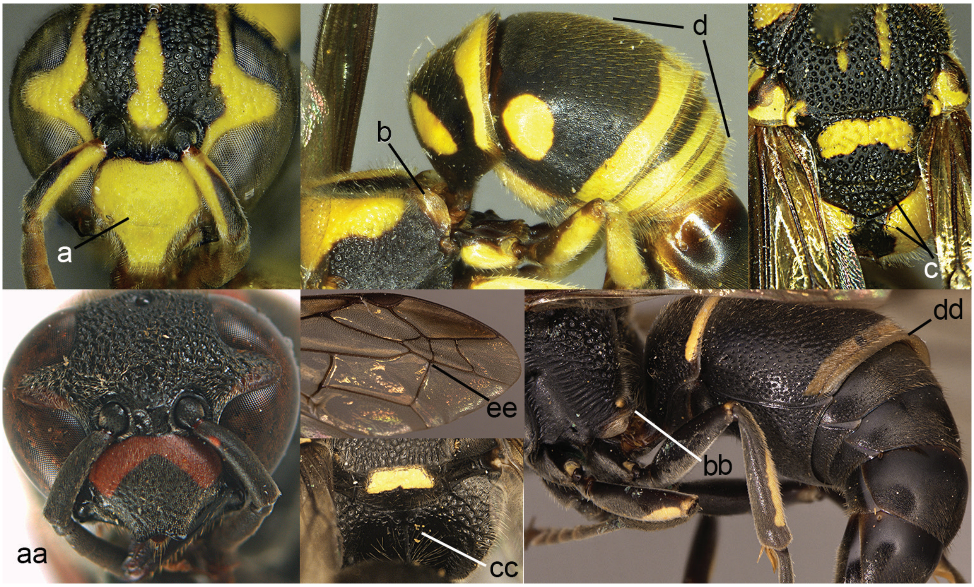

Figure 39. Head in frontal view (**a, aa**), part of meso- and metasoma (**b, d, bb, dd**), part of mesosoma in dorsal view (**c, cc**) and distal part of forewing (**ee**). **a–d** *Stenodyneriellus guttulatus* (de Saussure) **aa–ee** *Epsilon dyscherum* (de Saussure).

40 Axillary fossa in dorsal view much narrower than long, often slit-like (40a); tegula short, not exceeding parategula..**41**

– Axillary fossa in dorsal view not slit-like, at least as wide as long, oval (40aa); tegula usually equal to or exceeding parategula **45**

Figure 40. Part of mesosoma in dorsal view. **a** *Orientalicesa unifasciata* (von Schulthess) **aa** *Euodynerus p. posticus* (Herrich-Schäffer).

41 Propodeum with raised shelf-like part nearly at level of metanotum, metanotum flat (41a) **42**
– Propodeum below level of metanotum, metanotum various (41aa) **43**

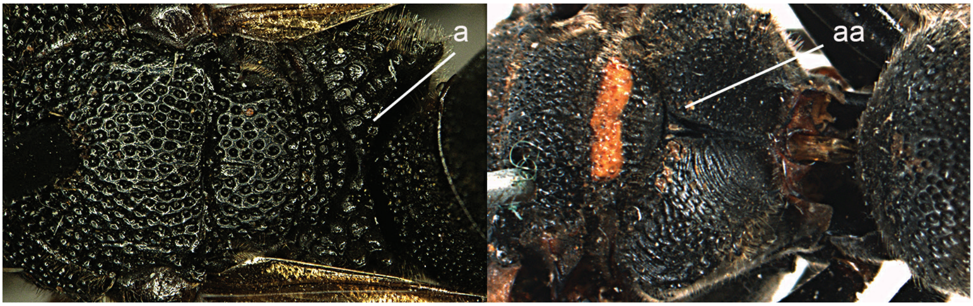

Figure 41. Part of mesosoma in dorsal view (**a**) and in dorso-caudal view (**aa**). **a** *Orientalicesa unifasciata* (von Schulthess) **aa** *Anterhynchium (Dirhynchium) flavopunctatum* (Smith).

42 Forewing with third submarginal cell separated from apex of marginal cell by about half its length (42a); male sternum VII with basal truncate process (42b) .... ***Allorhynchium* van der Vecht**
– Forewing with third submarginal cell separated from apex of marginal cell by about its own length (42aa); male sternum VII without process (42bb) .... ***Orientalicesa* Koçak and Kemal**

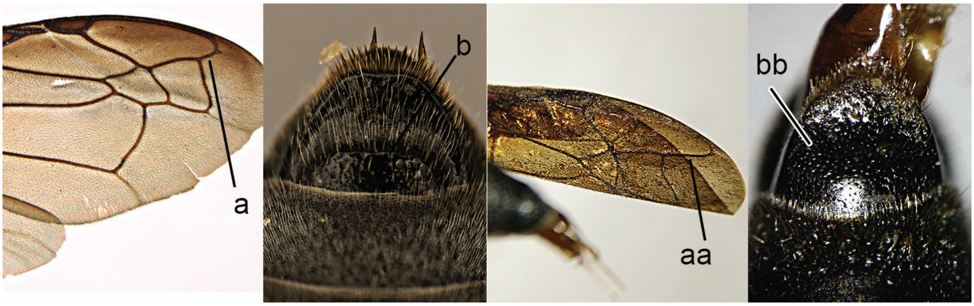

Figure 42. Distal part of forewing (**a, aa**) and terminal sternum of male (sternum VII) (**b, bb**). **a, b** *Allorhynchium argentatum* (Fabricius) **aa, bb** *Orientalicesa unifasciata* (von Schulthess).

43 Parastigma of forewing more than half length of pterostigma, measured along posterior part or nearly equal (43a); palpal formula 6:4 (38aa)..................**44**

– Parastigma shorter than half length of pterostigma, measured along posterior part (43aa); palpal formula 5:3 (38a) .... ***Okinawepipona* Yamane**

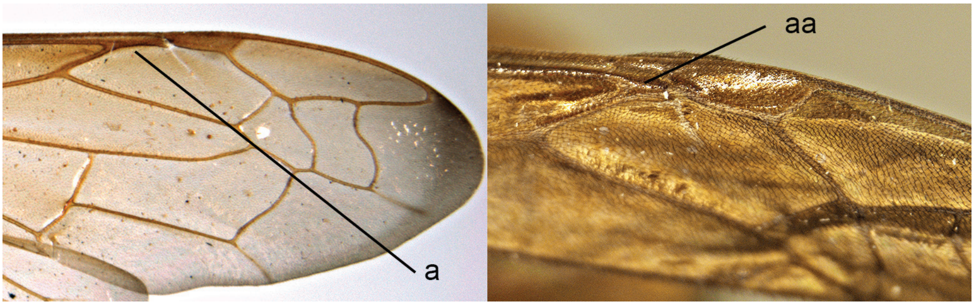

Figure 43. Part of forewing. **a** *Rhynchium carnaticum* (Fabricius) **b** *Okinawepipona kojimai* (Giordani Soika).

44 Mesoscutum posteriorly and scutellum smooth, very sparsely and finely punctate (44a); metanotum depressed medially (44b); male middle femur basally emarginated (44c)..***Rhynchium* Spinola**

– Mesoscutum and scutellum richly punctate throughout (44aa); metanotum not depressed medially (44bb); male middle femur not basally emarginate (44cc) ....***Anterhynchium* de Saussure**

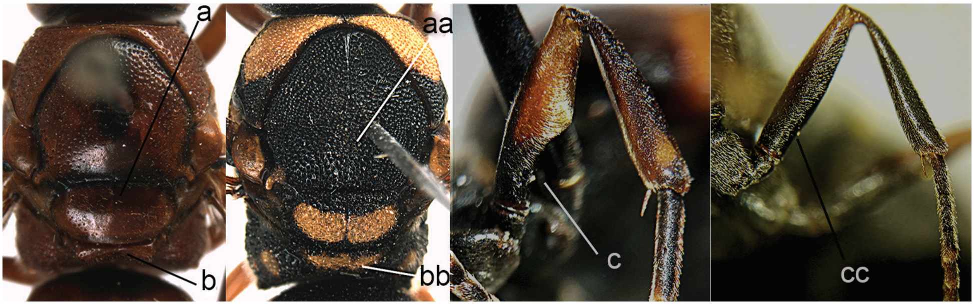

Figure 44. Mesosoma in dorsal view (**a, b, aa, bb**) and middle leg of male (**c, cc**). **a, b** *Rhynchium carnaticum* (Fabricius) **c** *Rhynchium q. quinquecinctum* (Fabricius) **aa, bb** *Anterhynchium flavomarginatum micado* (Kirsch) **cc** *Anterhynchium* sp.

45 Tergum I behind apical band with well-developed lamella (45a) **46**
– Tergum I behind apical band without well-developed lamella (45aa) **47**

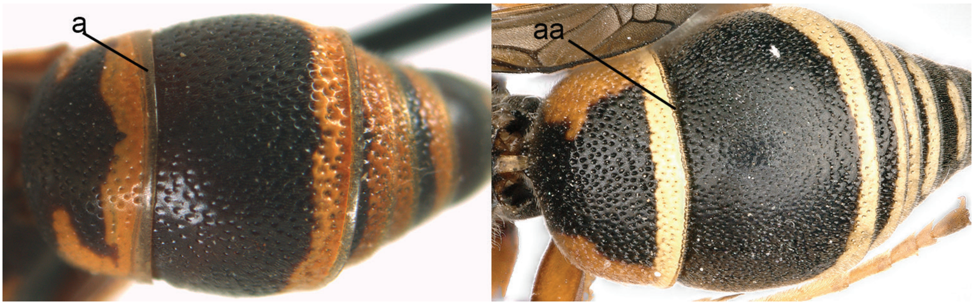

Figure 45. Metasoma in dorsal view. **a** *Euodynerus trilobus* (Fabricius) **aa** *Pseudepipona h. herrichii* (de Saussure).

46 Metanotum between horizontal and vertical area with hemi-circular carina (46a) .... ***Antodynerus* de Saussure**
– Metanotum between areas without hemi-circular shaped carina (46aa) .... ***Euodynerus* Dalla Torre**

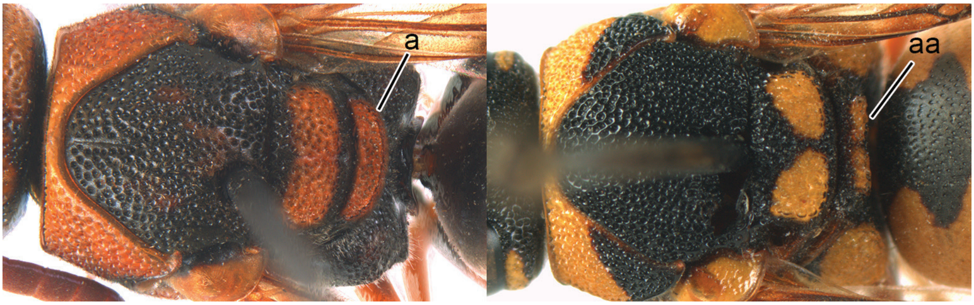

Figure 46. Mesosoma in dorsal view. **a** *Antodynerus limbatus* (de Saussure) **aa** *Euodynerus d. dantici* (Rossi).

47 Pretegular carina absent (47a) **48**
– Pretegular carina present, at least posteriorly (47aa) **49**

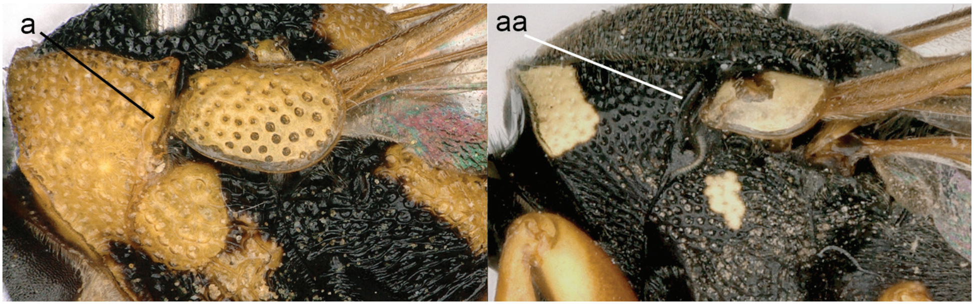

Figure 47. Part of mesosoma in lateral view. **a** *Brachyodynerus m. magnificus* (Morawitz) **aa** *Pseudepipona h. herrichii* (de Saussure).

48 Tegula sparsely punctate, slightly exceeding parategula and much smaller than scutellum (48a); mid-anterior face of pronotum smooth (48b); metanotum with lateral lamellae (48c); female with single cephalic fovea situated near occipital carina (48d) .... ***Parodontodynerus* Blüthgen**

– Tegula densely punctate, distinctly exceeding parategula, almost as large as scutellum (48aa); mid-anterior face of pronotum densely punctate (48bb); metanotum without lateral lamellae (48cc); female with single cephalic fovea situated halfway posterior ocelli and occipital carina (48dd) ....***Brachyodynerus* Blüthgen**

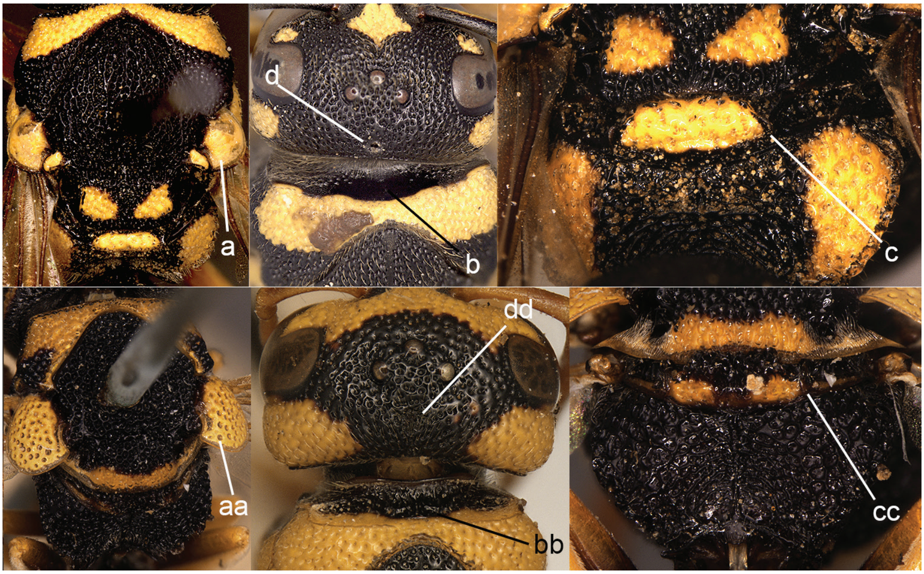

Figure 48. Mesosoma in dorsal view (**a, aa**), head and pronotum in dorsal view (**b, d, bb, dd**) and metanotum in dorsal view (**c, cc**). **a–d** *Parodontodynerus e. ephippium* (Klug) **aa–dd** *Brachyodynerus magnificus* (Morawitz).

49 Tegula narrower and longer, surpassing parategula posteriorly (49a). [female vertex with reniform fovea, about as wide as ocellar triangle; hind coxa with ventral lobes] ....***Allodynerus* Blüthgen**

– Tegula broad, equal to parategula posteriorly (49aa) **50**

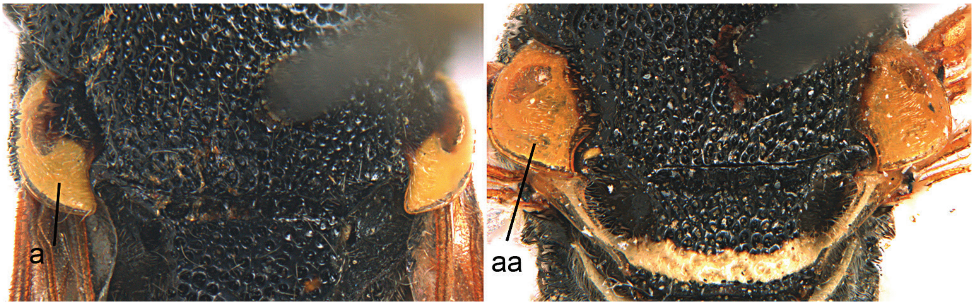

Figure 49. Part of mesonotum showing tegula and parategula. **a** *Allodynerus mandschuricus* Blüthgen **aa** *Pseudepipona herrichii siberia* Kurzenko.

50 Propodeal valvula mono-lamellate (50a), with transverse carina, and with a dentate ridge laterally (50b); [metanotum ridge roughly bidentate-shaped]... ....***Pseudepipona* de Saussure**

– Propodeal valvula bilamellate (50aa), without transverse carina, and without dentate ridge laterally; [small species (6 mm body length); anterior face of pronotum smooth; vertex with very small pits] ....***Asiodynerus* Kurzenko**

Figure 50. Propodeum in lateral view (**a, aa**) and in caudal view (**b**). **a, b** *Pseudepipona herrichii siberia* Kurzenko **aa** *Asiodynerus lucifer* (Kostylev), after Kurzenko (1977).

Checklist of the species of the subfamily Eumeninae from China

Allodynerus Blüthgen, 1938

Allodynerus Blüthgen, 1938 (1937), Konowia 16: 280; Type species: "*Lionotus floricola* Sauss. 1852" [= *Odynerus floricola* de Saussure, 1853].
Allodynerus delphinalis delphinalis (Giraud, 1866)
Allodynerus mandschuricus Blüthgen, 1953

Allorhynchium van der Vecht, 1963

Allorhynchium van der Vecht, 1963, Zool. Verh., Leiden 60: 57 (key), 58, genus. Type species: *Vespa argentata* Fabricius, 1804.
Allorhynchium chinense (de Saussure, 1862)
Allorhynchium lugubrinum (Cameron, 1900)
Allorhynchium metallicum (de Saussure, 1852)

Ancistrocerus Wesmael, 1836

Ancistrocerus Wesmael, 1836, Bull. Acad. R. Belg. 3: 45. Type species: *Vespa parietum* Linnaeus, 1758.
Ancistrocerus arcanus Giordani Soika, 1993
Ancistrocerus aureovillosus Giordani Soika, 1977
Ancistrocerus deqinensis You and Li, 2013
Ancistrocerus frigidus Giordani Soika, 1977 (1976)
Ancistrocerus hirsutus hirsutus (Meade-Waldo, 1910)
Ancistrocerus hirsutus supiensis Giordani Soika, 1977 (1976)
Ancistrocerus hirsutus tinkiensis Giordani Soika, 1977 (1976)

Ancistrocerus khangmarensis Giordani Soika, 1966
Ancistrocerus krausei Giordani Soika, 1966
Ancistrocerus melanocerus (Dalla Torre, 1894)
Ancistrocerus melanurus Morawitz, 1889
Ancistrocerus montuosus Gusenleitner, 1993
Ancistrocerus nigricornis (Curtis, 1791)
Ancistrocerus parapoloi Giordani Soika, 1966
Ancistrocerus parietum (Linnaeus, 1758)
Ancistrocerus rufofrustius Tan & Carpenter, **nom. n.**
Replacement name for *Ancistrocerus rufopictus* (Kostylev, 1940) (junior primary homonym of *Odynerus lineaticollis* var. *rufopictus* Meade-Waldo, 1915).
Ancistrocerus sikhimensis (Bingham, 1897)
Ancistrocerus terayamai Yamane, 1993
Ancistrocerus tibetanus Giordani Soika, 1966
Ancistrocerus transpunctatus You & Li, 2013
Ancistrocerus trifasciatus shibuyai (Yasumatsu, 1938)
Ancistrocerus waltoni (Meade-Waldo, 1910)

Antepipona de Saussure, 1855

Antepipona de Saussure, 1855, Ét. Fam. Vesp. 3: 244. Type species: *Odynerus silaos* de Saussure, 1853.
Antepipona asiamontana Gusenleitner, 2004
Antepipona biguttata (Fabricius, 1787)
Antepipona bipustulata (de Saussure, 1855)
Antepipona brunneola Giordani Soika, 1986
Antepipona deflenda (Saunders, 1853)
Antepipona excelsa excelsa Giordani Soika, 1982
Antepipona ferruginea Kim & Yamane, 2003
Antepipona ferruginea Kim & Yamane, 2003
Antepipona guttata diffinis (de Saussure, 1855)
Antepipona menkei Giordani Soika, 1986
Antepipona ovalis (de Saussure, 1853)
Antepipona plurimacula Giordani Soika, 1971
Antepipona rufescens (Smith, 1857)
Antepipona shantungensis Giordani Soika, 1993
Antepipona sexfasciata Soika, 1986
Antepipona tytides (Cameron, 1904)

Anterhynchium de Saussure, 1863

Anterhynchium de Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève 17: 205. Type species: *Rygchium* [= *Rhynchium*] *synagroides* de Saussure, 1852.
Anterhynchium (*Anterhynchium*) *mellyi* (de Saussure, 1852)
Anterhynchium (*Dirhynchium*) *flavomarginatum flavomarginatum* (Smith, 1852)

Anterhynchium (*Dirhynchium*) *flavomarginatum formosicola* (von Schulthess, 1934)
Anterhynchium (*Dirhynchium*) *flavopunctatum flavopunctatum* (Smith, 1852)
Anterhynchium (*Dirhynchium*) *flavopunctatum opulentum* (Giordani Soika, 1973)
Anterhynchium (*Dirhynchium*) *inamurai* (Sonan, 1937)
Anterhynchium (*Dirhynchium*) *yunnanensis* Giordani Soika, 1973

Antodynerus de Saussure, 1855

Antodynerus de Saussure, 1855, Ét. Fam. Vesp. 3: 287.Type species: "*Odynerus punctum* (Fabricius)" sensu de Saussure, 1853 [= *Vespa flavescens* Fabricius, 1775]
Antodynerus limbatus (de Saussure, 1852)

Apodynerus Giordani Soika, 1993

Apodynerus Giordani Soika, 1993, Boll. Mus. Civ. Stor. Nat. Venezia 42: 155. Type species: *Odynerus troglodytes* de Saussure, 1855.
Apodynerus formosensis continentalis Giordani Soika, 1994
Apodynerus formosensis formosensis (von Schulthess, 1934)
Apodynerus troglodytes troglodytes (de Saussure, 1855)
Apodynerus yayeyamensis yayeyamensis (Matsmura, 1926)

Archancistrocerus Giordani Soika, 1986

Archancistrocerus Giordani Soika, 1986, Boll. Mus. Civ. Stor. Nat. Venezia 35: 143, genus. Type species: *Archancistrocerus diffinis* Giordani Soika, 1986, monotypy.
Archancistrocerus diffinis Giordani Soika, 1986
Note: *Archancistrocerus* is a junior synonym and will be included in *Allorhynchium* (Tan et al. 2018b, submitted).

Asiodynerus Kurzenko, 1977

Asiodynerus Kurzenko, 1977, Ins. Mongol. 5: 557. Type species: *Odynerus lucifer* Kostylev, 1937.
Asiodynerus lucifer (Kostylev, 1937 (1936))

Brachyodynerus Blüthgen, 1938

Brachyodynerus Blüthgen, 1938, Deutsch. Entomol. Zeitschr.: 450, 459, genus. Type species: *Odynerus* (*Lionotus*) *magnificus* Morawitz, 1867.
Brachyodynerus perarrus Kurzenko, 1977

Calligaster de Saussure, 1852

Calligaster de Saussure, 1852, Ét. fam. Vesp. 1: 22, genus. Type species: *Calligaster cyanoptera* de Saussure, 1852.
Calligaster himalayensis (Cameron, 1904)

Coeleumenes van der Vecht, 1963

Coeleumenes van der Vecht, 1963, Zool. Verh., Leiden 60: 45, genus. Type species: *Montezumia impavida* Bingham, 1897

Coeleumenes burmanicus (Bingham, 1897)
Coeleumenes thoracicus (Sonan, 1939)

***Cyrtolabulus* van der Vecht, 1969**

Cyrtolabulus van der Vecht, 1969, Entomol. Ber., Amst. 29: 1, replacement name for *Cyrtolabus* van der Vecht, 1963, *non* Voss, 1925. Type species: *Cyrtolabus suavis* van der Vecht, 1963.
Cyrtolabulus exiguus (de Saussure, 1853)
Cyrtolabulus yunnanensis Lee, 1982

***Delta* de Saussure, 1855**

Delta de Saussure, 1855, Ét. Fam. Vesp. 3: 130, 132, 143. Type species: *Vespa maxillosa* DeGeer, 1775 [= *Vespa emarginata* Linnaeus, 1758]
Delta campaniforme campaniforme (Fabricius, 1775)
Delta conoideum (Gmelin, 1790)
Delta esuriens okinawae Giordani Soika, 1986
Delta pyriforme pyriforme (Fabricius, 1775)

***Discoelius* Latreille, 1809**

Discoelius Latreille, 1809, Gen. Crust. et Insect. 4: 140. Type species: *Vespa zonalis* Panzer, 1801, monotypy.
Discoelius dufourii dufourii (Lepeletier, 1841)
Discoelius dufourii manchurianus Yasumatsu, 1934
Discoelius emeishanensus Zhou and Li, 2013
Discoelius esakii Yasumatsu, 1934
Discoelius longinodus Yamane, 1996
Discoelius nigriclypeus Zhou & Li, 2013
Discoelius wangi Yamane, 1996
Discoelius zonalis (Panzer, 1801)

***Ectopioglossa* Perkins, 1912**

Ectopioglossa Perkins, 1912, Ann. Mag. Nat. Hist. (8) 9: 118, genus. Type species: *Ectopioglossa australensis* Perkins, 1912, monotypy.
Ectopioglossa ovalis Giordani Soika, 1993
Ectopioglossa taiwana (Sonan, 1938)

***Epsilon* Saussure, 1855**

Epsilon de Saussure, 1855, Ét. Fam. Vesp. 3: 229, 252. Type species: *Odynerus dyscherus* de Saussure, 1852.
Epsilon fujianense Lee, 1981

***Eumenes* Latreille, 1802**

Eumenes Latreille, 1802, Hist. Nat. Crust. Ins. 3: 360, genus. Type species: "*Eumenes coarctata*, Fab." [= *Vespa coarctata* Linnaeus, 1758].

Eumenes architectus Smith, 1859
Eumenes assamensis Meade-Waldo, 1910
Eumenes atrophicus (Fabricius, 1798)
Eumenes buddha Cameron, 1897
Eumenes coarctatus coarctatus (Linnaeus, 1758)
Eumenes coronatus coronatus (Panzer, 1799)
Eumenes ferrugiantennus Zhou, Chen & Li, 2012
Eumenes formosensis Giordani Soika, 1973
Eumenes fraterculus Dalla Torre, 1894
Eumenes fulvopilosellus Giordani Soika, 1965
Eumenes kangrae Dover, 1925
Eumenes kiangsuensis Giordani Soika, 1941
Eumenes labiatus flavoniger Giordani Soika, 1941
Eumenes labiatus labiatus Giordani Soika, 1941
Eumenes labiatus sinicus Giordani Soika, 1941
Eumenes mediterraneus manchurianus Giordani Soika, 1971
Eumenes micado Cameron, 1904 (Kim and Yoon (2001) state that the record is very doubtful)
Eumenes multipictus de Saussure, 1855
Eumenes nigriscutatus Zhou, Chen & Li, 2012
Eumenes pedunculatus pedunculatus (Panzer, 1799)
Eumenes pomiformis (Fabricius, 1781)
Eumenes punctatus de Saussure, 1852
Eumenes quadratus obsoletus Dover, 1926
Eumenes quadratus quadratus Smith, 1852
Eumenes quadratus urainus Sonan, 1939
Eumenes rubronotatus Pérez, 1905
Eumenes septentrionalis khangmarensis Giordani Soika, 1966
Eumenes septentrionalis septentrionalis Giordani Soika, 1940
Eumenes tosawae lofouensis Giordani Soika, 1973
Eumenes tosawae tosawae Giordani Soika, 1934
Eumenes transbaicalicus Kurzenko, 1984
Eumenes tripunctatus (Christ, 1791)
Eumenes variepunctatus Giordani Soika, 1941

Euodynerus **Dalla Torre, 1904**

Euodynerus Dalla Torre, 1904, Gen. Ins. 19: 38. Type species: *Vespa dantici* Rossi, 1790.
Euodynerus (*Euodynerus*) *caspicus caspicus* (Morawitz, 1873)
Euodynerus (*Euodynerus*) *dantici brachytomus* (Kostylev, 1940)
Euodynerus (*Euodynerus*) *dantici violaceipennis* Giordani Soika, 1973
Euodynerus (*Euodynerus*) *fastidiosus* (de Saussure, 1853)
Euodynerus (*Euodynerus*) *rufinus rufinus* Blüthgen, 1942

Euodynerus (*Euodynerus*) *semisaecularis semisaecularis* (Dalla Torre, 1889)
Euodynerus (*Euodynerus*) *variegatus kruegeri* (von Schulthess, 1928)
Euodynerus (*Pareuodynerus*) *adiacens* Giordani Soika, 1973
Euodynerus (*Pareuodynerus*) *deqinensis* Ma, Chen & Li, 2017
Euodynerus (*Pareuodynerus*) *ferrugineus* Ma, Chen & Li, 2017
Euodynerus (*Pareuodynerus*) *nipanicus nipanicus* (von Schulthess, 1908)
Euodynerus (*Pareuodynerus*) *nipanicus ryukyuensis* Tano, 1987
Euodynerus (*Pareuodynerus*) *nipanicus tonkinensis* Giordani Soika, 1973
Euodynerus (*Pareuodynerus*) *notatus notatus* (Jurine, 1807)
Euodynerus (*Pareuodynerus*) *quadrifasciatus quadrifasciatus* (Fabricius, 1793)
Euodynerus (*Pareuodynerus*) *similinipanicus* Ma, Chen & Li, 2017
Euodynerus (*Pareuodynerus*) *strigatus* (Radoszkowski, 1893)
Euodynerus (*Pareuodynerus*) *trilobus* (Fabricius, 1787)

Gribodia Zavattari, 1912

Gribodia Zavattari, 1912, Arch. Naturgesch. 78A (4): 161. Type species: *Monobia cavifrons* Gribodo, 1891 [= *Odynerus confluenta* Smith, 1857], monotypy.
Gribodia nigra Nguyen & Xu, 2015

Jucancistrocerus Blüthgen, 1938

Jucancistrocerus Blüthgen, 1938, Deutsch. Entomol. Zeitschr.: 442, 460.Type species: *Odynerus* (*Ancistrocerus*) *jucundus* Mocsáry, 1883, monotypy.
Jucancistrocerus (*Jucancistrocerus*) *alashanicus* Kurzenko, 1977
Jucancistrocerus (*Jucancistrocerus*) *angustifrons* (Kostylev, 1940)
Jucancistrocerus (*Eremodynerus*) *atrofasciatus* (Morawitz, 1885)
Jucancistrocerus (*Eremodynerus*) *chotanensis* (Blüthgen, 1942)

Katamenes Meade-Waldo, 1910

Katamenes Meade-Waldo, 1910, Ann. Mag. Nat. Hist. (8) 5: 46, genus. Type species: *Katamenes watsoni* Meade-Waldo, 1910, monotypy.
Katamene arbustorum arbustorum (Panzer, 1799)
Katamene indetonsus (Morawitz, 1895)
Katamene tauricus tauricus (de Saussure, 1855)

Labus de Saussure, 1867

Labus de Saussure, 1867, Reise Novara, Zool. 2 (1), Hym.: 3, genus. Type species: *Labus spiniger* de Saussure, 1867
Labus exiguus (de Saussure, 1855)
Labus lofuensis Giordani Soika, 1973

Leptochilus de Saussure, 1853

Leptochilus de Saussure, 1853, Ét. Fam. Vesp 1: 233. Type species: *Pterocheilus mauritianus* [!] [= *Pterocheilus mauritanicus* Lepeletier, 1841].

Leptochilus (*Lionotulus*) *chinensis* Gusenleitner, 2001
Leptochilus (*Lionotulus*) *gobicus* (Kostylev, 1940)
Leptochilus (*Lionotulus*) *incertus* (Kostylev, 1940)
Leptochilus (*Neoleptochilus*) *tibetanus* Giordani Soika, 1966

Lissodynerus **Giordani Soika, 1993**

Lissodynerus Giordani Soika, 1993, Boll. Mus. Civ. Stor. Nat. Venezia 42: 135. Type species: *Odynerus septemfasciatus* Smith, 1857.
Lissodynerus septemfasciatus feanus (Giordani Soika, 1941)

Leptomicrodynerus **Giordani Soika, 1985**

Leptomicrodynerus Giordani Soika, 1985, Lavori Soc. Ven. Sci. Nat. 10: 37. Type species: *Leptomicrodynerus tieshengi* Soika, 1985, monotypy.
Leptomicrodynerus tieshengi Giordani Soika, 1985
Note: The characteristics of this genus also fit well with *Eumenidiopsis* Giordani Soika, 1939, and further research is needed to solve the problem.

Nortozumia **van der Vecht, 1937 (new record)**

Nortozumia van der Vecht, 1937, Treubia 16: 263, genus. Type species: *Zethus rufofemoratus* Cameron, 1903.
Nortozumia sp.

Odynerus **Latreille, 1802**

Odynerus Latreille, 1802, Hist. Nat. Crust. Ins. 3: 362. Type species: *Vespa spinipes* Linnaeus, 1758.
Odynerus (*Odynerus*) *tristis tianshanicus* Kurzenko, 1977.

Okinawepipona **Yamane, 1987**

Okinawepipona Yamane, 1987, Mem. Kagoshima Univ. Res. Center S. Pacific 8: 52. Type species: *Anterhynchium kogimai* Giordani Soika, 1986, monotypy.
Okinawepipona curcipunctura Nguyen & Xu, 2014
Okinawepipona kogimai taiwana Yamane, 1987
Okinawepipona nigra Nguyen & Xu, 2014

Onychopterocheilus **Blüthgen, 1955**

Onychopterocheilus Blüthgen, 1955, Mitt. Münch. Entomol. Ges. 44/45: 406, 407. Type species: "*Pterocheilus daw* (Dusmet, 1909)" [= *Odynerus* (*Hoplomerus*) *daw* Dusmet, 1903], monotypy.
Onychopterocheilus (*Asiapterocheilus*) *bensoni* (Giordani Soika, 1941)
Onychopterocheilus (*Asiapterocheilus*) *nigropilosus* (Kostylev, 1940)
Onychopterocheilus (*Asiapterocheilus*) *rongsharensis* (Giordani Soika, 1977)
Onychopterocheilus (*Asiapterocheilus*) *tibetanus* (Meade-Waldo, 1913)
Onychopterocheilus (*Asiapterocheilus*) *waltoni* (Meade-Waldo, 1913)

Onychopterocheilus (*Onychopterocheilus*) *chinensis* Gusenleitner, 2005
Onychopterocheilus (*Onychopterocheilus*) *dementievi* (Kostylev, 1940)
Onychopterocheilus (*Onychopterocheilus*) *eckloni* (Morawitz, 1885)
Onychopterocheilus (*Onychopterocheilus*) *wuhaiensis* Gusenleitner, 2005

Orancistrocerus **van der Vecht, 1963**

Orancistrocerus van der Vecht, 1963, Zool. Verh., Leiden 60: 58 (key), 99, genus. Type species: *Odynerus drewseni* de Saussure, 1857
Orancistrocerus aterrimus aterrimus (de Saussure, 1852)
Orancistrocerus drewseni drewseni (de Saussure, 1857)
Orancistrocerus drewseni ingens (von Schulthess, 1934)
Orancistrocerus drewseni opulentissimus (Giordani Soika, 1941)
Orancistrocerus moelleri aulicus Giordani Soika, 1973

Oreumenes **Bequaert, 1926**

Oreumenes Bequaert, 1926, Ann. S. Afr. Mus. 23: 488. Type species: *Eumenes harmandi* Perez, 1905 [= *Eumenes decoratus* Smith, 1852], monotypy.
Oreumenes decoratus (Smith, 1852)

Orientalicesa **Koçak & Kemal, 2010**

Orientalicesa Koçak & Kemal, 2010, CESA Misc. Pap. 151: 4, replacement name for *Kennethia* Giordani Soika, 1994, non De Dekker, 1979. Type species: *Odynerus unifasciatus* von Schulthess, 1934.
Orientalicesa confasciatus Tan & Carpenter, nom. n.
Replacement name for *Orientalicesa unifasciatus* (von Schulthess, 1934) (junior primary homonym of *Odynerus unifasciatus* de Saussure, 1852).

Paraleptomenes **Giordani Soika, 1970**

Paraleptomenes Giordani Soika, 1970, Boll. Mus. Civ. Stor. Nat. Venezia 20/21: 79, genus. Type species: *Paraleptomenes nurseanus* Giordani Soika, 1970, monotypy.
Paraleptomenes kosempoensis (von Schulthess, 1934)
Paraleptomenes miniatus miniatus (de Saussure, 1855)

Parancistrocerus **Bequaert, 1925**

Parancistrocerus Bequaert, 1925, Trans. Am. Entomol. Soc. 51: 64. Type species: *Odynerus fulvipes* de Saussure, 1855 [= *O. "flavipes* Fabricius" *sensu* de Saussure, 1852, *non Vespa flavipes* Fabricius, 1775].
Parancistrocerus hongkongensis Gusenleitner, 2002
Parancistrocerus intermediatus (Sonan, 1939)
Parancistrocerus kuraruensis (Sonan, 1939)
Parancistrocerus nitobei (Sonan, 1939)
Parancistrocerus taihorinensis (von Schulthess, 1934)
Parancistrocerus taikonus (Sonan, 1939)

Parancistrocerus yachowensis konkunesis Giordani Soika, 1994
Parancistrocerus yachowensis yachowensis Giordani Soika, 1986
Parancistrocerus yamanei Gusenleitner, 2000

Pararrhynchium **de Saussure, 1855**

Pararrhynchium de Saussure, 1855, Ét. Fam. Vesp. 3: 173. Type species: *Rhynchium ornatum* Smith, 1852, monotypy.
Pararrhynchium ornatum bifasciatulum Giordani Soika, 1986
Pararrhynchium ornatum infrenis Giordani Soika, 1973
Pararrhynchium ornatum multifasciatum Giordani Soika, 1986
Pararrhynchium ornatum ornatum (Smith, 1852)
Pararrhynchium ornatum sauteri (von Schulthess, 1934)
Pararrhynchium paradoxum paradoxum (Gussakovskij, 1932)
Pararrhynchium sinense (von Schulthess, 1913)
Pararrhynchium smithii (de Saussure, 1855)
Pararrhynchium taiwanum Kim & Yamane, 2007

Pareumenes **de Saussure, 1855**

Pareumenes de Saussure, 1855, Ét. Fam. Vesp. 3: 133. Type species: *Eumenes quadrispinosus* de Saussure, 1855.
Pareumenes (*Nortonia*) *taiwanus* (Sonan, 1937)
Pareumenes (*Pareumenes*) *chinensis* Liu, 1941
Pareumenes (*Pareumenes*) *obtusus* Liu, 1941
Pareumenes (*Pareumenes*) *quadrispinosus acutus* Liu, 1941
Pareumenes quadrispinosus conjunctus Liu, 1941
Pareumenes (*Pareumenes*) *quadrispinosus interruptus* Liu, 1941
Pareumenes (*Pareumenes*) *quadrispinosus quadrispinosus* (de Saussure, 1855)
Pareumenes (*Pareumenes*) *quadrispinosus transitorus* Liu, 1941

Parodontodynerus **Blüthgen, 1938**

Parodontodynerus Blüthgen, 1938 (1937), Konowia 16: 280. Type species: *Eumenes ephippium* Klug, 1817.
Parodontodynerus laudatus (Kostylev, 1940)

Phimenes **Giordani Soika, 1992**

Phimenes Giordani Soika, 1992, Lavori Soc. Ven. Sci. Nat. 17: 41, 66, genus, replacement name for *Phi* de Saussure, 1855, non de Saussure, 1854. Type species: *Vespa arcuata* Fabricius, 1775.
Phimenes flavopictus flavopictus (Blanchard, 1804)
Phimenes flavopictus formosanus (Zimmermann, 1931)
Phimenes sparsipunctatus Gusenleitner, 2002

Pseudepipona de Saussure, 1856

Pseudepipona de Saussure, 1856, Ét. Fam. Vesp. 3: 309. Type species: *Odynerus herrichii* de Saussure, 1856, monotypy.
Pseudepipona (*Pseudepipona*) *augusta* (Morawitz, 1867)
Pseudepipona (*Pseudepipona*) *herrichii herrichii* (de Saussure, 1856)
Pseudepipona (*Pseudepipona*) *lativentris rubricans* Kurzenko, 1976
Pseudepipona przewalskyi (Morawitz, 1885)

Pseudonortonia Giordani Soika, 1936

Pseudonortonia Giordani Soika, 1936, Ann. Mus. Civ. Stor. Nat. Genova 59: 268, genus. Type species: *Odynerus difformis* de Saussure, 1853
Pseudonortonia abbreviaticornis Giordani Soika, 1941

Pseudozumia de Saussure, 1875

Pseudozumia de Saussure, 1875, Smithson. Misc. Coll. 254 (I): 128, division of genus *Montezumia* de Saussure. Type species: *Montezumia indica* de Saussure, 1855, monotypy.
Pseudozumia indica indica (de Saussure, 1855)
Pseudozumia indica paulonotata Giordani Soika, 1941
Pseudozumia indosinensis Giordani Soika, 1960

Pseumenes Giordani Soika, 1935

Pseumenes Giordani Soika, 1935, Ann. Mus. Civ. Stor. Nat. Genova 57: 145. Type species: *Eumenes eximius* Smith, 1861.
Pseumenes depressus depressus (de Saussure, 1855)
Pseumenes imperatrix (Smith, 1857)

Pterocheilus Klug, 1805

Pterocheilus Klug, 1805, Beitr. Naturk. 1: 143. Type species: *Vespa phalerata* Panzer, 1797.
Pterocheilus albofasciatus Smith, 1878
Pterocheilus napalkovi Kurzenko, 1977

Rhynchium Spinola, 1806

Rhynchium Spinola, 1806, Ins. Ligur. 1: 84. Type species: *Rygchium europaeum* Spinola, 1806 [= *Vespa oculata* Fabricius, 1781], monotypy.
Rhynchium brunneum brunneum (Fabricius, 1793)
Rhynchium quinquecinctum quinquecinctum (Fabricius, 1787)

Stenodyneriellus Giordani Soika, 1962

Stenodyneriellus Giordani Soika, 1962 (1961), Boll. Mus. Civ. Stor. Nat. Venezia 14: 65, 71. Type species: *Stenodyneriellus turneriellus* Giordani Soika, 1962.
Stenodyneriellus depressus Li & Chen, 2016

Stenodyneriellus guttulatus (de Saussure, 1862)
Stenodyneriellus maolanensis Li & Chen, 2016
Stenodyneriellus similiguttulatus Li & Chen, 2016

***Stenodynerus* de Saussure, 1863**

Stenodynerus de Saussure, 1863, Mém. Soc. Phys. Hist. Nat. Genève 17: 228. Type species: *Odynerus chinensis* de Saussure, 1863.
Stenodynerus baronii Giordani Soika, 1975
Stenodynerus bluethgeni van der Vecht, 1971
Stenodynerus chinensis chinensis (de Saussure, 1863)
Stenodynerus clyppeopictus (Kostylev, 1940)
Stenodynerus copiosus Gusenleitner, 2012
Stenodynerus frauenfeldi (de Saussure, 1867)
Stenodynerus funebris (André, 1884)
Stenodynerus incurvitus Gusenleitner, 2003
Stenodynerus morawitzi Kurzenko, 1977
Stenodynerus morbillosus Giordani Soika, 1979
Stenodynerus nepalensis Giordani Soika, 1985
Stenodynerus ninglangensis Ma & Li, 2016
Stenodynerus nudus (Morawitz, 1889)
Stenodynerus pappi luteifasciatus Kim & Yamane, 2004
Stenodynerus pappi pappi Giordani Soika, 1976
Stenodynerus pullus Gusenleitner, 1981
Stenodynerus reflexus Ma & Li, 2016
Stenodynerus similibaronii Ma & Li, 2016
Stenodynerus taiwanus Kim & Yamane, 2004
Stenodynerus tenuilamellatus Ma & Li, 2016
Stenodynerus tergitus Kim, 1999

***Subancistrocerus* de Saussure, 1855**

Subancistrocerus de Saussure, 1855, Ét. Fam. Vesp. 3: 206. Type species: *Odynerus sichelii* de Saussure, 1855.
Subancistrocerus camicrus (Cameron, 1904)
Subancistrocerus compressus Li & Chen, 2014
Subancistrocerus jinghongensis Li & Chen, 2014
Subancistrocerus kankauensis (von Schulthess, 1934)
Subancistrocerus sichelii (de Saussure, 1855)

***Symmorphus* Wesmael, 1836**

Symmorphus Wesmael, 1836, Bull. Acad. R. Belg. 3: 45. Type species: *Odynerus elegans* Wesmael, 1833.
Symmorphus ambotretus Cumming, 1989
Symmorphus angustatus (Zetterstedt, 1838)

Symmorphus apiciornatus (Cameron, 1911)
Symmorphus aurantiopictus Giordani Soika, 1986
Symmorphus bifasciatus (Linnaeus, 1761)
Symmorphus cavatus Li and Chen, 2014
Symmorphus foveolatus Gussakovskij, 1933
Symmorphus fuscipes (Herrich-Schaeffer, 1838)
Symmorphus hoozanensis (von Schulthess, 1934)
Symmorphus lucens (Kostylev, 1938)
Symmorphus mizuhonis Tsuneki, 1977
Symmorphus nigriclypeus Li & Chen, 2014
Symmorphus ornatus Gusenleitner, 2000
Symmorphus sichuanensis Lee, 1981
Symmorphus sublaevis (Kostylev, 1940)
Symmorphus tianchiensis Li & Chen, 2014
Symmorphus violaceipennis Giordani Soika, 1966
Symmorphus yananensis Gusenleitner, 2002
Symmorphus yunnanensis Gusenleitner, 2002

***Tropidodynerus* Blüthgen, 1939**

Tropidodynerus Blüthgen, 1939, Veröff. Deutsch. Kolon. Übersee Mus. Bremen 2: 259, 260. Type species: "*Hoplomerus interruptus* (Brullé, 1832) = *H. mandibularis* Morawitz, 1885" [= *Polistes interrupta* Brullé, 1832].
Tropidodynerus concavus Li & Chen, 2015
Tropidodynerus liupanshanensis Li & Chen, 2015

***Zethus* Fabricius, 1804**

Zethus Fabricius, 1804, Syst. Piez.: xii, 282. Type species: "*Zethus coeruleo-pennis* Fab." [= *Vespa coeruleopennis* Fabricius, 1798].
Zethus dolosus Bingham, 1897
Zethus malayanus Gusenleitner, 2010
Zethus nanlingensis Nguyen & Xu, 2017
Zethus taiwanus Yeh & Lu, 2017
Zehtus velamellatus Tan, 2018
Zethus nigerrimus Gusenleitner, 2001

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